# Retention of ciliates and flagellates by the oyster Crassostrea gigas in French Atlantic coastal ponds: protists as a trophic link between bacterioplankton and benthic suspension-feeders

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# Retention of ciliates and flagellates by the oyster *Crassostrea giga*s in French Atlantic coastal ponds: protists as a trophic link between bacterioplankton and benthic suspension-feeders.

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## Abstract

In French Atlantic coastal ponds of Charente, oysters can grow under conditions where phytoplankton production is limited by nutrients exhaustion. Such ponds typically show a high concentration of ciliates and flagellates during the growing season (1 x $10^4$ to 3 x $10^5$ cells $l^{-1}$ in June 1997). In order to evaluate the importance of the "protozoan trophic link " for energy transfer from the " microbial food web" to large benthic suspension feeders, we offered a coastal pond community of ciliates and flagellates as potential prey to the oyster, *Crassostrea gigas*. Clearance rate, filtered particles and relative retention efficiency were evaluated. In the grazing experiment, 94 % of ciliates and 86 % of flagellates (size between 4 and 72 µm), were retained by the oyster. Whatever their size, protists were similarly retained by the oyster gills. In terms of carbon, oyster retain on average 126 µg carbon (C) $h^{-1}$ $g^{-1}$ dry weight, a value over 4 times higher than reported for phytoplankton. These results indicate that a field community of protists can contribute in coastal oyster rearing ponds to the energy requirements of the oyster *Crassostrea gigas*. We report here the first experimental evidence of a significant retention of a protist community by oysters, supporting the role of protists as a trophic link between picoplankton and benthic filter-feeding bivalves.

## Key-words

Bivalve, oyster, food source, coastal pond, microbial food web, protist, picoplankton, trophic link

# INTRODUCTION

Oysters obtain energy resources by filtering particles from sea water and their growth depends upon the nutritive value of the retained seston (Berg & Newell, 1986) and the trophic capacity of coastal waters (Héral, 1987). The natural habitats of the oyster *Crassostrea gigas* are open coastal ecosystems, rocky shores or mud flats. Charente Maritime, on the French Atlantic coast, is the most important European oyster farming area. Shellfish culture has developed in muddy bays (rearing areas of 4 800 ha) and in semi-closed coastal ponds (3 000 ha), characterized by relative confinement and low water renewal rates.

The importance of phytoplankton in the nutrition of oysters is well documented (Héral, 1987; Pastoureaud et al., 1996). However, in oyster rearing environments, such as the particularly light-limited turbid estuary of Marennes-Oléron, or in coastal ponds of Charente where nutrients are quickly exhausted, phytoplankton cannot entirely account for the energy requirements of oysters (Héral, 1987).

In the oceans, more than 50 % of the primary production is due to unicellular organisms less than 3 µm in size (Platt et al., 1983; Li et al., 1983; Glover et al., 1986), which constitutes a nutrient source of particulate and dissolved organic matter for heterotrophic organisms. Dissolved organic matter (DOM) present in coastal waters (Pomeroy and Wiebe, 1993) provides a potential for high bacterial production. Thus, in the Atlantic coastal ponds, bacterioplankton constitutes 50 % of the planktonic carbon biomass (Frikha et al., 1987). Such heterotrophic bacterioplankters, with typically high growth rates and growth efficiencies, represent a significant energy pathway by recycling DOM into particles potentially available to upper trophic levels (Pomeroy, 1974; Azam et al., 1983; Fenchel, 1988).

However, small sized bacteria and autotrophic picoplankton are not retained by gills of bivalves, particularly oysters (Shumway et al., 1985; Héral, 1987; Riisgård, 1988; Barillé et al., 1993). Flagellate and ciliate protists, which consume bacteria and phytoplankton, are abundant in coastal ecosystems (Revelante & Gilmartin, 1983; Sherr et al., 1986 a; Fenchel, 1988; Leakey et al., 1992**)** and are preyed upon by numerous organisms of zooplankton, particulary copepods (Berk et al., 1977; Jonsson & Tiselius, 1990; Gifford & Dagg, 1991; Hartmann et al., 1993). Protozoa have been suggested as a major trophic link between picoplankton and micro or macroplankton (Porter et al., 1979; Conover, 1982; Sherr et al., 1986 b; Stoecker & Capuzzo, 1990).

Likewise, protists might represent a trophic link between bacteria and filter-feeding bivalves. Some data support this assumption. Tintinnids were observed in the stomachs of oysters (Paulmier, 1972). Moreover, filter-feeding benthic molluscs retain protists, as examplified by contaminations of bivalves by toxic flagellates (Sournia et al., 1991). In a mixed cell suspension of phytoplankton and dinoflagellates, six different species of bivalves were able to selectively clear and digest dinoflagellates (Shumway et al., 1985). Recently, Bardouil et al. (1996) showed that *Crassostrea gigas* easily consumes a non toxic dinoflagellate and Kreeger and Newell (1996) clearly demonstrated in mussels the ingestion and assimilation of bacterial carbon *via* heterotrophic flagellates. Le Gall *et al.* (1997) reported experimental significant retention and ingestion of cultured bacterivorous ciliates, *Uronema* sp., by the oyster *Crassostrea gigas*. Heterotrophic protists, which are abundant in coastal ecosystems, may thus constitute an alternative or complementary food resource for benthic filter feeders allowing the indirect recuperation of DOM and picoplanktonic production, otherwise not accessible to them.

We present evidence of oyster grazing on protists: a ciliate and flagellate community from a coastal oyster rearing pond was offered to oysters in a laboratory experimental system. Clearance rate, filtered particles and relative retention efficiency were determinated by following the taxonomic composition and relative abundance of the protist community over time in presence or absence of actively filtering oysters.

## MATERIALS AND METHODS

### Oyster collection and acclimation

Oysters were collected in June 1997 from our oyster pond research facility " Marais du Plomb" (L'Houmeau, near La Rochelle, French Atlantic coast). Twenty adult *Crassostrea gigas* (1 year old, shell length 5 cm and mean dry tissue weight 1.64 $\pm$ 0.29 g) were transported to the laboratory, removed of epibionts and acclimated overnight at the ambient field temperature of 18°C, in GF/C (Whatman) filtered coastal pond water. Just before the experiment, 10 actively filtering oysters were selected and placed in 1 liter pyrex rectangular trays containing 800 ml of GF/C (Whatman) filtered coastal pond water.

**Protist community: sampling and enumeration**

The field planktonic community provided as potential food to the experimental oysters came from the coastal pond. Natural unfiltered oyster pond water was collected, using a sampling 2.5 l "Van Doorn" bottle (Wildco) and held in the laboratory at 18 °C in an opaque carboy until use. Ciliates and flagellates were fixed, stained and enumerated according to methods modified from Haas (1982), Caron (1983) and Sherr et al. (1994). For ciliate examination, 20 ml samples were stained live for 10 minutes by adding proflavin hemisulfate solution (Sigma, 0.033 % w/v, final concentration, 0.00066 %): preliminary comparative experiments showed that live staining had no deleterious effects on the ciliate community. Ciliates were then preserved by adding glutaraldehyde (Sigma electron microscopy grade, 25 % v/v in 0.2 µm filtered seawater, final concentration 1 %). The cells were enumerated in Utermöhl settling chambers (Hydro-Bios combined plate chambers), using a reverse epifluorescence microscope (Leitz DMIRB, 100 W mercury lamp and blue light excitation). Ciliate taxons were enumerated and identified under combined epifluorescence and interference contrast illumination (magnification: x 400 or x 630). Sizes of all cells (length and width) were mesured through a calibrated ocular micrometer. Mean cell volume of each ciliate taxon was calculated by equating the shape to standard geometric configurations. The cell volume was converted into carbon units, using a theoretical carbon/volume ratio of 0.17 pg Carbon (C) $\mu m^{-3}$ (Putt and Stoecker, 1989), corrected for glutaraldehyde fixative, according to Leakey et al. (1994)).

