Autotrophic and heterotrophic nanoplanckton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*

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**Abstract.** The ingestion of autotrophic and heterotrophic nanoplanckton by two estuarine copepods, *Eurytemora affinis* and *Acartia bifilosa*, was measured in various environmental conditions using the incubation method and epifluorescence microscopy. Egg production of the species was also determined in order to estimate their carbon requirements. Assuming a gross efficiency of egg production of 0.3, nanoplanctonic carbon ingested always met the carbon requirements suggesting that, most of the time, other carbon sources could be unnecessary. Nanoplankton ingestion by *A. bifilosa* (from 128 to 1693 cells ind.\(^{-1}\) h\(^{-1}\)) was dominated by autotrophic forms (60–97%) and was seriously affected by high (>100 mg l\(^{-1}\)) suspended particulate matter (SPM) concentrations. Nanoplankton ingestion by *E. affinis* (from 300 to 1049 cells ind.\(^{-1}\) h\(^{-1}\)) was relatively stable in comparison, but this latter species seemed to switch its grazing pressure from autotrophic to heterotrophic forms when SPM concentrations increased. Thus, two copepod species, living in the same estuary, presented two different feeding behaviours, probably to maximize energy input per unit of energy expenditure. Such differences could contribute to the spatial and seasonal segregation of these species which is usually observed.

**Introduction**

Historically, the dominant view in zooplankton ecology has been that ingestion, growth and fecundity of suspension-feeding copepods are governed by phytoplankton availability. Therefore, copepod herbivory has been largely investigated (reviewed in Frost, 1980). More recently, numerous species have been thought to be omnivorous (Carrick *et al.*, 1991; Ohman and Runge, 1994) and suggestions have been repeatedly made that heterotrophic protists could provide a major portion of the total nutrition, as well as much of the energy for growth and reproduction (Gifford and Dagg, 1988; Stoecker and Capuzzo, 1990). If protozoans are effectively preyed upon by mesozooplankton, the nature of energy transfer in the pelagic food web could be different or more complex than previously thought (see Legendre and Rassoulzadegan, 1995). Additionally, diversity in mesozooplankton diets may introduce nutritional variability and, in turn, affect processes such as growth and egg production (Kleppel *et al.*, 1991). Subsequently, the relative role of autotrophic and heterotrophic resources in the diet of planktonic crustaceans appears to be important in helping to understand the dynamics of pelagic ecosystems.

Little is known, however, about the composition of the natural diets of most copepods, and about the relative importance of autotrophic and heterotrophic prey. Evidence from laboratory experiments, such as a higher clearance rate for ciliates than for phytoplankton in *Acartia tonsa* (Stoecker and Egloff, 1987), cannot be accurately extrapolated to the field where naturally occurring prey assemblages are definitely more complex. Additionally, attempts to describe
mesozooplankton diets in situ have frequently involved gut pigment content determination (Mackas and Bohrer, 1976; Swadling and Marcus, 1994), providing little or no indication of the importance of the heterotrophic dietary component (but see Kleppel et al., 1988).

In turbid estuaries, several copepods are already known to be omnivorous. *Eurytemora affinis*, for instance, can ingest ciliates (Berk et al., 1977) or detritus (Heinle et al., 1977) as well as algae. However, information about the relative contribution of the different food sources to in situ ingestion and to natural growth is limited. Part of this scarcity stems from the large amount of terrestrial inert particles in estuarine waters which renders it difficult to apply most of the methods used in other aquatic environments. In the Gironde estuary, suspended particulate matter (SPM) is mainly composed of silt (Castaing et al., 1984). SPM concentrations often exceed 500 mg l⁻¹ at the water surface and 1 g l⁻¹ near the bottom. By comparison, chlorophyll (Chl) concentrations rarely exceed 10–20 µg l⁻¹ (Irigoien and Castel, 1996). Because of the high SPM concentration, which induces light limitation, the primary production in such an environment is often very low and contrasts with the high densities of copepods (Castel, 1981). These observations highlight the question of the relative role of heterotrophic food since the primary production is probably not sufficient to sustain the secondary production (Heinle and Flemer, 1975; Castel and Feurtet, 1989).

Copepods can consume prey ranging in size from 5 to 200 µm. In general, they retain the largest particles more efficiently than the smallest ones (Frost, 1972; Price et al., 1983). However, in estuaries, and especially in the Gironde, the largest particles (>20 µm) are scarce compared to the large amount of smaller particles (Castaing et al., 1984). In such conditions, it has been demonstrated by Richman et al. (1977) that estuarine copepods graze predominantly on nanoplanktonic size prey (5–20 µm), probably because they shift their grazing pressure to the size where the peak concentration of the particles occurs (Poulet, 1973, 1974).

