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Grazing activity of mesoplanktonic copepods in a shallow bay during an algal spring bloom (Marennes-Oléron Bay, France)

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In situ grazing activity of mesoplanktonic copepods was investigated by the fluorometric method during an algal spring bloom in a zone of oyster farming in Marennes-Oléron Bay. The grazing activity of copepods was overall higher during the night than during the day for three species (*Temora longicornis*, *Paracalanus parvus* and *Acartia clausi*), but peaks also appeared during the day for all of them. Individual ingestion rates and daily rations were higher during neap tide (low suspended particulate matter (SPM) concentrations) than during spring tide (high SPM concentrations). During ebb tide (when SPM concentrations were the lowest) the feeding activity of *T. longicornis*, *P. parvus* and *A. clausi* was significantly negatively correlated with algal concentration. Our work suggests that during the algal spring bloom in the farming area of Marennes-Oléron Bay the pressure exerted by mesoplanktonic copepods on the algal stock was very low, as a consequence of: (i) high algal concentrations in the field (resuspension and high phytoplanktonic production); (ii) low ingestion rates when high algal concentrations were observed. The likely ingestion of non-fluorescent particles by copepods is discussed.

INTRODUCTION

Coastal ecosystems are known to support high rates of autochtonous organic production plus, in many estuarine systems, high rates of allochtonous production derived from the land (Kemp et al., 1997). The fate of phytoplankton is a combination of grazing by micro- and mesozooplankton, remineralization and sedimentation. Studies on the fate of phytoplankton are of particular interest in such ecosystems with high productivity where herbivorous invertebrate farmed species such as oysters and mussels are abundant. Nutritional availability for breeding species depends on the competition between them and the other primary consumers. Among them, herbivorous zooplankton and especially copepods, due to their high densities (Sautour & Castel, 1995), could exert an important grazing pressure on the algal stock. This has been observed in the open sea (Menzel & Ryther, 1961), but grazing pressures exerted by metazoan zooplankton on phytoplankton are generally low in coastal zones (Kiørboe & Nielsen, 1994; Sautour et al., 1996).

In semi-enclosed coastal areas such as Marennes-Oléron Bay, detritus forms an important part of suspended particulate matter (SPM). The great quantity of these suspended particles in the water column can affect copepods (Irigoien et al., 1993) and imposes great nutritional adaptability. Although copepods were considered as herbivorous for a few years, a lot of coastal species are also now known to have detritivorous (e.g. Roman, 1984) or carnivorous (e.g. Verity & Paffenhöfer, 1996) diets. The wide adaptability of coastal copepods in highly variable areas is also due to their capacity to feed as suspension feeders on immobile particles and/or as predators on larger ones which are individually detected (Price et al., 1983; Kiørboe et al., 1996) and to their capacity to rapidly migrate in the water column (Williamson et al., 1996). The opportunistic trends of these plankters allow them to utilize their nutritive environment optimally.

The grazing activity of planktonic copepods was studied in the characteristic zone of oyster farming in the Marennes-Oléron Bay during an algal spring bloom by means of the gut fluorescence method. This method does not permit the estimation of the ingestion of non-chlorophyll particles but it does allow us to quantify the impact of the herbivorous copepod community on the algal stock.

MATERIALS AND METHODS

Study area and sampling strategy

The sampling station was situated in the middle of the bay (Figure 1) where two opposite tidal flows meet and create a 'wantij' (Héral et al., 1983). One of them is due to neritic water, entering the bay through the Pertuis d'Antioche, and mixing with estuarine water (Charente Estuary). The second flow is less important and penetrates the south of the bay through the Pertuis de Maumusson. The sampling area is characterized by its shallowness (~6 m at high tide at our sampling station) and by an important turbulence and by high concentrations of SPM. A net water flow is observed in the bay from the north to the south, taking about five to nine days.

Two series of samples were taken during the algal spring bloom (May 1988): one during neap tide and one during spring tide at two hour intervals during a 24 h cycle. At each sampling, temperature, salinity, SPM and chlorophyll pigments were measured (unpublished data