For flagellate counting, 20 ml samples were preserved with formaldehyde (paraformaldehyde powder Sigma, 8 % w/v in 0.2 µm filtered seawater, final concentration 1%); each sample was concentrated to 10 ml in a filtration tower mounted with black a 0.6 µm-pore polycarbonate membrane (Nuclepore) and a cellulosic backing filter (Whatman 1 µm) and stained by primulin (direct yellow 59 from Sigma; working solution was according to Sherr et al. (1994): 250 µg primulin in 100 ml of 0.1 M Trizma HCl at pH 4.0; 50 µg $ml^{-1}$ final concentration). The primulin method allows observation of cell outlines and permits distinguishing autotrophic from heterotrophic flagellates by repeated interchange of the filter sets (Caron, 1983): phototrophic cells (crimson under UV 365 nm excitation and red colored under green 450-490 nm excitation) and heterotrophic cells (blue under UV excitation and invisible under green excitation) were separately enumerated. Fields were viewed first for primulin fluorescence to locate flagellates, and then for chlorophyll *a* fluorescence (by changing the filter set) to confirm which of these cells were

pigmented. Length and width of 100 flagellates were mesured (observation under UV 365 nm excitation and magnification x 630) from triplicate samples. However, the presence of the black Nuclepore filter did not allow any observation of the flagellates under light microscopy and thus prevented identification of taxon or species.

### Experimental protocol for the study of protist retention

The possible influence of oyster filtration upon the natural protist community was studied during 90 minutes in an experimental chamber at 18°C by comparing the evolution of protist abundances in triplicate suspensions with or without filtering oysters. At the start of the feeding period, 6 oysters were transferred to individual 500 ml pyrex rectangular trays containing 400 ml natural unfiltered oyster pond water, gently homogeneized with a magnetic rod to prevent sedimentation. As protists are fragile organisms, only a moderate homogenization was processed in order to avoid cell damage; because of this restriction, the volume of the protist suspension could not be more than 400 ml, to maintain an homogenous concentration of living protists.

Two experimental treatments were performed each in triplicate: the natural ciliate and flagellate suspensions were (1) allowed to evolute as controls, in presence of 3 living but non filtering oysters, tightly tied up by a knoted string (controls for physical sedimentation of the suspension), or (2) delivered to 3 actively filtering oysters. It is to be noticed that, at natural food concentration used in this study, there was no visible production of pseufaeces. Dry tissue weight of each oyster was recorded at the end of the experiment and clearance rates and filtered particles were expressed per g of oyster dry tissue.

### Calculation of clearance rate, filtered particles and relative retention efficiency

In order to control the normality of oyster filtration in our laboratory experiments, the clearance rate was estimated and compared to litterature data. Defined as the theoretical water volume entirely cleared from particles (assuming 100 % retention) per unit time and per oyster dry tissue weight (l $h^{-1}g^{-1}$) (Bayne & Widdows, 1978), the clearance rate was calculated from the evolution in ciliate or flagellate cell concentration in the triplicate suspensions with filtering oysters. During the first five minutes of the experiment, individual variations in the settling of a regular oyster filtration prevented any reliable study of the protist abundance evolution in the triplicate suspensions: therefore, we selected the subsequent sampling time (15 mn) as the most appropriate "standard" time

in our clearance experiment. Assuming exponential decline of the retained cells, the clearance rate was calculated according to Coughlan (1969) during the first 15 minutes:

$$F = \frac{LnCo - LnCt}{t - to} xV$$

where F = clearance rate (l $h^{-1}$), V = volume of the suspension (l), $C_o$ = initial concentration of the suspension (cells $l^{-1}$), $C_t$ = concentration at time t (cells $l^{-1}$) and $(t-t_o)$ = time interval (h).

Taking into account that the weight specific filtration decreases with increasing body size, standardized clearance rates were calculated according to Riisgård (1988): $F/W^b$

where F = clearance rate (l $h^{-1}$), W = dry tissue weight (g) and b = 0.73 for *Crassostrea virginica* (Riisgård, 1988).

The filtered particles, which is the number of each protist taxon retained per unit time and per g of oyster dry tissue (cells $h^{-1} g^{-1}$), was calculated directly from the difference of cells present between $t_0$ and $t_{15}$ minutes.

To investigate the possibility of a differential grazing by the oyster among the various protist taxons, we compared the relative retention efficiencies for each ciliate taxon and each ciliate and flagellate order. Defined as the number of a specific cell type retained during 15 mn, related to the initial available number of the same cell type at the beginning of the experiment, each relative retention efficiency was calculated from the difference in abundances at $t_0$ and $t_{15}$ minutes, related as a percentage to the abundance at $t_o$:

$$Er\ (\%) = 100 \times [(C_0 - C_t)/C_0]$$

where Er = relative retention efficiency, $C_0$ = initial particle concentration (cells $l^{-1}$) at $t_o$

and $C_t$ = particle concentration (cells $l^{-1}$) at 15 minutes.

Initial ciliate and flagellate abundances from the triplicate experiments with filtering or closed oyster were compared using a t-Student test (data were previously tested for nomality by Kolmogorov-Smirnov test). Evolution during the 90 minutes experiment of ciliate and flagellate abundances in triplicate controls was followed by comparing the 5 time points sampled (0, 5, 15, 45 and 90 minutes) with a regression test.

# RESULTS

## Taxonomic composition and standing stocks of protists in the coastal oyster pond in June 1997

In the summer period of the experiment, the ciliate community of the coastal pond was abundant (23 700 ± 3 600 cells $l^{-1}$) and dominated by members of the subclass Choreotrichia, mainly represented by the order Choreotrichida, with *Tintinnopsis* spp**.** (10 000 to 11 200 cells $l^{-1}$) and by the order Oligotrichida, dominated by *Strombidium* spp*.* (5 700 to 8 500 cells $l^{-1}$). Other common taxa from the subclass Haptoria and order Haptorida *(Mesodinium* sp., *Askenasia* sp.) were also representative of the assemblage (3 400 to 5 700 cells $l^{-1}$). Ciliate sizes ranged from 8 µm length for a *Mesodinium* sp., to 72 µm for *Strombidium conicum* (table 1). Prevalant ciliate cell lengths were between 16 and 48 µm. **Table 1 near here**

Flagellate abundances in the coastal pond varied from 4.2 to 6.7 x $10^6$ cells $l^{-1}$ and flagellates accounted for about 99.5 % of the protists enumerated in water samples. Mean flagellate sizes ranged from 4 µm for heterotrophic to 6 µm for autotrophic flagellates.

Tintinnina biovolumes as well as cell carbon were much higher than Oligotrichida and Haptorida ones (for the most abundant taxon in each order, 19 181 $\mu m^3$ for *Tintinnopsis* sp. (48 µm-24 µm), 5 579 $\mu m^3$ for *Strombidium* sp. (32 µm-24 µm) and 2 145 $\mu m^3$ for *Mesodinium* sp. (16 µm-16 µm)). By multiplying the taxon abundances at the beginning of experiment by the individual carbon content of each ciliate taxon, we estimated the quantity of ciliate carbon available for oysters: on average, 63.5 µg C $l^{-1}$**.** In this study, the flagellate carbon was not evaluated because flagellate taxonomy and biovolumes could not be determined.