Thus, the aim of this study was to quantify the in situ ingestion of autotrophic and heterotrophic nanoplankton by the dominant copepod species of the Gironde estuary (*E. affinis* and *Acartia bifilosa*). It was also examined whether (i) the ingestion of one or the other of these prey groups is sufficient, (ii) both are necessary or (iii) another food source (non-living particles, larger prey) has to be included to sustain the production which was measured by the fecundity. This investigation was conducted taking into account the environmental factors which could influence copepod ingestion.

**Method**

Sampling and experiments were carried out once a month from April to November 1995 at two stations of the Gironde estuary (Figure 1). Station F was located in the downstream area of the estuary where *A. bifilosa* is generally the dominant species, whereas station E was located in the middle part of the estuary where *E. affinis* is the most abundant. All samples were taken 0.5 m below the surface.

Temperature and salinity were measured using a conductivity–temperature
Nanoplankton in the diet of *E. affinis* and *A. bifilosa*

Fig. 1. Map of the Gironde estuary (SW France) showing the sampling stations.
system YSI 33, and oxygen concentrations were obtained with an Orbisphere Model 2609 oxymeter. SPM water content was determined as dry weight (60°C, 24 h) after filtration of 100-250 ml of water through 47 mm Whatman GF/C filters.

For ingestion experiments, copepods were collected using a standard WP2 plankton net (200 µm mesh size). Nine glass bottles were filled with 100 ml of natural filtered (63 µm) estuarine water and ~30 adults of the dominant copepod species (E.affinis or A.bifilosa) were gently pipetted and distributed into three of them (final density 10 adults per 100 ml, mainly females). Three bottles without copepods were fixed immediately, whereas the other bottles (three with copepods and three controls) were incubated in a tank for 24 h under natural conditions of temperature and light, corresponding to the sampling depth. Nothing was added to the control bottles to compensate for copepod excretion as it was assumed to be negligible compared to nutrient concentrations of the water (N = 100 µM; P = 2-5 µM; Irigoien and Castel, 1996). Samples were preserved with 1% glutaraldehyde and 0.1% paraformaldehyde (final concentrations) and stored in the dark at 4°C (Lovejoy et al., 1993).

When back in the laboratory, the nanoplanクトon were enumerated in each bottle. The sample was gently mixed by inversion and left to stain for 15 min with the fluorochrome 4'-6-diamidino-2-phenylindole (DAPI; final concentration of 0.1 µg ml⁻¹). Three to ten millilitre quantities (depending on SPM concentration) were carefully filtered through 25 mm diameter, 5 µm pore size, translucent isopore membranes at a vacuum of <5 mmHg. Then, the membranes were mounted on a glass slide and examined by epifluorescence microscopy with a UV excitation filter block and 1000X oil immersion. Using this procedure, it was possible to locate and differentiate the nanozooplankton from the nanophytoplankton by visualizing the DAPI-stained nuclei (blue) and the Chl a autofluorescence (red). Translucent membranes were preferred to black ones because they allowed organisms to be identified in the most turbid samples by alternating epifluorescence and transmission microscopy. The 5 µm pore size was chosen as it allowed an important part of suspended mineral particles to go through and because it was not our purpose to count bacteria.

The number of cells per unit volume was calculated according to Sherr and Sherr (1983) by multiplying the average number of cells per microscope field by the number of fields per membrane, and dividing the result by the volume filtered. For each slide, at least 100 fields were examined, and between 30 and 130 cells per 100 fields were usually counted.

Finally, nanoplanクトon ingestion rates of copepods were calculated as the number of cells ingested per individual and per hour using the equations of Frost (1972). These ingestion rates were converted to terms of carbon using the mean volume of 30 cells and a conversion factor of 0.15 g C ml⁻¹ (Carrick et al., 1991).

The carbon requirement (Cr) of adult copepods can be estimated by the egg production rate, using the equation Cr = (F × Ce)/Ki (Peterson et al., 1990), where F is the egg production rate (eggs female⁻¹ day⁻¹), Ce is the carbon content of an egg and Ki is the gross efficiency of egg production.