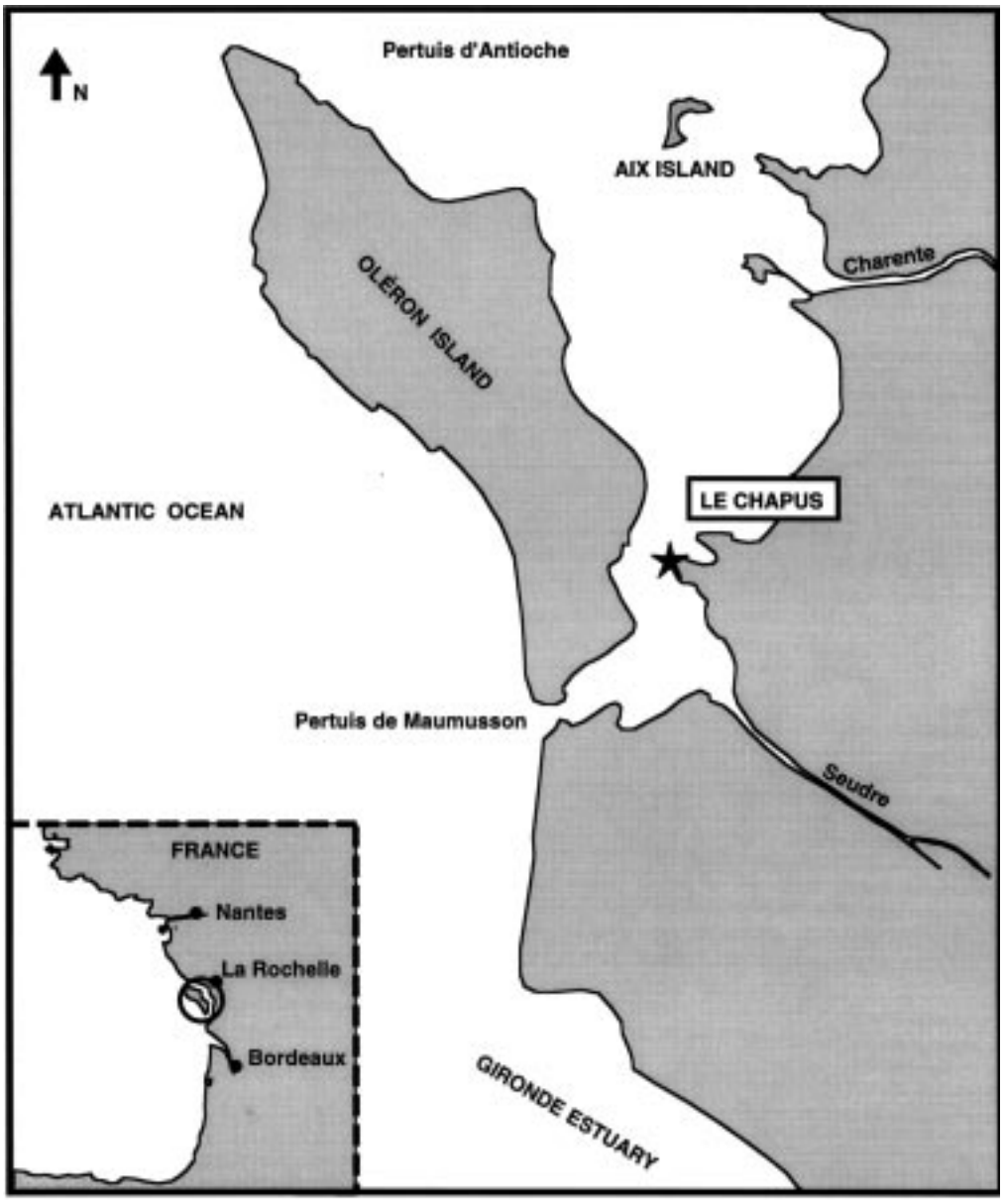

Figure 1. Marennes-Oléron Bay (France). Sampling station.

from the Laboratoire des Écosystèmes Conchylicoles IFREMER). Chlorophyll pigments were obtained by filtering 1 l onto a GF/C filter and were measured by the fluorometric method (Parsons et al., 1984). Suspended particulate matter was estimated as dry weight (60°C, 24 h) after filtration (1 l) onto a GF/C filter. Two zooplankton samples were also collected: a quantitative one to determine zooplankton density; and a qualitative one to measure copepod gut fluorescence. These two zooplankton samples were taken by means of a pump (1.5 m from the bottom, average discharge: 6 m^3 h^{-1}) and filtered through a sieve (mesh size: 200-μm). The quantitative samples were rinsed with filtered seawater and preserved in seawater buffered formalin for estimation of species abundances in the laboratory. The qualitative samples were immediately deep-frozen and stored in liquid nitrogen until the determination of gut fluorescences.

Zooplankton density and biomass

An aliquot of each quantitative sample was used to determine zooplankton abundance. Zooplankton were sorted and counted under a binocular microscope. Copepods were determined to species level. Results were transformed to abundance per cubic metre. The individual dry weights of the herbivorous copepods were determined by weighing three aliquots of 30 individuals of each species on a Mettler ME22 microbalance (sensitivity: 0.1 μg); individuals having been previously rinsed with distilled water and dried at 60°C for 24 h. Biomass was given in weight of carbon by multiplying dry weights by a factor 0.4 (Simard et al., 1985).

Copepod gut content and ingestion rates

The grazing estimation was made by measuring the amount of chlorophyll pigments present in the gut of the

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copepods with the gut fluorescence method (Mackas & Bohrer, 1976). The qualitative samples were rapidly deep-frozen in order to minimize faecal pellet production of individuals (Saiz et al., 1992). This technique does not affect the fluorescence of chlorophyll pigments in the gut of the copepods (Bautista et al., 1988). In the laboratory, 25 individuals of each dominant species were picked at random from the frozen samples under a binocular microscope and a cool light. Animals were washed with filtered seawater to remove adherent algae, transferred and crushed in tubes with 5 ml of 90% acetone. The fluorescence of the extracts was measured after 2 h extraction (4°C in the dark) before and after acidification with a fluorometer (Turner model 112). The equations of Lorenzen (1966) were used to calculate the average gut chlorophyll pigment content of copepods (G). They were obtained from the addition of chl-*a* and phaeopigments (pheophorbides expressed in chl-*a* equivalents: chl-*a* eq) and expressed in ng chl-*a* eq.

Classically, the fluorometric method uses chlorophyll pigments as natural tracers postulating that the degradation of chlorophyll ends with phaeopigments (Shuman & Lorenzen, 1975). However, Wang & Conover (1986) and Kiørboe & Tiselius (1987) noted that results obtained with this method could be underestimated. The bias could be due to a destruction of chlorophyll pigments to non-fluorescent compounds during their passage through the gut of the copepods widely depending on circumstances: feeding history, food concentration, light, diel feeding behaviour (Head, 1992; Head & Harris, 1996). Very high levels of pigment destruction have occasionally been observed (90–99%) inducing underestimates of ingestion rate by an order of magnitude (Conover et al., 1986). However, in these experiments it is unknown if the loss of pigments occurs in the gut of copepods or in the faecal pellets. Comparisons between the gut fluorescence and other methods (Kiørboe & Tiselius, 1987) and measurements of pigment budget (Pasternak & Drits, 1988) suggest that this estimate is not valuable for copepods in general and that instantaneous destruction is probably not great if it occurs (10–11%). Destruction of pigments to non-fluorescent compounds during their passage through the gut of the copepods was not measured during our study. Consequently, all our values found for gut content were corrected for pigment destruction using a common level of pigment destruction: 33% (Dam & Peterson, 1988; Atkinson et al., 1996).

Individual hourly ingestion rates of copepods (*Ic*, ng chl-*a* eq $\mathrm{ind}^{-1}\mathrm{h}^{-1}$) were estimated by multiplying copepod gut contents by the gut clearance rate constants (k, min^{-1}):

$$Ic = 60\,k\,G \tag{1}$$

The daily rations (in percentage of body carbon) were calculated for the six species by dividing the individual daily ingestion rate (converted to carbon from the carbon to chlorophyll ratio: C=50 chl-*a*) by the individual carbon weight.

Gut clearance rate constants (k) were determined in the laboratory for the four dominating species: *Acartia clausi*, *Centropages hamatus*, *Euterpina acutifrons* and *Temora longicornis* (gut clearance rates given by Huntley et al. (1987) were used for *Paracalanus parvus* and *Calanus helgolandicus*). The determination of the gut clearance rate constant was made by measuring the decrease of chlorophyll pigments in the gut of starved copepods. Copepods were acclimatized for two days in the laboratory at constant temperature (19°C) and fed with the prymnesiophycae: *Isochrysis galbana*. At the beginning of the experiment copepods were placed, in the dark, in beakers containing filtered seawater (five animals per 50 ml beaker). At regular intervals (10 min), from 0 to 60 min, three pools of five copepods were gently picked out and transferred into tubes with 5 ml of 90% acetone. The extraction of chlorophyll pigments and the determination of the gut content were made as described above.

An exponential model is classically used to describe the decrease of chlorophyll pigments in the gut of starved copepods according to the time (Mackas & Bohrer, 1976; Kiørboe et al., 1985; Wang & Conover, 1986; Bautista et al., 1988):

$$G_t = G_0 \mathrm{e}^{-kt} \tag{2}$$

(where G_0 is the initial gut pigment content cop-l; G_t the gut content cop-l at time t; k the gut clearance rate constant). The gut clearance rate constants were calculated from this model. These experimental values obtained at 19°C were extrapolated to the field temperature using a Q_{10} value of about 2.21 (Dam & Peterson, 1988).