## Grazing experiments

The initial concentration in the natural suspension sampled for the grazing experiment was 25 000 $\pm$ 3 900 ciliates $l^{-1}$ and 4.5 x $10^6$ $\pm$ 1.12 x $10^6$ flagellates $l^{-1}$. Since all suspensions originated from the same coastal pond sample, initial protist abundances in the experimental trays showed no significant difference between controls and oyster treatments (t Student test, n= 6, p >> 0.05). In the 3 control suspensions, ciliate and flagellate

abundances remained relatively constant over 90 minutes (figure 1) with regression test ($r^2$ = 0.17, p >> 0.05 for ciliates and $r^2$ = 0.23, p >> 0.05 for flagellates). **Figure 1 here**

In the 3 experimental trays with filtering oysters, ciliates whose size was between 20 and 40 µm were 100% retained; the relative retention efficiency in the experimental suspension within 15 minutes was 96 % for Haptorida and Tintinnina (figure 2-a and -b)) and 91 % for Oligotrichida, (figure 2 c). Similarly, flagellates decreased by 86 % within 15 minutes in the trays with the filtering oyster (figure 2-d). At the end of the experiment (90 minutes), virtually all ciliates and 96 % of the flagellates had been retained by the bivalves. **Figure 2 here**

The relative retention efficiency for each protist taxon, related to the protist sizes present in the suspension remained constant in the studied size range (figure 3), unless a slight decrease was noticed for the smaller and larger taxons: only 84 % of the 4 µm particles and 88 % of the 72 µm particles were retained. For concentrations below the pseudofeces threshold, all protist from 4 to 72 µm were similarly retained by the oyster gills. **Fig 3 here**

**Clearance rates, filtered particles** **Table 2 near here**

Clearance rates of oysters averaged 4.0 $\pm$ 1.3 l $h^{-1}g^{-1}$ for flagellates and 7.2 $\pm$ 3.5 l $h^{-1}g^{-1}$ for Oligotrichida ciliates (table 2). The filtered particles, calculated between 0 and 15 minutes (table 3) were dependent on protist taxon. Tintinnina were more retained (27 000 $\pm$ 11 500 cells $h^{-1}g^{-1}$) than Haptorida (8 800 $\pm$ 4 400 cells $h^{-1}g^{-1}$) or Oligotrichida (19 600 $\pm$ 10 200 cells $h^{-1}g^{-1}$). By multiplying filtered particles (cells $h^{-1}g^{-1}$) by the individual carbon content of each taxon, we obtained the quantity of ciliate carbon retained per hour per gram oyster dry weight (µg C $h^{-1}g^{-1}$), which averaged 126 µg C $h^{-1}g^{-1}$ (table 3). **Table 3 near here**

## DISCUSSION

Marine planktonic protists (ciliates and flagellates) have recently been shown to be abundant in Atlantic coastal ponds: our estimations of protist abundances in our coastal pond at the time of the grazing experiment were respectively 23 700 ± 3 600 ciliate $l^{-1}$ and 4.5 x $10^6$ $\pm$ 1.12 x $10^6$ flagellates $l^{-1}$. These protist abundances fell within the

range estimated in the same pond by Robin (pers.com.), 10 000 to 30 000 cells $l^{-1}$ for ciliates and 53 x $10^4$ to 2.2 x $10^6$ flagellates $l^{-1}$.

In absence of published report on ciliate abundances in the Atlantic coastal ecosystem near the coastal pond, we compared our data to results from distant estuaries and bays. In other temperate estuaries, ciliate abundances were in the same range, from 200 to 19 000 cells $l^{-1}$ (Saint-Laurent estuary, Sime Ngando et al., 1995) and from 220 cells $l^{-1}$ to 56 000 cells $l^{-1}$ (Northern Adriatic, River Po estuary, Revelante & Gilmartin, 1983). However, in the Gulf of Maine, ciliate abundances were higher: 350 000 to 6 000 000 cells $l^{-1}$ (Montagnes et al., 1988).

In our study, the ciliate community was dominated by the order Choreotrichida with *Tintinnopsis* spp. (10 000 to 11 200 cells $l^{-1}$) and by the order Oligotrichida with *Strombidium* spp. (5 700 to 8 500 cells $l^{-1}$). Robin (pers. com.) observed up to 300 000 Tintinnina $l^{-1}$ in June 1996 in the same coastal pond of L'Houmeau. Tintinnina are also abundant in the Mediterranean Sea: 10 000 ciliate $l^{-1}$ in Villefranche-sur-mer (Rassoulzadegan & Gostan, 1976) and 8 000 cells $l^{-1}$ in the south-eastern mediterranean Alger Bay (Vitiello, 1964). On the opposite, in a Northern Mediterranean coastal lagoon (Etang de Thau), Tintinnina abundance was only 75 cells $l^{-1}$ (Lam-hoai et al., 1997), a value much lower than our. Oligotrichida abundances (5 700 to 8 500 cells $l^{-1}$) were in the range of values collected by Robin (pers. com.) during the spring of 1996 (4 300 to 11 500 cells $l^{-1}$) but lower than abundances (90 000 cells $l^{-1}$) during the summer in Mediterranean Sea (Rassoulzadegan, 1977).

Our values for flagellate abundances were close to those obtained in the Saint-Laurent estuary: 1.9 x $10^6$ to 6 x $10^6$ cells $l^{-1}$ (Lovejoy et al., 1993) or in the marine shallow-water Limfjorden in Denmark: 2 x $10^6$ cells $l^{-1}$ (Andersen & Sorensen, 1986).

The wide range of these data shows the natural variability of protist abundances in the field. Moreover, since the coastal ponds are periodically closed systems in which the plankton community undergoes rapid fluctuations, it remains difficult to establish valid criteria for comparisons with open coastal systems. Nevertheless, in terms of potential carbon resources available to the oysters, the amounts calculated for ciliates (63.5 µg C $l^{-1}$) were at the

high level for protozoan carbon levels in coastal waters (Saint-Laurent Estuary: 0.23 to 51.6 µg C $l^{-1}$, Sime Ngando et al, 1995).

When a coastal pond planktonic community was provided as potential food, clearance rates of oysters for protists (4.0 ± 1.3 l $h^{-1}g^{-1}$ for flagellates and 7.2 ± 3.5 l $h^{-1}g^{-1}$ for Oligotrichida ciliates) were in a range similar to values measured for phytoplankton by Gerdes (1983): 4.8 l $h^{-1}$ $g^{-1}$, Deslous-Paoli et al. (1987): 4.7 l $h^{-1}g^{-1}$ , Riisgård (1988): 6.8 l $h^{-1}g^{-1}$ and Soletchnik et al. (1991): 3 to 4 l $h^{-1}g^{-1}$. However, in our experimental closed system, the concentration of particles is rapidly declining during the experiment (figure 2); the standard time for our clearance experiment (15 mn), selected to avoid drawbacks related to the irregular settling of oyster filtration during the first five minutes, is tardily to allow accurate evaluation of clearance rates. Nevertheless, the possible negative effects of our suboptimal laboratory experimental conditions on the bivalve filter pump efficiency (Jorgensen, 1996) may have only resulted in the underestimation of our experimental values: field clearance rates of oysters for protists might be even higher.