The egg production rates were estimated using the method of Kimmerer (1984). Approximately 100 adults from the same haul as for ingestion experiments were
pipetted and placed in 5 l incubation bottles filled with natural filtered (63 µm) water. Three replicates were incubated for 24 h at in situ temperature. Concerning experiments conducted with *E. affinis*, which is an egg-carrying species, eggs were introduced with females at the beginning of the incubation. Therefore, subsamples were taken and fixed with 5% formalin at the beginning and at the end of the incubation. From each subsample, the number of females and the total number of eggs and nauplii were counted (only females appearing intact were taken into account). The egg production rate was calculated from the change in the mean number of eggs per female against time, considering nauplii as eggs and assuming that the egg production rate remains linear during the experiment. Concerning experiments conducted with *A. bifilosa*, which is a free-spawning species, there were no eggs at the beginning of the incubation. In this case, the egg production rate was calculated from the total number of eggs and nauplii collected at the end of the incubation, divided by the number of females and by the duration of the experiment.

For each experiment, the carbon content was estimated from the mean volume of 30 eggs and applying a carbon to volume conversion factor of 0.14 g C ml\(^{-1}\) (Kiørboe et al., 1985).

The gross efficiency of egg production for estuarine copepods is variable, between 0.09 and 0.18 (Heinle et al., 1977) for *E. affinis* and 0.49 (Kiørboe et al., 1985) for *A. tonsa* (no data are available for *A. bifilosa*). A mean value of 0.30 was assumed for the calculation, but the consequences of another choice will be discussed.

**Results**

Results of nanoplankton ingestion experiments are summarized in Table I. There was a significant ingestion of nanophytoplankton (Student’s *t*-test, H0: prey number in control bottles = prey number in copepod bottles) for all experiments with *E. affinis* and for 5/8 of the experiments with *A. bifilosa*. Nanozooplankton were less often significantly ingested: 3/8 with *E. affinis* and 1/8 with *A. bifilosa*. Thus, even if nanophytoplankton seem to be more frequently ingested than nanozooplankton, both autotrophic and heterotrophic nanoplankton can be included in the natural diet of these copepods, at least in some circumstances.

For *A. bifilosa*, the ingestion rate of total nanoplankton (autotrophic + heterotrophic) varied seasonally (Table I) with a maximum in June (1693 ± 213 cells ind.\(^{-1}\) h\(^{-1}\)). This period usually corresponds to the maximum development rate of this species (Castel, 1993). Most of the variability was due to changes in nanophytoplankton ingestion, whereas in comparison nanozooplankton ingestion alone remained relatively low and stable (June excepted). Moreover, nanophytoplankton ingestion by *A. bifilosa* was higher than nanozooplankton ingestion in most of the experiments (significantly for 4/8).

For *E. affinis*, the ingestion rate of total nanoplankton did not vary significantly between experiments: only the value obtained in July (300 ± 86 cells ind.\(^{-1}\) h\(^{-1}\)) was significantly different from the others (between 1049 ± 90 and 876 ± 65 cells ind.\(^{-1}\) h\(^{-1}\)). Conversely, nanophytoplankton ingestion or nanozooplankton ingestion alone were clearly more variable, with changes depending on stations (in
April) as well as on seasons. Nanophytoplankton ingestion was sometimes higher (significantly in April, station F) and sometimes lower (significantly in November, station E) than nanozooplankton ingestion. This suggests that the composition of *E. affinis* diet could change in relation to environmental conditions.

Environmental conditions corresponding to ingestion experiments are grouped in Table II. For both copepod species, no clear relationships have been found between ingestion rates and the environmental parameters (temperature, prey concentration) which are classically known to affect ingestion. This lack of relationships could be due to the dependence of ingestion rate on several of these factors (or other ones). Furthermore, supposed relationships were not compulsorily linear. Conversely, ingestion rates appeared to be affected by SPM concentration (Figure 2A and B). Maximum nanophytoplankton ingestion rates by *E. affinis* corresponded to relatively low SPM concentrations, whereas maximum nanozooplankton ingestion rates corresponded to higher SPM values (Figure 2A). The results suggest that this copepod shifted its grazing pressure from one kind of prey to the other when the SPM concentration increased. On the other hand, maximum ingestion rates by *A. bifilosa* always corresponded to low (<100 mg l\(^{-1}\)) SPM values (Figure 2B), suggesting that ingestion of this latter species was strongly limited for higher concentrations.