Species ingestion rates and grazing impact

Species ingestion rates were determined by multiplying the individual ingestion rate (I_c) by the abundance per cubic metre (N) of the corresponding species. Consumption by the copepod community (I_t) was calculated by summing the species ingestion rates.

Grazing pressure (P) by the copepod community on the algal stock was estimated by dividing the quantity of chlorophyll pigments per cubic metre in the field (C) by the consumption by the copepod community per cubic metre (I_t):

$$P = \frac{C}{I_t} 100 \tag{3}$$

RESULTS

Environmental conditions

Short-term variations due to tidal cycles were observed for SPM and phytoplankton (Figure 2). Maximum SPM concentrations were observed at the beginning of the flood tide (period between low water and high water) due to local erosion. Other smaller peaks were observed at high tide due to the SPM coming from both the north of the bay and the Charente Estuary. The lowest SPM concentrations were observed during ebb tide (period between high water and low water). This corroborates the common scheme observed in the middle part of the bay by Raillard (1991) indicating that low SPM concentrations were observed during ebb tide when tidal

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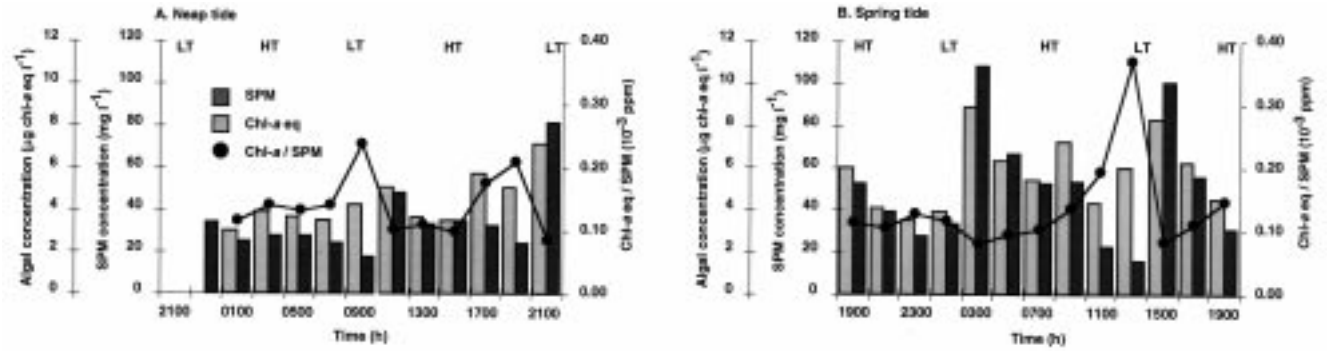

Figure 2. Changes in algal concentration (μg chl-*a* eq l^{-1}), SPM concentration (mg l^{-1}) and chl-*a*/SPM ratio (10^{-3} ppm) during (A) neap tide and (B) spring tide. HT, high tide; LT, low tide.

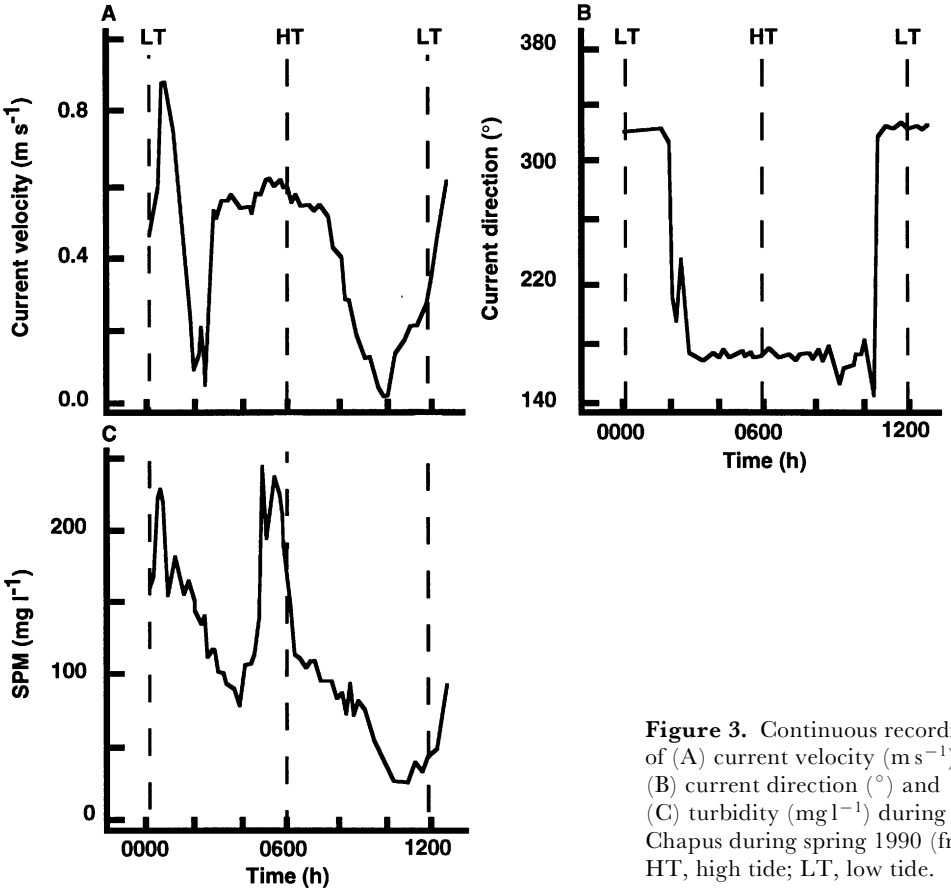

Figure 3. Continuous recording of (A) current velocity (m s^{-1}), (B) current direction (°) and (C) turbidity (mg l^{-1}) during spring tide at Le Chapus during spring 1990 (from Raillard, 1991). HT, high tide; LT, low tide.

currents were at their lowest, inducing sedimentation of suspended particles and that the highest SPM concentrations were usually observed during flood tide due to local erosion induced by important tidal currents (Figure 3). High chlorophyll pigment concentrations were nearly always observed at low tide. Variations were also observed between spring and neap tides (Table 1): SPM concentrations were on average 1.5 times higher and the concentrations varied on a larger-scale during spring tide than during neap tide (which is classically observed in this zone: Raillard, 1991). Generally, during the algal spring bloom in the middle part of the bay, organic matter represented 10–20% of the SPM, the lowest relative values being observed during spring tide (ash-free dry weight: M. Héral, personal communication).