The relative retention efficiency was 94 % for the ciliates and 86 % for the flagellates within 15 minutes from 400 ml suspensions. This finding supports the results of Le Gall *et al.* (1997), who demonstrated that the oyster *Crassostrea gigas* retained *Uronema* sp., a cultured ciliate isolated from the oyster pond, with a 85 % relative retention efficiency when present at a concentration close to field ciliate abundances. It also corroborates the observations by Paulmier (1972), who reported Tintinnids to be abundant in the stomachs of wild oysters from the Atlantic coast. Likewise, Kreeger & Newell (1996) estimated that 58 % and 44 % respectively of the cultured heterotrophic nanoflagellates were retained by *Geukensia demissa* and *Mytilus edulis*, compared to values of 66 % and 77 %, respectively, for the autotroph *Isochrysis galbana.* Ciliates and flagellates thus represent a potentially valuable food source and might be a significant component in the natural diet of suspension-feeding bivalves, given that their relative abundance is sufficiently high in the available seston.

To investigate the possible influence of particle size on oyster retention, we separately followed the evolution of each protist taxon abundance in the experimental suspensions. In our experiments, ciliates and flagellates in a size range from 4 to 72 µm were retained by the oyster, but the smallest heterotrophic flagellates (4 µm) and the largest ciliates (*Strombidium conicum*, 72 µm x 32 µm) displayed a slightly lower relative retention efficiency than the

ciliates, whose size was between 20 and 40 µm. Indeed, the flagellate sizes in our suspensions were at the lower end of the particle size spectrum, known to be retained by *Crassotrea gigas.* Barillé et al. (1993) showed that this oyster has a limited capacity to retain small particles: 4 µm particles (equivalent spherical diameter, ESD) were retained with 100% retention efficiency when sestonic load was low, but the limit increased to 12 µm for higher sestonic loads; for particles below these thresholds, retention efficiency quickly decreased. Similarly Deslous-Paoli et al. (1987) demonstrated that the oyster is not able to retain small particles. Bougrier et al. (1997) reported that the selection of algae by the oyster, *Crassostrea gigas* was independent of the size, volume or carbon content of each species (size between 3.65 and 9 µm ESD). They observed, nevertheless, that some algae were preferentially filtered or rejected, due to cell shape and flexibility.

Conversely, mussels are able to retain even picoplankton-size particles (Kemp et al., 1990; Kreeger & Newell, 1996): in particular, in high-quality food suspensions (expressed as percent of particles with chlorophyll fluorescence) prey retention and selection in *Mytilus edulis* is not dependent on the prey size (Newell et al., 1989). Reduction in food quality induced a drop in the ability to select living cells from silt particles, independently of size. These investigations demonstrated however, as for oysters, a selectivity based on cell shape (Newell et al., 1989). Since unlike the mussel, *Crassostrea gigas* cannot retain picoplankton-size particles at natural concentrations, the picoplankton-protozoa trophic pathway (Le Gall et al., 1997) may represent a significant energy source for the oyster (figure 4).

Ciliates are more nutritious prey than phytoplankton cells. They are relatively rich in nitrogen (C:N ratio near 4 , Putt & Stoecker, 1989; Ohman & Snyder, 1991, as compared to > 5 for phytoplankton, Heinbokel et al., 1978; Burkhardt et al., 1997), and contain more carbon per cell than phytoplankton : our estimations of cell carbon contents, which are comparable to values previously reported in litterature (3 100 pg cell$^{-1}$ for *Strombidium* sp. (43 µm - 42 µm), Stoecker & Egloff, 1987; 1 100 pg C cell$^{-1}$ for *Strombidium* sp. (43 µm - 30 µm), Jonsson & Tiselius, 1990) were much higher than phytoplankton carbon content per cell from 10 to 21 pg C cell$^{-1}$ for *Skeletonema costatum* (Strathmann, 1967; Burkhardt et al., 1997; Bougrier et al., 1997), 1.61 pg C cell$^{-1}$ for *Phaedactylum tricornatum* (Fiala-Medioni et al., 1983) and 10.3 pg C cell$^{-1}$ for *Navicula filata* (Bougrier et al., 1997). In our experiment, on average, oysters retained 126 µg ciliate C h$^{-1}$ g$^{-1}$ for a ciliate concentration of 25 000 $\pm$ 3 900 cells l$^{-}$

[1]. Fiala-Mediono et al. (1983) estimated that oyster filtering *Phaedactylum tricornatum* retained 27.5 µg C $h^{-1}$ $g^{-1}$ for a phytoplankton concentration of 1 x $10^6$ cells $l^{-1}$. Ciliates may thus contribute to the carbon requirements of *Crassostrea gigas* in the same way as do heterotrophic flagellates for the mussels *Geukensia demissa* and *Mytilus edulis* (Kreeger & Newell, 1996).

Most studies that have examined the nutritional importance of protist as a "trophic link" have focused on pelagic consumers, such as zooplankton (Berk et al., 1977; Porter et al.,1979; Sherr et al., 1986 b, Jonsson and Tiselius, 1990; Gifford & Dagg, 1991; Hartmann et al., 1993). Hovewer, only few studies have done the same for benthic consumers (Kreeger & Newell, 1996 ; Le Gall et al, 1997). Trophic coupling between pelagic protists and benthic suspension-feeders is poorly documented in aquatic food models (e.g. see Legendre & Le Fèvre, 1995).

In open water oyster beds, primary producers, in particular phytoplankton and resuspended microphytobenthos can be considered important food sources for bivalves suspension feeders (Blanchard et al., 1997**)**. Otherwise in coastal ponds, the resuspension of microphytobenthos is low, due a lack of turbulence: even if it may attain up to 25 times higher levels than phytoplankton (Zanette, 1980; Robert, 1983), the microphytobenthos is unlikely to be an important direct resource. However, the DOM released by these autotrophs contributes to the important bacterial biomass that develops in coastal ponds: bacterioplankton constitutes 50 % of the planktonic C biomass in oyster ponds of the Charente (Frikha et al., 1987). The bacteria, in turn, will be primary food for heterotrophic/ mixotrophic ciliates and flagellates which develop biomasses comparable to phytoplankton: in our coastal pond, the protist biomass was similar to the phytoplankton biomass of coastal oyster ponds from Bourgneuf Bay (Robert, 1983). Since bacterivorous ciliates have a gross growth efficiency of about 40 % (Johnson et al., 1982; Ohman & Snyder, 1991), relatively large amounts of bacterial C must be recovered by oysters *via* the protist trophic link.

In coastal pond habitats, bivalve molluscs are abundant and may be the dominant consumers of seston. Oysters are most likely opportunist omnivores, balancing their C (and N) requirements by utilizing a wide variety of living and dead material (Riera & Richard, 1996) including protists. In addition to phytoplankton which cannot entirely account for the energy requirements of *Crassostrea gigas* (Héral, 1987), oysters can derive nutrition from microzooplankton, in particular from protists. Our experiment presents the first data about oyster nutrition on a field community of protists. These results clearly show that suspension-feeding bivalves feed on ciliates and

flagellates. Such a trophic relationship could be of primary importance for the transfer of C, and probably N, from the microbial food web to higher trophic levels in the benthos.