Additional information was obtained by plotting the ratio of autotrophic:total nanoplankton ingested against the same ratio in the water (Figure 3). Only experiments where ingestion was significantly different from zero have been used. The plot shows that the ratio ingested is often significantly above, or very near, the ratio in the water and never below for both species. This result indicates that nanophytoplankton were eaten in disproportion to their numerical abundance in the nanoplankton. In other words, the predation pressure exerted
Table II. Nanoplankton abundances (means ± SE), temperatures (T), salinities (S), oxygen saturations (O₂) and suspended particulate matter concentrations (SPM) at the beginning of ingestion experiments

<table>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>Autotrophic cells (no. ml⁻¹)</th>
<th>Heterotrophic cells (no. ml⁻¹)</th>
<th>T (°C)</th>
<th>S (psu)</th>
<th>O₂ (%)</th>
<th>SPM (mg l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11/04</td>
<td>F</td>
<td>727 ± 44</td>
<td>205 ± 22</td>
<td>12.3</td>
<td>8.5</td>
<td>−</td>
<td>− 57</td>
</tr>
<tr>
<td>12/04</td>
<td>E</td>
<td>512 ± 128</td>
<td>3442 ± 226</td>
<td>14.1</td>
<td>0.8</td>
<td>−</td>
<td>− 305</td>
</tr>
<tr>
<td>23/05</td>
<td>E</td>
<td>4510 ± 885</td>
<td>9021 ± 1459</td>
<td>17.3</td>
<td>4.0</td>
<td>83.7</td>
<td>410</td>
</tr>
<tr>
<td>07/06</td>
<td>E</td>
<td>3936 ± 588</td>
<td>5043 ± 668</td>
<td>20.0</td>
<td>5.1</td>
<td>78.5</td>
<td>136</td>
</tr>
<tr>
<td>05/07</td>
<td>E</td>
<td>4223 ± 872</td>
<td>10661 ± 603</td>
<td>24.5</td>
<td>7.2</td>
<td>82.1</td>
<td>225</td>
</tr>
<tr>
<td>15/11</td>
<td>E</td>
<td>1148 ± 144</td>
<td>3451 ± 266</td>
<td>15.1</td>
<td>8.5</td>
<td>84.0</td>
<td>252</td>
</tr>
<tr>
<td>22/05</td>
<td>F</td>
<td>3936 ± 596</td>
<td>2870 ± 241</td>
<td>17.5</td>
<td>8.8</td>
<td>83.9</td>
<td>94</td>
</tr>
<tr>
<td>06/06</td>
<td>F</td>
<td>4202 ± 526</td>
<td>3219 ± 397</td>
<td>18.9</td>
<td>11.4</td>
<td>82.8</td>
<td>87</td>
</tr>
<tr>
<td>04/07</td>
<td>F</td>
<td>4920 ± 376</td>
<td>1967 ± 161</td>
<td>22.1</td>
<td>14.9</td>
<td>82.6</td>
<td>48</td>
</tr>
<tr>
<td>19/09</td>
<td>F</td>
<td>4510 ± 249</td>
<td>3075 ± 702</td>
<td>18.3</td>
<td>21.2</td>
<td>86.6</td>
<td>78</td>
</tr>
<tr>
<td>20/09</td>
<td>E</td>
<td>6424 ± 731</td>
<td>8952 ± 566</td>
<td>22.0</td>
<td>8.7</td>
<td>84.0</td>
<td>284</td>
</tr>
<tr>
<td>17/10</td>
<td>F</td>
<td>3954 ± 609</td>
<td>1558 ± 177</td>
<td>18.8</td>
<td>16.1</td>
<td>80.5</td>
<td>49</td>
</tr>
<tr>
<td>18/10</td>
<td>E</td>
<td>5826 ± 623</td>
<td>5125 ± 1097</td>
<td>19.3</td>
<td>8.0</td>
<td>77.7</td>
<td>374</td>
</tr>
<tr>
<td>14/11</td>
<td>F</td>
<td>348 ± 61</td>
<td>697 ± 93</td>
<td>13.5</td>
<td>14.9</td>
<td>85.8</td>
<td>111</td>
</tr>
</tbody>
</table>

on nanophytoplankton was significantly higher than that on nanozooplankton. Nevertheless, concerning *E. affinis*, the ratio ingested tended to increase with the ratio in the water. This could partially explain the relationship with SPM concentration described above since the autotrophic:total nanoplankton ratio in the water decreased strongly as SPM increased (Figure 4). A similar observation cannot be made for *A. bifilosa*.