Table 1. *Salinity, temperature, suspended particulate matter (SPM), phytoplankton stock, zooplankton and copepod abundance in Marennes-Oléron Bay during the algal spring bloom (May 1988).*

	Neap tide	Spring tide
Salinity (psu)	28.5 ±0.3	30.0 ±0.3
Temperature (°C)	16.1 ±0.9	16.6 ±1.0
SPM (mg l^{-1})	34 ±16	51 ±27
Phytoplankton stock (μg chl-*a* eq l^{-1})	4.4 ±1.2	5.8 ±1.7
Phytoplankton/SPM	0.14 ±0.05	0.14 ±0.07
Zooplankton (ind m^{-3})	2760 ±2173	2960 ±1872
Copepods (ind m^{-3})	1897 ±1582	2107 ±1566

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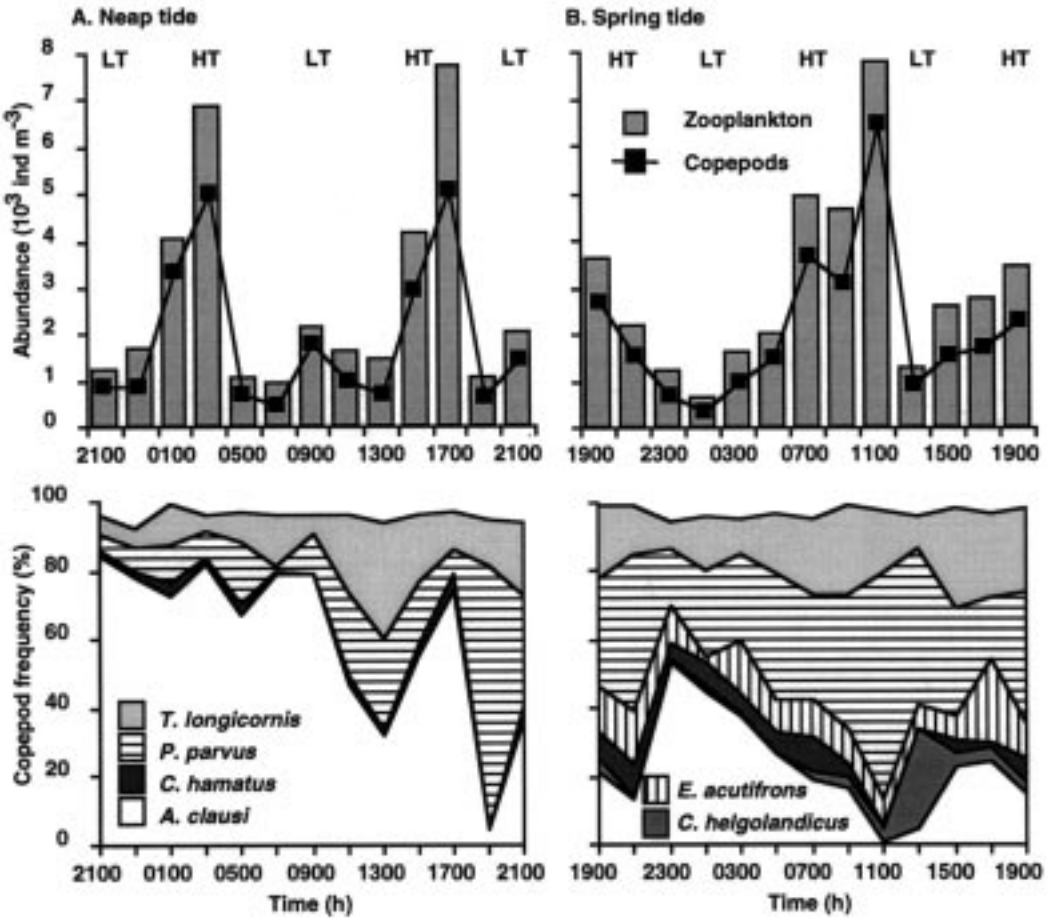

Figure 4. Zooplankton and copepod abundance (ind m^{-3}) and relative abundance of the main copepod species in the copepod community during (A) neap tide and (B) spring tide. HT, high tide; LT, low tide.

Table 2. *Individual carbon weights, gut content, daily rations (in percentage of body carbon) and daily consumption of copepod species during neap tide (NT) and spring tide (ST).*

	Weight (μg C),	Gut content (ng chl-*a* eq cop^{-1}),		Daily ration (%)		Daily consumption (μg chl-*a* eq m^{-3} d^{-1})	
		NT	ST	NT	ST	NT	ST
Arcartia clausi	1.25 ±0.02	0.88 ±0.96	0.31 ±0.20	80	30	21.9 ±23.7	2.3 ±2.0
Centropages hamatus	2.78 ±0.21	0.90 ±0.49	0.81 ±0.54	103	96	3.9 ±6.0	3.5 ±3.1
Paracalanus parvus	1.40 ±0.13	0.31 ±0.16	0.15 ±0.10	15	7	1.0 ±1.0	2.1 ±4.3
Temora longicornis	3.90 ±0.17	0.54 ±0.35	0.32 ±0.18	135	84	29.7 ±40.3	24.1 ±20.1
Calanus helgolandicus	16.31 ±1.65	—	2.51 ±2.02	—	42	—	6.6 ±7.7
Enterpina acutifrons	0.68 ±0.02	—	0.47 ±0.48	—	149	—	3.7 ±3.6

Classically, the phytoplankton stock is mainly composed of *Nitzschia seriata*, *Schroderella delicatula*, *Thalassiosira hyalina* and *Rhizosolenia* sp. during the algal spring bloom in the bay (Héral et al., 1983). During our study the mean stock (±SD) increased from 4.40±1.23 μg chl-*a* eq l^{-1} during neap tide to 5.75±1.70 μg chl-*a* eq l^{-1} during spring tide (*t*-test, $P<0.05$). Chlorophyll pigment concentrations were strongly linked to SPM ($P<0.05$ during neap tide and $P<0.01$ during spring tide). Chlorophyll pigment concentrations/SPM ratios were used as an index of food accessibility to copepods. No significant difference was observed between neap tide and spring tide, but values found during ebb tide were significantly higher than those found during flood tide (*t*-test, $P<0.01$).