*Acknowledgments.* This work was supported by the CNRS (INSU-SDV), the IFREMER (DRV-RA), the LBBM (La Rochelle University) and by a doctoral grant from the "Conseil Général de Charente -Maritime" (Région Poitou-Charentes). We also thank Mr Knutsen for reviewing the English.

## LITERATURE CITED

Andersen P, Sorensen HM (1986) Population dynamics and trophic coupling in pelagic microorganisms in eutrophic coastal waters. Mar Ecol Prog Ser 33:99-109

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257-263

Bardouil M, Bohec M, Bougrier S, Lassus P, Truquet P (1996) Feeding responses of *Crassostrea gigas* (Thunberg) to inclusion of different proportions of toxic dinoflagellates in their diet. Oceanol Acta 19:177-182

Barillé L, Prou J, Héral M, Bougrier S (1993) No influence of food quality, but ration-dependent retention efficiencies in the japanese oyster *Crassostrea gigas*. J Exp Mar Biol Ecol 171:91-106

Bayne BL, Widdows J (1978) The physiological ecology of two populations of *Mytilus edulis* L. Oecologia 37: 137-162

Berk SG, Brownlee DC, Heinle DR, Kling HJ, Colwell RR (1977) Ciliates as a food source for marine planktonic copepods. Microb Ecol 4:27-40

Berg JA, Newell RIE (1986) Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. Estuar Coast Shelf Sci 23:375-386

Blanchard G, Sauriau PG, Cariou-Le Gall V, Gouleau D, Garet MJ, Olivier F (1997) Kinetics of tidal resuspension of microbiota: testing the effects of sediment cohesiveness and bioturbation using flume experiments. Mar Ecol Prog Ser 151:17-25

Bougrier S, Hawkins AJS, Héral M (1997) Preingestive selection of different microalgal mixtures in *Crassostrea gigas* and *Mytilus edulis*, analysed by flow cytometry. Aquaculture 150:123-134

Burkhardt S, Riebesell U (1997) $CO_2$ avaibility affects elemental composition (C:N:P) of the marine diatom *Skeletonema costatum*. Mar Ecol Prog Ser 155: 67-76

Caron DA (1983) Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. Appl Environ Microbiol 46:491-498

Conover RJ (1982) Interrelations between microzooplankton and other plankton organisms. Ann Inst Océanogr 58:31-46

Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. Mar Biol 2:356-358

Deslous-Paoli JM, Héral M, Goulletquer P, Boromthanarat W, Razet D, Garnier J, Prou J, Barillé L, (1987) Evolution saisonnière de la filtration de bivalves intertidaux dans des conditions naturelles. Oceanis 13:575-579

Fenchel T (1988) Marine plankton food chains. Ann Rev Ecol Syst 19:19-38

Fiala-Medioni A, Copello M, Colomines JC (1983). Relations trophiques entre huître et milieu; influence de la concentration et de la taille des particules. Bases biologiques de l'aquaculture, IFREMER, Montpellier, Actes de colloques n°1, p 63-74

Frikha MG, Linley EAS and Delmas D (1987) Evolution annuelle et saisonnière de la microbiomasse d'une claire à huîtres : importance des populations bactérioplanctoniques. Oceanis 13:433-447

Gerdes D (1983) The pacific oyster *Crassostrea gigas*. Part I. Feeding behaviour of larvae and adults. Aquaculture 31:195-219

Gifford DJ, Dagg MJ (1991) The microzooplankton-mesozooplankton link: consumption of planktonic protozoa by the calanoid copepods *Acartia clausi* Dana and *Neocalanus plumchrus* Murukawa. Mar Microb Food Webs 5:161-177

Glover HE, Campbell L, Prézelin BB (1986) Contribution of *Synechococcus* spp. to size-fractioned primary productivity in three water masses in the Northwest Atlantic Ocean. Mar Biol 91:193-203

Hartmann HJ, Taleb H, Aleya L and lair N (1993) Predation on ciliates by the suspension-feeding calanoid copepod *Acanthodiaptomus denticornis*. Can J Fish aquat Sci 50:1382-1393

Haas LW (1982) Improved epifluorescence microscopy for observing planktonic microorganisms. Ann Inst Océanogr 58:261-266

Heinbokel JF (1978) Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. Mar Biol 47:177-189

Héral M (1987) Shellfish Culture Development and Management - Aquaculture International Seminar, La Rochelle 4-9 mars 1985. Evaluation of the carrying capacity of molluscan shellfish ecosystems. IFREMER, Brest

Jonhson PW, Huai-Shu X, Sieburth J McN (1982) The utilization of chroococoid cyanobacteria by marine zooplankters but not by calanoid copepods. Ann Inst Océanogr 58:297-308

Jonsson Pr, Tiselius P (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. Mar Ecol Prog Ser 60:35-44

J□rgensen CB (1996) Bivalve filter feeding revisited. Mar Ecol Prog Ser 142: 287-302

Kemp PF, Newell SY, Krambeck C (1990) Effects of filter-feeding by the ribbed mussel *Geukensia demissa* on the water-columm microbiota of a *Spartina alterniflora* salt-marsh. Mar Ecol Prog Ser 59:119-131

Kreeger DA, Newell RIE (1996) Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa* and *Mytilus edulis* (Bivalvia, Mollusca). Aquat Microb Ecol 11:205-214

Lam-Hoai T, Rougier C, Lasserre G (1997) Tintinnids and rotifers in a northern Mediterranean coastal lagoon. Structural diversity and function through biomass estimations. Mar Ecol Prog Ser 152:13-25

Leakey RJG, Burkill PH, Sleigh MA (1992) Planktonic ciliates in Southampton water: abundance, biomass, production, and role of pelagic carbon flow. Mar Biol 114:67-83

Leakey RJG, Burkill PH, Sleigh MA (1994) A comparison of fixatives for the estimation of abundance and biovolume of marine planktonic ciliate populations. J Plankton Res 16:375-389

Le Gall S, Bel Hassen M, Le Gall P (1997) Ingestion of a bacterivorous ciliate by the oyster *Crassostrea gigas*: protozoa as a trophic link between picoplankton and benthic suspension-feeders. Mar Ecol Prog Ser 152:301-306

Legendre L, Le Fèvre J (1995) Microbial food webs and the export of biogenic carbon in oceans. Aquat Microb Ecol 9:69-77

Li KW, Subba Rao DV, Harrison GW, Smith CJ, Cullen JJ, Irwin B, Platt T (1983) Autotrophic picoplankton in the tropical ocean. Science, 219: 292-295.