Finally, carbon requirements to sustain observed egg production (see Method) were compared with carbon ingestion (Figure 5). Egg production values, ranging from 0.30 to 5.49 eggs female⁻¹ day⁻¹ for *A. bifilosa* and from 0.34 to 4.79 eggs female⁻¹ day⁻¹ for *E. affinis*, will be detailed in a further paper. For both species, total nanoplanktonic carbon ingested was always above or very near the carbon requirement. This suggests that nanoplankton (auto and/or heterotrophic) could provide an important part of the energetic requirements and that other food sources could be unnecessary. Concerning *E. affinis*, ingestion of nanophytoplankton alone was not always sufficient to meet carbon requirement (2/6 significant differences, *P* < 0.05), whereas total nanoplankton ingestion, including nanozooplankton, appeared to be always sufficient. On the other hand, nanophytoplankton ingestion by *A. bifilosa* never differed significantly from the carbon requirements. The relative importance of nanozooplanktonic cell carbon seems very low for this latter species. In the only experiment where nanozooplankton ingestion was significant, ingested carbon exceeded carbon requirement.

Discussion

The results of this study suggest that both copepods *A. bifilosa* and *E. affinis* ate nanophytoplankton when available instead of nanozooplankton. Considering the
classical food chain in aquatic environments, a trophic relationship between copepods and phytoplankton is not surprising. However, in estuarine turbid environments such as the Gironde, where phytoplankton resources are in relatively short supply, and considering that omnivory has been demonstrated for estuarine copepods (Berk et al., 1977; Stoecker and Egloff, 1987), the important relative role of nanophytoplankton in the diet of the studied species was not expected. Furthermore, it can be reasonably supposed that nanophytoplankton were selected from the total amount of nanoplanckton since they were often eaten in disproportion to their relative abundance in the 5–20 μm size range.

Nevertheless, nanozooplankton cannot be excluded as a possible complementary or alternative food source. From this point of view, results were substantially different between the studied species. For *A. bifilosa*, nanozooplankton ingestion was rarely important (7/8 values were <200 cells ind.⁻¹ h⁻¹) and the only significant value occurred when nanophytoplankton ingestion was also high. Thus, nanozooplankton sometimes appeared as a complementary food source for this copepod, but never as its bulk food. On the contrary, *E. affinis* nanozooplankton ingestion was important only when nanophytoplankton ingestion was low. This

![Graph showing nanophytoplankton and nanozooplankton ingestion by *E. affinis* and *A. bifilosa*](image)

**Fig. 2.** Nanophytoplankton (black squares) and nanozooplankton (open circles) ingested by *E. affinis* (upper panel) and by *A. bifilosa* (lower panel) as a function of SPM concentrations (means ± SE).
suggests that *E. affinis* could use nanozooplankton as an alternative food to compensate for low nanophytoplankton availability, and thereby that nanozooplankton could sometimes be its bulk food if larger (and not investigated) prey were not ingested at a higher rate. This latter species seems then to present an opportunistic feeding behaviour, eating most available food rather than specific food.

Assuming a gross efficiency of egg production of 0.3, the total nanoplanktonic carbon ingested always met the carbon requirements, thus suggesting that other carbon sources could be unnecessary. For *A. bifilosa*, nanophytoplankton alone seemed to cover the largest part of the energetic requirements during most of the experiments, whereas nanozooplankton did not. On the contrary, the energetic requirements of *E. affinis* were sometimes covered by nanophytoplankton alone (4/6 of experiments) and sometimes by nanozooplankton alone (2/6 of experiments).

However, if the use of another gross efficiency of egg production does not affect the ratio between autotrophic and heterotrophic nanoplankton ingestion,
a lower value should make other food sources indispensable. Concerning *E. affinis*, the use of the lowest gross efficiency value found in the literature (0.09; Heinle et al., 1977) reduces the part of carbon requirements covered by nanoplankton ingestion to 74% on average. Then, detritus (Heinle et al., 1977) or microzooplankton (White and Roman, 1992) could constitute part of the diet of this copepod, even if nanoplankton remain its bulk food. Moreover, applying the same minimum gross efficiency to data obtained with *A. bifilosa*, carbon requirements covered by nanoplankton do not exceed 43% on average. In this case, other prey than nanoplankton, such as detritus, large ciliates, rotifers or nauplii, could represent the main source of carbon, even if nanoplankton remain a significant food for this species. Such low values of the gross efficiency of egg production are relatively scarce in the literature and correspond usually to laboratory experiments with high levels of food. Egg production rates measured in this study (see Results) were very low compared to values usually reported in the literature for *E. affinis* (up to 34 eggs female$^{-1}$ day$^{-1}$; Ban, 1994) or for *Acartia sp.* (>40 eggs female$^{-1}$ day$^{-1}$; Kjørboe et al., 1985). These observations probably reflected poor feeding conditions in the Gironde estuary (Burdloff et al., submitted). In such conditions, a generally well-accepted view is that the gross efficiency of egg production is high (Heinle et al., 1977). Thus, a gross efficiency value around 0.3 seems realistic and has been confirmed during preliminary experiments (unpublished data).