Zooplankton density

Zooplankton abundance varied according to tidal cycle (Figure 4): the highest values were observed at high tide (which is linked to the influence of water masses coming from the north of the bay: Sautour & Castel, 1993). Zooplankton abundances were not significantly different between the two cycles. Copepods constituted on average >65% of the zooplankton abundance during the two cycles. During neap tide, *Acartia clausi* dominated the

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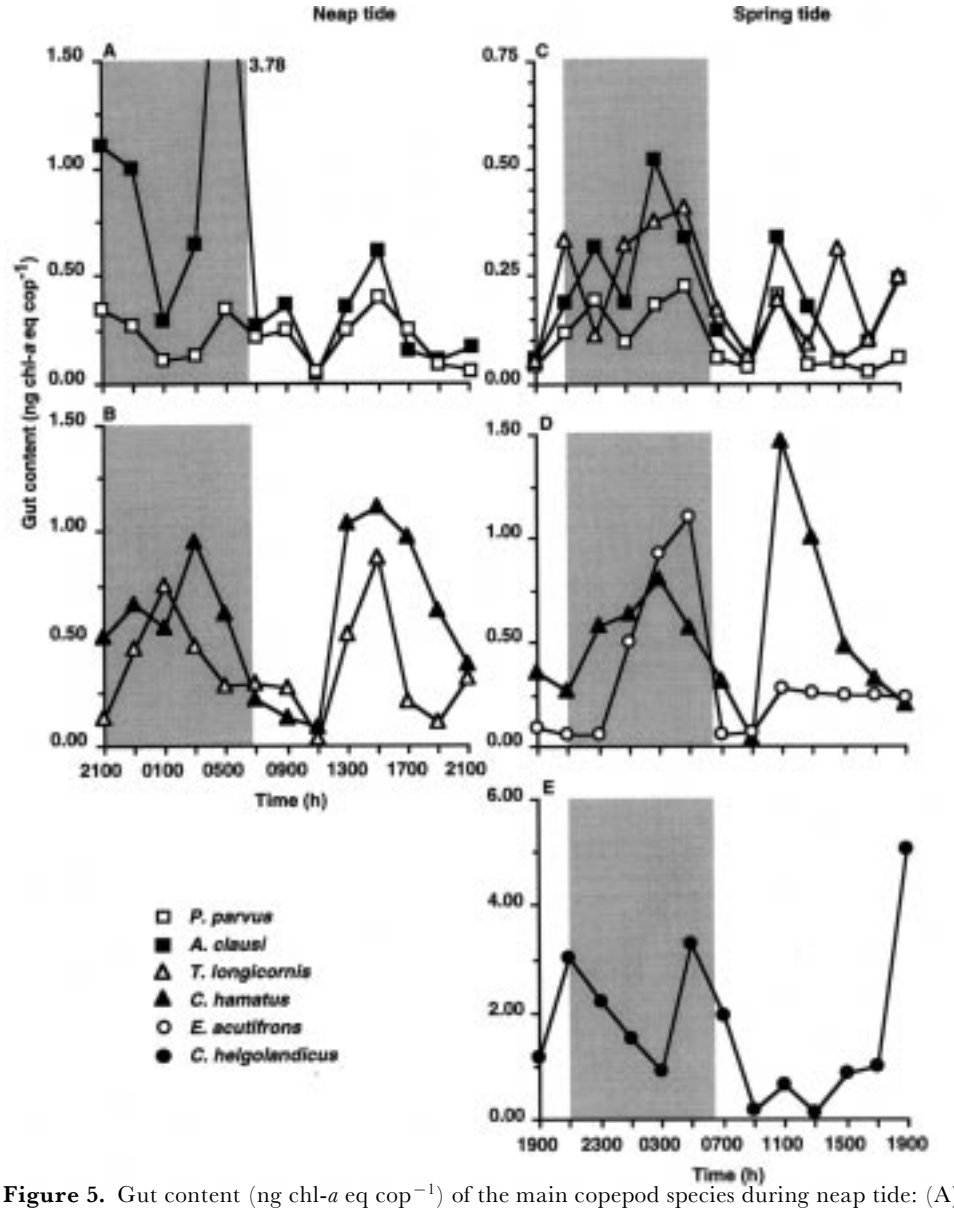

Figure 5. Gut content (ng chl-*a* eq cop^{-1}) of the main copepod species during neap tide: (A) *Paracalanus parvus* and *Acartia clausi*; (B) *Temora longicornis* and *Centropages hamatus*. During spring tide: (C) *A. clausi*, *P. parvus*, *T. longicornis*; (D) *C. hamatus*, *Euterpina acutifrons*; (E) *Calanus helgolandicus*. Shaded area indicates night-time period.

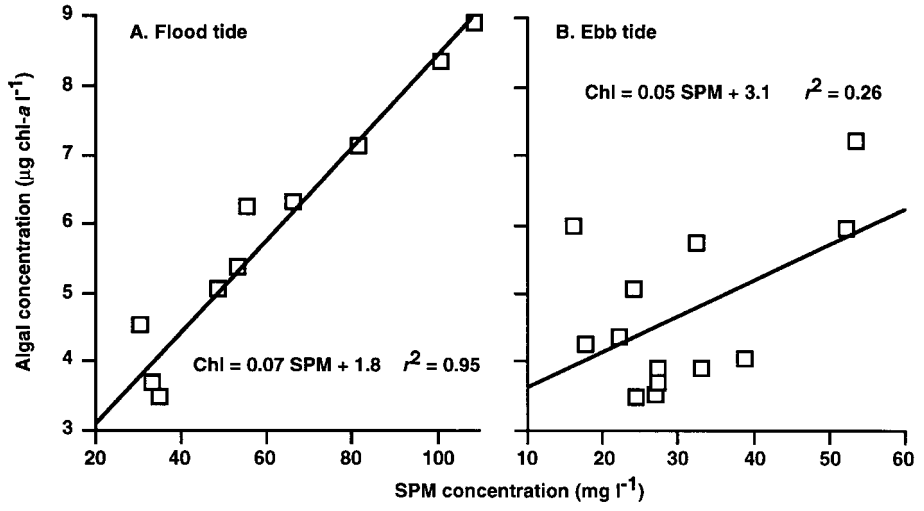

Figure 6. Suspended particulate matter concentration ($mg\,l^{-1}$) in relation to chlorophyll pigment concentration (μg chl-*a* $eq\,l^{-1}$): (A) flood tide; (B) ebb tide.