Lovejoy C, Vincent WF, Frenette JJ, Dodson JJ (1993) Microbial gradients in a turbid estuary: application of a new method for protozoan community analysis. Limnol Oceanogr 38:1295-1303

Montagnes DJS, Lynn DH, Roff JC, Taylor WD (1988) The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. Mar Biol 99:21-30

Newell CR, Shumway SE, Cucci TL, Selvin R (1989) The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availibility for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. J Shellfish Res 8, 1: 187-196

Ohman MD, Snyder RA (1991) Growth kinetics of the omnivorous oligotrich ciliate *Strombidium* sp. Limnol Oceanogr 36:922-935

Pastoureaud A, Héral M, Prou J, Razet D, Russu P (1996) Particle selection in the oyster *Crassostrea gigas* (Thunbert) studied by pigment HPLC analysis under natural food conditions. Oceanol Acta 19:79-87

Paulmier G (1972) La nutrition des huîtres en relation avec les sources trophiques. Rev Trav Inst Pêches Marit 36:456-506

Platt T , Subba-Rao DV , Irwin B (1983) Photosynthesis of picoplankton in the oligotrophic ocean. Nature 301

Pomeroy LR (1974) The ocean's food web, a changing paradigm. Bioscience 24:499-504

Pomeroy LR, Wiebe WJ (1993) Energy sources for microbial food webs. Mar Microb Food Webs 7:101-118

Porter KG, Pace ML, Battey JF (1979) Ciliate protozoans as links in freshwater planktonic food chains. Nature 277:563-565

Putt M, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnol Oceanogr 34:1097-1103

Rassoulzadegan F, Gostan J (1976) Répartition des ciliés pélagiques dans les eaux de Villefranche-sur-mer. Remarques sur la dispersion du microzooplancton en mer et à l'intérieur des échantillons dénombrés par la méthode d'Utermöhl. Ann Inst Océanogr 52:175-188

Rassoulzadegan F (1977) Evolution annuelle des ciliés pélagiques en Méditerrannée nord-occidentale. Ciliés oligotriches "non tintinnides" (Oligotrichina). Ann Inst Océanogr 53:125-134

Revelante N, Gilmartin M (1983**)** Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. Oceanol Acta 6:407-415

Riera P, Richard P (1996) Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the Estuarine Bay of Marennes-Oléron. Estuar Coast Shelf Sci 42:347-360

Riisg□rd HU 1988 Efficiency of particle retention and filtration rate in 6 species of North east American bivalves. Mar Ecol Prog Ser 45:217-223

Robert JM (1983) Fertilité des eaux des claires ostréicoles et verdissement : utilisation de l'azote par les diatomées dominantes. Thèse Doctorat ès Sciences Nantes, Nantes

Sherr EB, Sherr BF, Fallon R, Newell SY (1986 a) Small aloricate ciliate as a major component of the marine heterotrophic nanoplankton. Limnol Oceanogr 31 (1):177-183

Sherr EB, Sherr BF, Paffenhöfer GA (1986 b) Phagotrophic protozoa as food for metazoans: a "missing" trophic link in marine pelagic food webs? Mar Microb Food Webs 1:61-80

Sherr EB, Caron DA, Sherr BF (1994) Staining of heterotrophic protists for visualisation *via* epifluorescence microscopy. In: Kemp PF, Sherr BF, Sherr EB, Cole JJ (eds) Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, Ann Arbor, London, Tokyo, p 213-227

Shumway SE, Cucci TL, Newell RC, Yentsch CM (1985) Particle selection, ingestion, and absorption in filter-feeding bivalves. J Exp Mar Biol Ecol 91:77-92

Sime-Ngando T, Gosselin M, Roy S, Chanut JP (1995) Significance of planktonic ciliated protozoa in the Lower St. Lawrence Estuary: comparison with bacterial, phytoplankton, and particulate organic carbon. Aquat Microb Ecol 9:243-258

Soletchnik P, Prou J, Héral M, Barille L, Razet D, Guezennec L (1991) Influence de la charge particulaire sur la filtration d'une population d'huître *Crassostrea gigas* dans le bassin estuarien de Marennes-Oléron (France) : analyse de deux cycles de marée. Conseil International pour l'Exploitation de la Mer

Sournia A, Belin C, Berland B, Erard-Le Denn , Gentien P, Grzebyk D, Marcaillou-Le Baut C, Lassus P, Partensky F (1991) Le Phytoplancton nuisible des Côtes de France. De la biologie à la prévention. IFREMER-CNRS, Brest

Stoecker DK, Capuzzo JMD (1990) Predation on protozoa: its importance to zooplankton. J Plankton Res 12:981-908

Stoecker DK, Egloff DA (1987) Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J Exp Mar Biol Ecol 110:53-68

Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol Oceanogr 12:411-418

Vitiello P (1964) Contribution à l'étude des Tintinnides de la baie d'Alger. Pelagos 2: 5-18

Zanette Y (1980) Intervention de quelques facteurs dans l'évolution de la biomasse des claires de Marennes-Oléron. Cons Inst Exp Mer, C. M., L, 45; 11p.

| Order | Suborder | Family | Taxon | Species | Length (µm) | Width (µm) | Biovolume (µm$^3$) | Carbon per cell (pg C cell$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Choreotrichida | Tintinnina | | | | | | | |
| | | Codonellidae | | | | | | |
| | | | *Tintinnopsis* | *sp.* | 35 | 24 | 13994 | 2379 |
| | | | *Tintinnopsis* | *sp.* | 40 | 24 | 15984 | 2717 |
| | | | ***Tintinnopsis*** | ***sp.*** | **48** | **24** | **19181** | **3261** |
| | | | *Tintinnopsis* | *sp.* | 48 | 40 | 53281 | 9058 |
| | | | *Tintinnopsis* | *sp.** | 51 | 40 | 56632 | 9627 |
| | | | *Tintinnopsis* | *sp.* | 56 | 24 | 22378 | 3804 |
| | | Codonellopsidae | | | | | | |
| | | | *Stenosemella* | *sp.** | 24 | 22 | 7603 | 1293 |
| Oligotrichida | | | | | | | | |
| | | Halteriidae | | | | | | |
| | | | *Halteria* | *sp.* | 27 | 19 | 3024 | 514 |
| | | Strombidiidae | | | | | | |
| | | | *Strombidium* | *sp. ** | 24 | 19 | 2617 | 445 |
| | | | *Strombidium* | *sp.* | 25 | 22,5 | 4307 | 732 |
| | | | ***Strombidium*** | ***sp.*** | **32** | **24** | **5579** | **948** |
| | | | *Strombidium* | *sp.* | 35 | 25,6 | 6863 | 1167 |
| | | | *Strombidium* | *sp.* | 40 | 28,5 | 9569 | 1627 |
| | | | *Strombidium* | *conicum* | 72 | 32 | 20642 | 3509 |
| Haptorida | | | | | | | | |
| | | Didiniidae | | | | | | |
| | | | *Didinium* | *sp.** | 64 | 54 | 97716 | 16612 |
| | | Mesodiniidae | | | | | | |
| | | | non identified | | 16 | 16 | 2145 | 365 |
| | | | non identified | | 27 | 14 | 2771 | 471 |
| | | | *Mesodinium* | *sp.** | 8 | 8 | 268 | 45 |
| | | | ***Mesodinium*** | ***sp.*** | **16** | **16** | **2145** | **365** |
| | | | *Mesodinium* | *pulex* | 14 | 10 | 733 | 125 |
| | | | *Askenasia* | *sp.* | 24 | 16 | 3217 | 547 |
| **Autotrophic flagellate** | | | | | 6,2 | 4,2 | | |
| **Heterotrophic flagellate** | | | | | 4,1 | 3,5 | | |

Table 1: Taxonomic composition, sizes, biovolumes and carbon content per cell of the protist community in the coastal pond in June 1997. Taxa printed in bold type were abundant and represented in all samples. Taxa identified by an * were rare and/or not present in all samples. When species unidentified, taxa were typified by their size.