Concerning relationships between nanoplankton ingestion and environmental factors, the type and/or the quantity of ingested nanoplanktonic prey seems to be linked to SPM concentration, whereas temperature or nanoplankton abundances had no distinguishable influence during experiments. Because the SPM concentration and nanophytoplankton ratio in the water were closely related, it cannot be decided whether the SPM impact on ingestion was direct (hindering prey capture, for instance), indirect (influencing prey availability),
or both. Consequently, in the following assumptions, SPM is just used as an indicator of nutritional conditions.

For *E. affinis*, total nanoplankton ingestion appeared relatively stable, whereas the ratio of ingested nanophytoplanktonic prey decreased when SPM increased. Phytoplanktonic prey are usually selected by this copepod for relatively low (<100 mg/l) SPM concentration (Tackx *et al.*, 1995). Thus, it can be supposed that the above observation corresponded to a decrease in selection efficiency and that this species did not significantly reduce or stop feeding when its preferred food was not available. On the other hand, the proportion of nanophytoplankton in the diet of *A. bifilosa* did not show any significant changes as a function of SPM and remained relatively high. It was the total nanoplankton ingestion (dominated by autotrophic forms) which seemed to decrease strongly when SPM increased. We can subsequently suppose that *A. bifilosa* reduced its ingestion rate rather than

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**Fig. 5.** Nanophytoplanktonic carbon ingested (black squares) and nanophytoplanktonic + nanozooplanktonic carbon ingested (open circles) against carbon requirements to sustain observed egg production of *E. affinis* (upper panel) and of *A. bifilosa* (lower panel). Carbon requirements are defined from egg production using a gross efficiency of 0.3. Symbols correspond to means ± SE.
ingest a lot of 'undesirable' prey by reducing selection. Thus, in the same estuary, two copepod species present two different feeding behaviours which could correspond to different ways to maximize energy input per unit of energy expenditure.

Such differences in feeding behaviour have already been suggested by Irigoien et al. (1996) and they proposed *E. affinis* as a species adapted to highly turbid environments while *A. bifilosa* would be food limited. Results obtained in this study corroborate these assumptions. However, if *E. affinis* seemed able to maintain ingestion in terms of quantity, this does not mean that the nutritional value of ingested prey does not change. In fact, there are some indications in the literature of a lower copepod development linked to high SPM concentration (Castel and Feurtet, 1993; Gasparini et al., submitted). Therefore nanozooplankton, which seem to be dominant in this case, could have a lower nutritional value than nanophytoplankton (a lower C:N ratio for instance).

In macrotidal estuaries such as the Gironde, both dominant calanoid copepods are clearly spatially and seasonally separated. *Acartia bifilosa* lives in the mesohaline area and is more abundant in summer, whereas *E. affinis* lives in the oligohaline area with maximum abundances during spring and autumn (Castel, 1993). The oligohaline area corresponds generally to the most turbid zone. With the help of the above observations, it can be supposed that environmental factors such as salinity or temperature are not sufficient to explain this distribution, and that more complex mechanisms like feeding behaviour must be involved. *Acartia bifilosa* seems to profit from the summer phytoplankton bloom seaward of the maximum turbidity zone (Irigoien et al., 1996) and is probably not able to use food resources when turbidity becomes too high. On the contrary, *E. affinis* seems able to use several food sources in or slightly upstream of the maximum turbidity zone with a preference for phytoplankton. The apparent discrepancy of a phytoplankton selection in a turbid environment, where primary production is very low, could correspond to the use of inputs from the upper river or from the bank by the copepods. Therefore, the origin of phytoplankton appears to be an interesting question for future research.

Acknowledgements

This study was supported by the 'Region Aquitaine' (Aquitaine/Euskadi project) and by IFREMER (Contract 95-2-480 402 DEL). Thanks are due to G.Oggian, captain of the RV 'Ebalia'.

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Received on August 31, 1996; accepted on February 2, 1997