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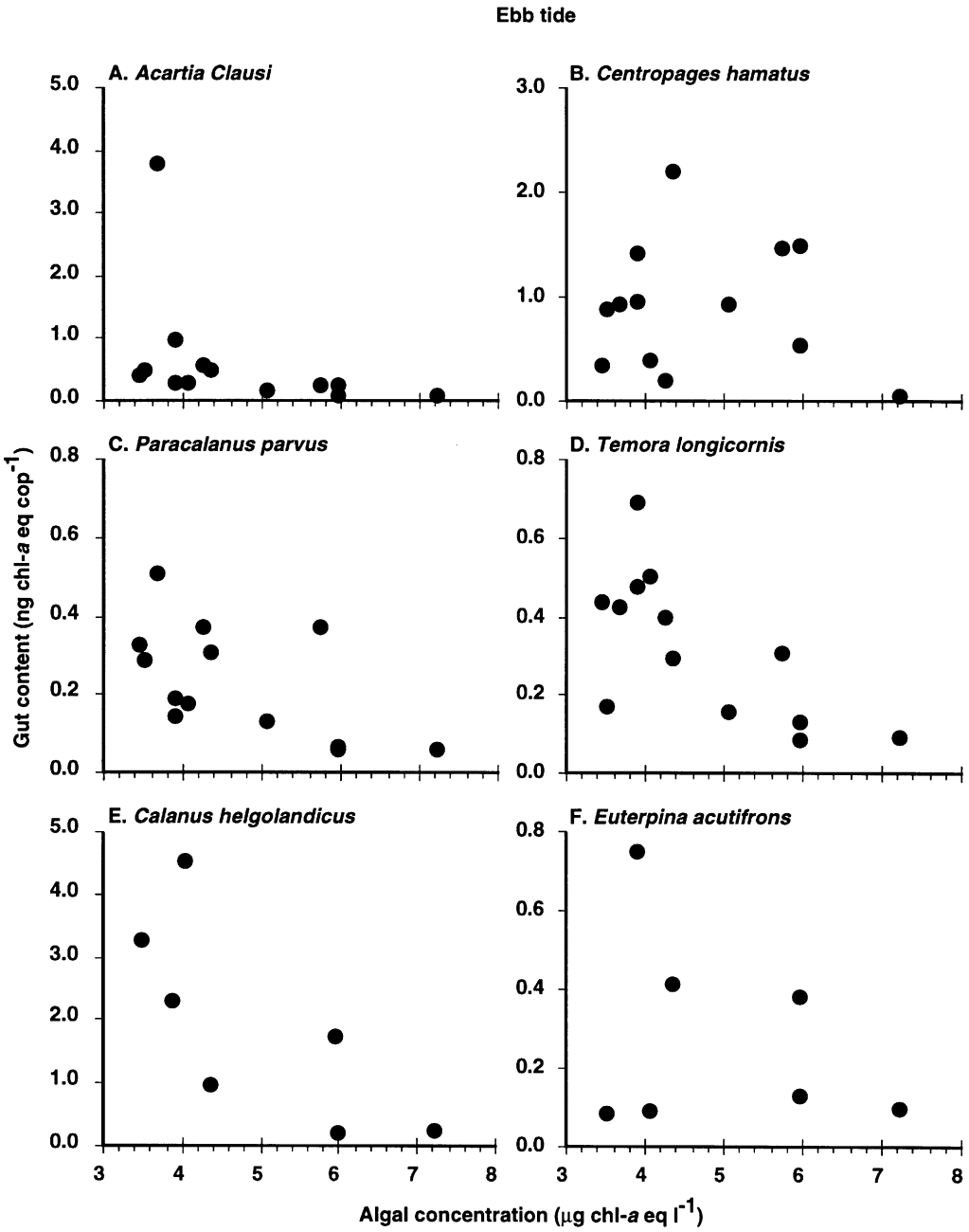

Figure 7. Gut content (ng chl-*a* eq cop^{-1}) of the main copepod species during ebb tide in relation to chlorophyll pigments in the field (data from the two cycles were pooled together). (A) *Acartia clausi*; (B) *Centropages hamatus*; (C) *Paracalanus parvus*; (D) *Temora longicornis*; (E) *Calanus helgolandicus*; (F) *Euterpina acutifrons*.

Table 3. *Summary of statistical models (see text) fitted to the data on gut clearance experiments. Copepods previously fed with* Isochrysis galbana.

Species	Model	Evacuation rate (k, min^{-1})
Acartia clausi	$G_t = 4.22\ e^{-0.020t}$ ($r^2 = 0.75$, N = 18)	0.020
Centropages hamatus	$G_t = 0.32\ e^{-0.055t}$ ($r^2 = 0.87$, N = 15)	0.055
Euterpina acutifrons	$G_t = 0.10\ e^{-0.036t}$ ($r^2 = 0.60$, N = 15)	0.036
Temora longicornis	$G_t = 4.27\ e^{-0.172t}$ ($r^2 = 0.91$, N = 12)	0.172

G_t, gut content at time t; temperature, 19°C.

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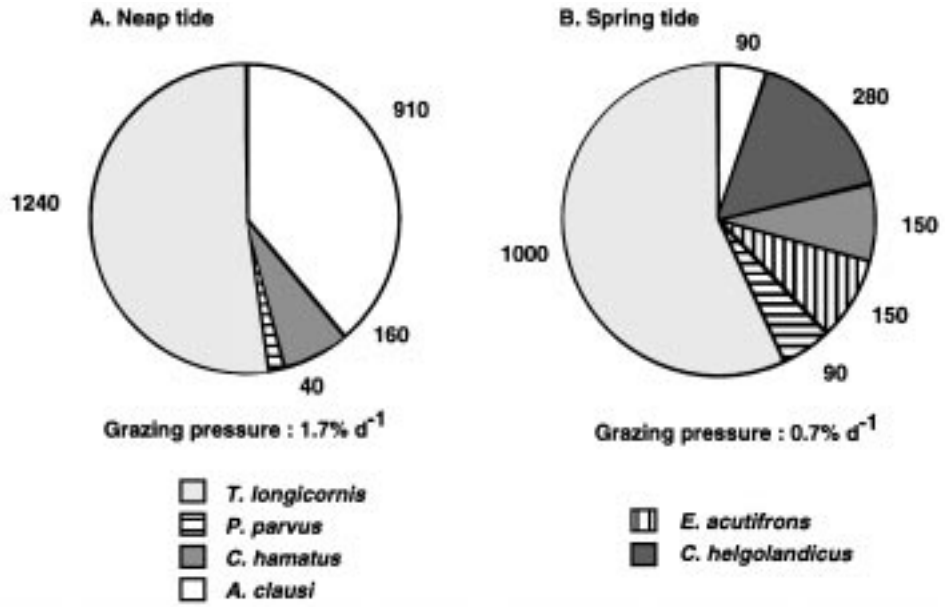

Figure 8. Average hourly algal consumption of the main copepod species (ng chl-*a* eq cop^{-1} h^{-1}) and daily copepod grazing pressure (% d^{-1}) on the algal stock during (A) neap tide and (B) spring tide.

copepod community (61±25%) which also comprised *Temora longicornis* (19±20%), *Paracalanus parvus* (14±9%) and *Centropages hamatus* (2±2%). These four species constituted 96±2% of the copepod community. The remainder of the zooplankton community was composed of gastropod, cirripede and decapod larvae and sporadically bivalve larvae and chaetognaths. During spring tide, the copepod community was essentially composed of *P. parvus* (35±13%), *A. clausi* (23±15%), *T. longicornis* (19±7%), *Euterpina acutifrons* (11±5%), *C. hamatus* (5±3%) and *Calanus helgolandicus* (4±8%). Gastropod, bivalve, cirripede and decapod larvae plus chaetognaths dominated the remainder of the zooplankton.