| Taxon (length-width in µm) | Cell abundances (cells $l^{-1}$) at To in experimental suspension with an actively filtering oyster | | Standardized clearance rate ($l\ h^{-1}g^{-1}$) | |
|---|---|---|---|---|
| | **Mean** | **SD** | **Mean** | **SD** |
| **Haptorida** | | | | |
| ***Mesodinium sp.* (16-16)** | 1178 | 237 | 3.6 | 0.7 |
| ***Mesodiniidae* (16-16)** | 1748 | 776 | 7.9 | 4.3 |
| ***Mesodinium pulex* (14-10)** | 2736 | 3178 | 4.1 | 4.5 |
| ***Askenasia* (24-16)** | 76 | 132 | 2.5 | 4.4 |
| **Haptorida average** | **5738** | **4192** | **5.5** | **2.3** |
| **Oligotrichida** | | | | |
| ***Strombidium sp.* (25-22,5)** | 1026 | 1777 | 3.7 | 6.5 |
| ***Strombidium sp.* (32-24)** | 3648 | 3288 | 4.9 | 6.4 |
| ***Strombidium sp.* (35-25,6)** | 2318 | 4015 | 4.1 | 7.1 |
| ***Strombidium sp.* (40-28,5)** | 114 | 197 | 2.7 | 4.7 |
| ***Strombidium conicum* (72-32)** | 1064 | 628 | 4.9 | 3.5 |
| ***Halteria sp. (27-19)*** | 76 | 132 | 0.0 | 0.0 |
| **Oligotrichida average** | **8284** | **2028** | **7.2** | **3.5** |
| **Tintinnina** | | | | |
| ***Tintinnopsis sp.* (35-24)** | 152 | 174 | 4.9 | 4.3 |
| ***Tintinnopsis sp.* (40-24)** | 1102 | 1425 | 8.7 | 2.2 |
| ***Tintinnopsis sp.* (48-24)** | 9082 | 3933 | 6.5 | 5.8 |
| ***Tintinnopsis sp.* (48-40)** | 760 | 1316 | 3.6 | 6.2 |
| ***Tintinnopsis sp.* (56-24)** | 114 | 114 | 4.7 | 4.1 |
| **Tintinnina average** | **11210** | **2146** | **7.8** | **1.5** |
| **Flagellates** | | | | |
| **Autotrophic flagellate** | 1.38E+06 | 1.07E+06 | 4.9 | 3.0 |
| **Heterotrophic flagellate** | 3.55E+06 | 5.00E+04 | 3.1 | 1.8 |
| **Flagellate average** | **4.93E+06** | **2.47E+06** | **4.0** | **1.3** |

Table 2: Cell abundances in experimental suspensions (cells $l^{-1}$ at To) and standardized clearance rates by *Crassostrea gigas* ($l\ h^{-1}g^{-1}$) for the different ciliate and flagellate taxa (mean ± SD, n=3). When species unidentified, taxa were typified by their size by their size (length and width in µm).

| Taxon (length-width in µm) | Filtered particles (cells $h^{-1}g^{-1}$) Mean | SD | Carbon per cell (pg C $cell^{-1}$) | Filtered particles (ng C $h^{-1}g^{-1}$) Mean | SD |
|---|---|---|---|---|---|
| **Haptorida** | | | | | |
| ***Mesodinium sp.* (16-16)** | 2707 | 823 | 365 | 988 | 301 |
| ***Mesodiniidae* (16-16)** | 4441 | 2933 | 365 | 1621 | 1070 |
| ***Mesodinium pulex* (14-10)** | 1488 | 1394 | 125 | 186 | 174 |
| ***Askenasia* (24-16)** | 227 | 393 | 547 | 124 | 215 |
| **Haptorida sum** | **8863** | **4390** | | **2919** | **1583** |
| **Oligotrichida** | | | | | |
| ***Strombidium sp.* (25-22,5)** | 3063 | 5305 | 732 | 2242 | 3883 |
| ***Strombidium sp.* (32-24)** | 7811 | 7739 | 948 | 7405 | 7337 |
| ***Strombidium sp.* (35-25,6)** | 6919 | 11985 | 1167 | 8075 | 13986 |
| ***Strombidium sp.* (40-28,5)** | 276 | 479 | 1627 | 450 | 779 |
| ***Strombidium conicum* (72-32)** | 2154 | 1126 | 3509 | 7560 | 3953 |
| ***Halteria sp.* (27-19)** | 158 | 274 | 514 | 81 | 141 |
| **Oligotrichida sum** | **19643** | **10285** | | **25812** | **8643** |
| **Tintinnina** | | | | | |
| ***Tintinnopsis sp.* (35-24)** | 432 | 528 | 2379 | 1029 | 1256 |
| ***Tintinnopsis sp.* (40-24)** | 2382 | 2899 | 2717 | 6472 | 7876 |
| ***Tintinnopsis sp.* (48-24)** | 22770 | 14798 | 3261 | 74254 | 48257 |
| ***Tintinnopsis sp.* (48-40)** | 1583 | 2742 | 9058 | 14342 | 24841 |
| ***Tintinnopsis sp.* (56-24)** | 318 | 342 | 3804 | 1210 | 1303 |
| **Tintinnina sum** | **27487** | **11584** | | **97307** | **32081** |
| **Mean sum for all ciliates** | **55993** | | | **126038** | |

Table 3: Retention of various ciliate taxa by *Crassostrea gigas*, expressed as filtered particles per unit time and unit oyster dry weight (cell $h^{-1}g^{-1}$ or ng C $h^{-1}g^{-1}$, mean ± SD, n = 3). When species unidentified, taxa were typified by their size (length and width in µm).