Copepod gut pigment content

The amount of pigment in the gut of copepods varied widely during the sampling periods. Gut content was significantly lower during spring tide than during neap tide (Table 2) for *A. clausi* ($P<0.05$, *t*-test) and *P. parvus* ($P<0.01$), when the concentration of chlorophyll pigments in the field were higher during spring tide than during neap tide ($P<0.05$). No significant differences were observed for *T. longicornis* and *Centropages hamatus*. Two periods of high ingestion rate were observed: one during the day and one during the night (Figure 5). Diurnal periods of high gut pigment content occurred at 1500 hours (UT) during neap tide and possibly one at 1100 hours during spring tide. Nocturnal periods of high grazing activity varied between species. Average nocturnal gut pigment contents (2100–0500 hours) were higher than diurnal ones both during spring tide and neap tide for *A. clausi* ($P<0.05$, *t*-test), and only during spring tide for *P. parvus* and *T. longicornis* ($P<0.02$).

When gut contents measured during the two cycles were pooled (both neap+spring tides), significant decreases of gut pigment contents were observed when chlorophyll pigments increased for *A. clausi* and *P. parvus* ($P<0.01$, hypothesis test for Spearman's coefficient).

Data obtained during ebb tide (low SPM) and during flood tide (high SPM) were analysed separately. No significant differences were observed between ebb tide gut content and flood tide gut content. During flood tide, chlorophyll pigment concentration and SPM concentration were strongly linked ($P<0.005$; Figure 6) pointing out the importance of local erosion and resuspension of inorganic and detrital material due to tidal currents (Raillard, 1991). No significant relationship was found between gut content and algal concentration during flood tide. During ebb tide, (high chlorophyll/SPM ratios, low tidal currents, settlement of SPM), strong decreases of gut content were measured when algal concentration increased (Figure 7; *P. parvus*, $P<0.05$; *Celanus helgolandicus*, *A. clausi* and *T. longicornis*, $P<0.01$).

Copepod consumption and grazing impact

Results of the gut clearance experiments were as expected (Table 3). Initial gut content was highly different from one species to the other and for each species the exponential model described the decrease of chlorophyll pigments in the gut of starved copepods. Clearance rate constants were similar to those obtained in the literature (Simard et al., 1985; Wang & Conover, 1986; Kiørboe & Tiselius, 1987; Sautour et al., 1996).

During neap tide, ingestion rate was dominated by the most important species *A. clausi* and *T. longicornis* (Figure 8). The algal consumption was far lower for the two other species due to low abundance of *Centropages hamatus* and low individual ingestion rates for *P. parvus*. During spring tide, *T. longicornis* was again the most important phytoplankton consumer (57% of the copepod consumption)

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and the consumption due to the other species was far lower. Summing the species ingestions per cubic metre together, average daily ingestion rates of 56 μg chl-*a* eq $m^{-3} d^{-1}$ during neap tide and 42 μg chl-*a* eq $m^{-3} d^{-1}$ during spring tide were obtained. The average grazing impact of the copepod community on the algal standing stock was 1.7% d^{-1} during neap tide and 0.7% d^{-1} during spring tide.

DISCUSSION

Gut pigment contents obtained in Marennes-Oléron Bay during this study were within the values reported in the literature for the same species or for similar ones (Kiørboe et al., 1985; Simard et al., 1985; Bautista et al., 1988; Sautour et al., 1996).

Rhythms of grazing activity

Short-term fluctuation of gut contents were observed during our study: bimodal rhythms of grazing activity were shown by several species. The classical higher nocturnal grazing activity (Mackas & Bohrer, 1976; Dagg & Wyman, 1983; Kiørboe et al., 1985; Simard et al., 1985; Christoffersen & Jespersen, 1986; Bautista et al., 1988) was observed for *Acartia clausi* during the two cycles and only during spring tide for *Paracalanus parvus* and *Temora longicornis*. The increase in grazing activity during the night shown for these species was attributed to endogenous rhythms of grazing activity by Duval & Geen (1976). Significant higher nocturnal grazing activity was not shown for other species due to important peaks observed during the day. Periods of high diurnal grazing activity as we observed in Marennes-Oléron Bay were also described in other sites (Nicolajsen et al., 1983; Christoffersen & Jespersen, 1986). The position of these increases throughout the day varies according to the sampling site (Dagg & Wyman, 1983) or according to the position of the individuals in the water column (Kiørboe et al., 1985). Vertical migration of copepods has been used to explain variations in gut content (Simard et al., 1985; Tande & Bamstedt, 1985; Roman et al., 1988; Williamson et al., 1996): individuals can migrate from a water mass with low phytoplankton concentration to a water mass with high algal concentration. However, the influence of vertical migration of copepods is probably very limited in Marennes-Oléron Bay due to the shallowness and probably only partially explains short-term variation in grazing activity.

Grazing activity and nutritional environment

Grazing activity of copepods appears to be a combination of stochastic and deterministic processes (Kleppel, 1993) and variations of grazing activity also depend on the food environment of the plankters. The relationship between the grazing activity of copepods and their nutritional environment have often been studied in the laboratory (Demott, 1995; Sanders et al., 1996) and in the field (Bautista & Harris, 1992; Dagg, 1995; Brussard et al., 1995). Classically, in the laboratory, grazing rates increase with algal concentration and reach a plateau (Frost, 1972). However, almost no significant relationship between gut content and algal concentration was found in our study and the relationship we found for *P. parvus* and *A. clausi* indicates a negative correlation between the grazing activity and algal concentration. This overall lack of correlation between ingestion rates and algal concentrations is quite general in field studies (e.g. Tande & Bamstedt, 1985), although positive correlations were sometimes observed (e.g. Bautista et al., 1988). Changes in algal concentrations are not sufficient to solely explain variations in grazing activity (Paffenhöfer, 1988). Important changes in both quality and quantity of SPM in Marennes-Oléron Bay are induced by both important oceanic (through Pertuis d'Antioche) and continental inputs (Seudre and Charente rivers) and by tidal currents, increasing the environmental variability. In such a shallow area, the nutritional environment of plankters is composed of phytoplankton 'diluted' with inorganic matter, detritus, microphytobenthos and microheterotrophs from different origins, whose relative abundance depends on the hydrological conditions. Each change in the nutritional environment of copepods induces periods of adjustment in their feeding activity; during these periods their grazing activity may be disturbed (Price & Paffenhöfer, 1984). Both periods of adaptation and the capability of copepods to feed upon other food sources than phytoplankton may increase the discrepancy observed between our results (and more generally between *in situ* studies) and the relationship found between gut content and chlorophyll pigment concentration in the laboratory.

The differences in copepod gut content (in terms of chlorophyll pigments) between neap and spring tides could be attributed to changes in the age structure of the copepod populations. However, the greater variability of gut contents during neap tide than during spring tide, indicates that other parameters probably strongly influenced variations in gut content. The influence of non-fluorescent particles (organic or inorganic) on the grazing activity of copepods can be detected by measuring the differences in copepod gut contents between neap and spring tides. The turbidity in the middle part of Marennes-Oléron Bay during the algal spring bloom was 1.5 times higher during spring tide than during neap tide and the highest relative values of inorganic SPM were found during spring tide. Thus, the general decrease of ingestion of algae during spring tide can be explained by: (i) a 'dilution' of the phytoplankton stock with mainly inorganic non-fluorescent particles; and also probably (we have no data to support these two points) by: (ii) a clogging of the filtering appendages of copepods during spring tide due to abundant non-fluorescent particles leading to a decrease in the filtration efficiency; and (iii) ingestion of non-fluorescent organic particles (heterotrophic microzooplankters) due to their abundance in this kind of shallow area submitted to riverine inputs (Carlsson et al., 1995). This last hypothesis underlies that these particles can be ingested by copepods and that their potential nutritive value is of consequence (Gifford & Dagg, 1988; Koshikawa et al., 1996). According to the copepod species, ingestion rates were more or less lower during spring tide than during neap tide, indicating different capabilities of adaptability towards the variations of the nutritive environment. *Centropages hamatus* appeared to be the least sensitive to these variations: its ingestion rate on phytoplankton only decreased by 7% during spring tide.

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As ingestion rates of copepods declined when SPM concentrations increased, we examined the relationship between gut content and chlorophyll pigment concentration when both SPM concentrations were at their lowest and chlorophyll/SPM ratios were the highest and vice versa. During flood tide (highest SPM concentrations), SPM concentrations were strongly correlated with chlorophyll pigment concentrations (Figure 6) indicating resuspension of microphytobenthos and detrital algae (Raillard, 1991) and a constant proportion of potential algal and non-algal food items. During these periods gut content was not correlated with algal concentration, which was probably due to: (i) rapid changes in the nutritional environment of the copepods (in terms of quality and quantity) linked to the great turbulence observed in this zone of 'wantij' (Tesson, 1973); and (ii) selection of microzooplankton as prey which can be favoured by turbulence (Kiørboe et al., 1996). The lowest SPM concentrations were typically observed during ebb tide when chlorophyll/SPM ratios were the highest and varied a lot indicating variable proportion of potential algal and non-algal food sources. During this period, gut content strongly decreased with increasing algal concentration, except for *C. hamatus* (Figure 7). For *A. clausi* and *T. longicornis*, high gut content observed at low algal concentrations coincided with nocturnal data (Figure 7) indicating that the relationship found between algal concentration and gut contents could be influenced by an important nocturnal grazing activity of these two species. On the contrary, high nocturnal ingestion rates did not influence the relationship between algal concentration and gut content for *P. parvus*. During ebb tide, the highest chlorophyll concentrations often coincided with the highest amounts of SPM indicating resuspension: phytoplankton stock consisted probably mostly of dying or unpalatable algal cells. For *P. parvus*, and probably also for *A. clausi* and *T. longicornis*, the low gut content observed when chlorophyll concentrations were high, probably linked to the poor quality of the phytoplankton stock. In this case copepods can select their food and reject unavailable or undesirable particles (White & Roman, 1992), particularly when other high-quality food sources are abundant (Burns & Hegarty, 1994).

Feeding behaviour

As a result, from our study we can distinguish between different feeding behaviour for the four dominant copepod species. Grazing activity of *C. hamatus* was never correlated to chlorophyll concentration and the daily rations calculated for both spring tide (high SPM concentrations) and neap tide (low SPM concentrations) were high and similar (Table 2). This indicates no apparent modification of the grazing activity according to algal concentration and a good adaptation of this species to the great environmental variability in this shallow bay. Detrital algae were probably accessible to this species through the microbial food web. The omnivory of 'herbivorous' copepods is now well known and only a few groups of obligate herbivores or carnivores exist (Paffenhöfer, 1988; Froneman et al., 1996; Koshikawa et al., 1996). Daily rations found for *T. longicornis* were high, indicating that this species was also well adapted to the phytoplankton stock found in this nearshore environment. However, both the strong decrease of daily ration observed during spring tide and the decrease of grazing activity when algal concentration increased during ebb tide highlight the sensitivity of this species to changes in its nutritional algal environment and its capability to modify its feeding behaviour. These observations and the high gut clearance rate constant observed for this species could be attributed to an opportunistic species having an important grazing activity varying according to its nutritional environment. Our results corroborate previous results obtained for *C. hamatus* and *T. longicornis* indicating that these two species are omnivores, the first one being mainly 'carnivorous', the second one mainly 'herbivorous' (Paffenhöfer & Knowles, 1980).

The low daily ration values observed for *A. clausi* and *P. parvus*, the highly important decreases in daily rations from neap tide to spring tide, and the significant decrease of grazing activity when algal concentration increased during ebb tide illustrate their sensitivity to variation in their algal environment. In addition, the constant presence of these two species in Marennes-Oléron Bay (Sautour & Castel, 1993) suggests they are capable of completing their diet with other food sources. In this case, the populations were probably mainly supported by microzooplankton which can constitute important alternative food items (Gifford & Dagg, 1988), represent a significant amount of the daily ration (see review in Kleppel, 1993) and which is a trophic intermediary between the microbial food web and larger mesozooplankton (Froneman et al., 1996).

Copepod grazing impact

Simple links between grazing activity of copepods and the nutritional environment are difficult to determine with traditional methods in littoral areas such as Marennes-Oléron Bay. The main problems are due to: (i) the great variability of suspended particulate matter; (ii) the great variability of food sources available for copepods; and (iii) the variable feeding behaviour of copepods. These parameters act together on the instantaneous grazing activity of copepods, but also on the life story of their feeding activity (Head, 1988). The gut fluorescence method allows an evaluation of the grazing impact of the plankters on the phytoplankton stock. It can be noticed from our work that, as a consequence of: (i) high algal concentration in the field (resuspension and high phytoplanktonic production); (ii) low ingestion rate when high algal concentration was observed; and (iii) likely ingestion of non-fluorescent particles by copepods, the pressure exerted by mesoplanktonic copepods on the algal stock was very low during the algal spring bloom in the characteristic farming area of Marennes-Oléron Bay. The grazing pressure on the algal stock (in terms of chl-*a* eq) is even low when it is multiplied by 2 (Conover & Mayzaud, 1984; Sautour & Castel, 1998) in order to estimate the pressure of the whole copepod community (mesozooplanktonic copepods+larval stages and young copepodids): 1.4% d^{-1} during spring tide to 3.4% d^{-1} during neap tide. The daily grazing pressures on algal stock in Marennes-Oléron Bay were far lower than those observed

in open areas (Menzel & Ryther, 1961). However, these values are common in littoral areas (Nicolajsen et al., 1983; Tackx et al., 1990). The estimation of this impact is important in semi-enclosed ecosystems where herbivorous farmed species are abundant and compete for food with zooplankton. From our study, we can conclude that in Marennes-Oléron Bay during the algal spring bloom the most important part of the phytoplankton stock remains available for trophic competitors of zooplankton.

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