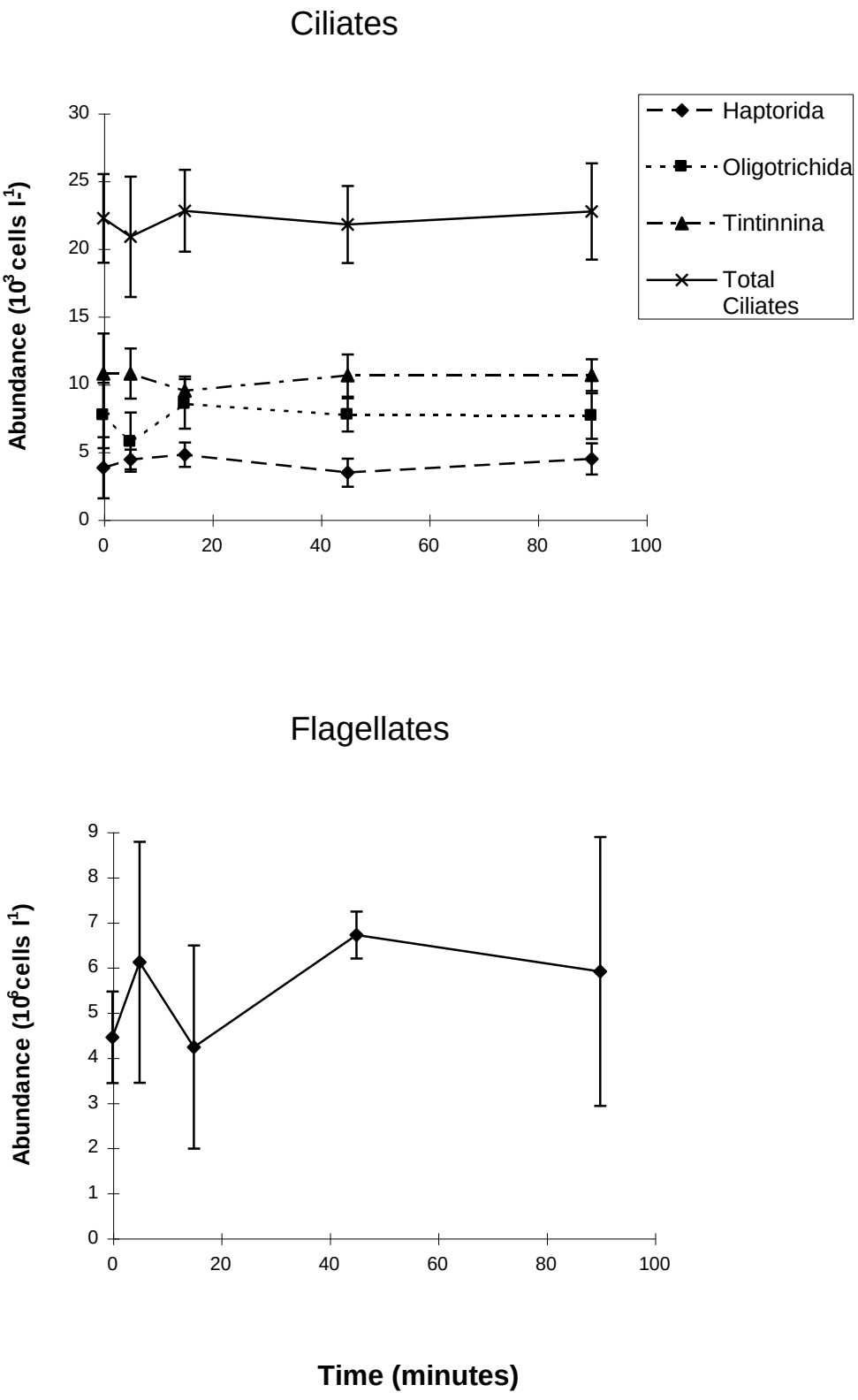


Figure 1: Evolution of ciliate and flagellate abundances in control suspensions. Abundance data (mean $\pm$ SD, n = 3) were collected from 3 separate experiments, performed with a closed non-filtering oyster in 400 ml suspension of coastal pond water.

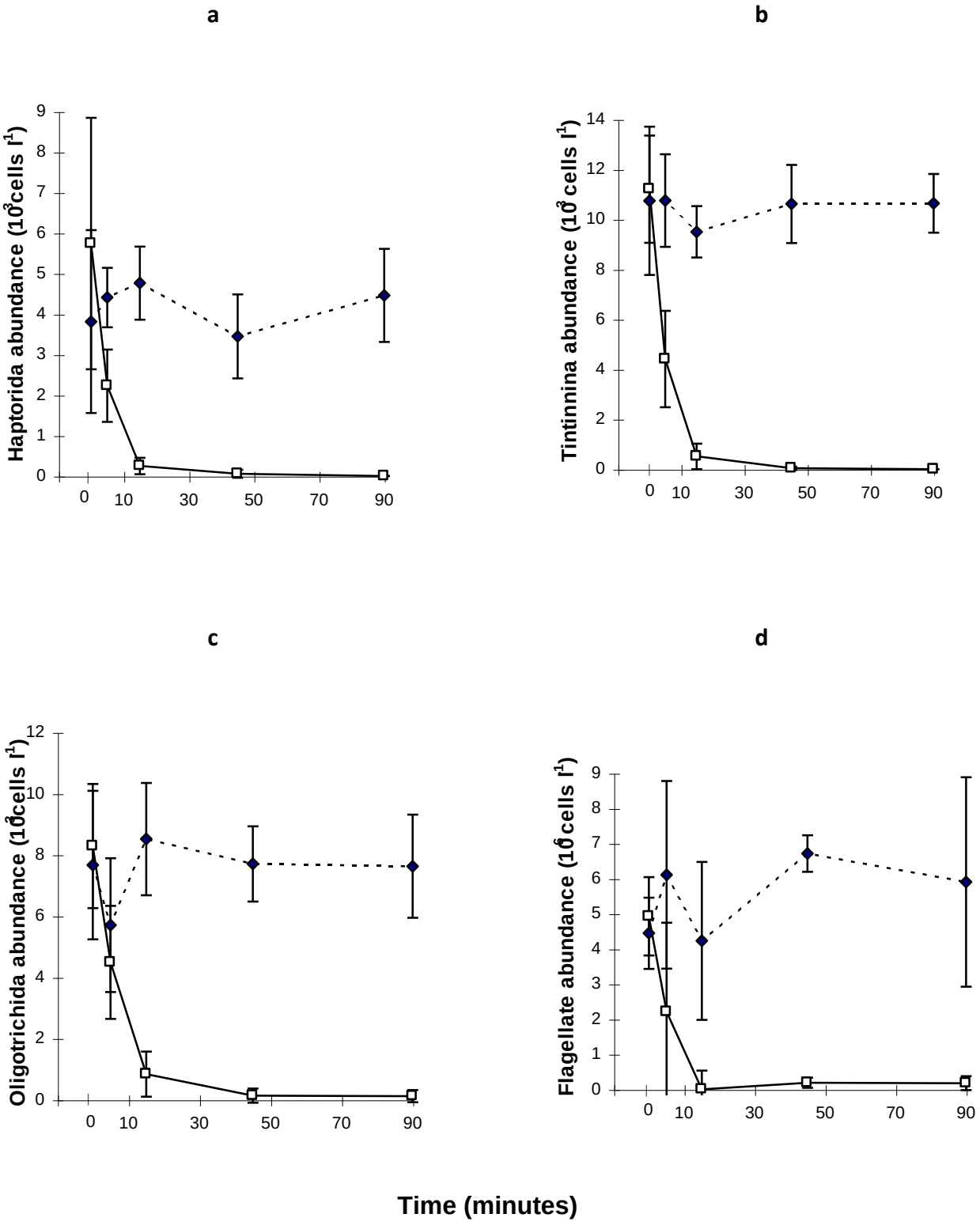


Figure 2: Retention of various protist taxons by the oyster *Crassostrea gigas* (Haptorida (a), Tintinnina (b) and Oligotrichida (c) and flagellates (d). Protist abundance data (mean ± SD, n = 3) were collected from 6 separate experiments performed in 400 ml marine pond water suspensions with a closed non-filtering oyster (◆ and dashed lines) or with a filtering oyster (□ and solid lines).

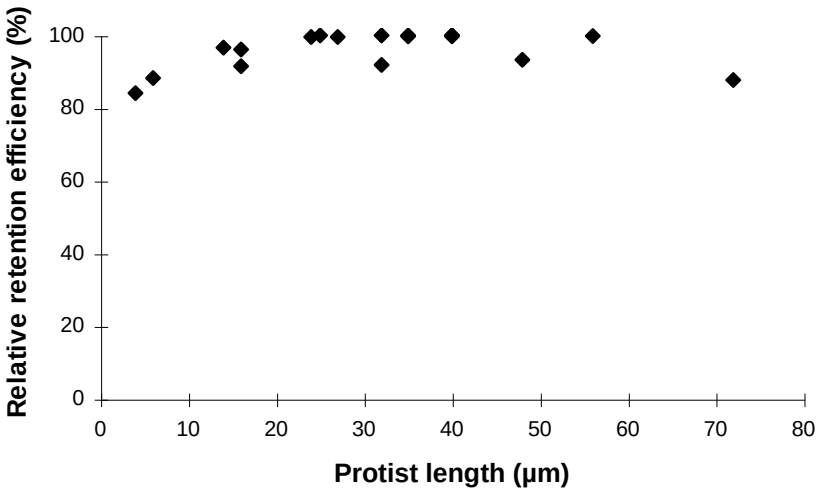


Figure 3: Relative retention efficiencies of protists related to their size class.

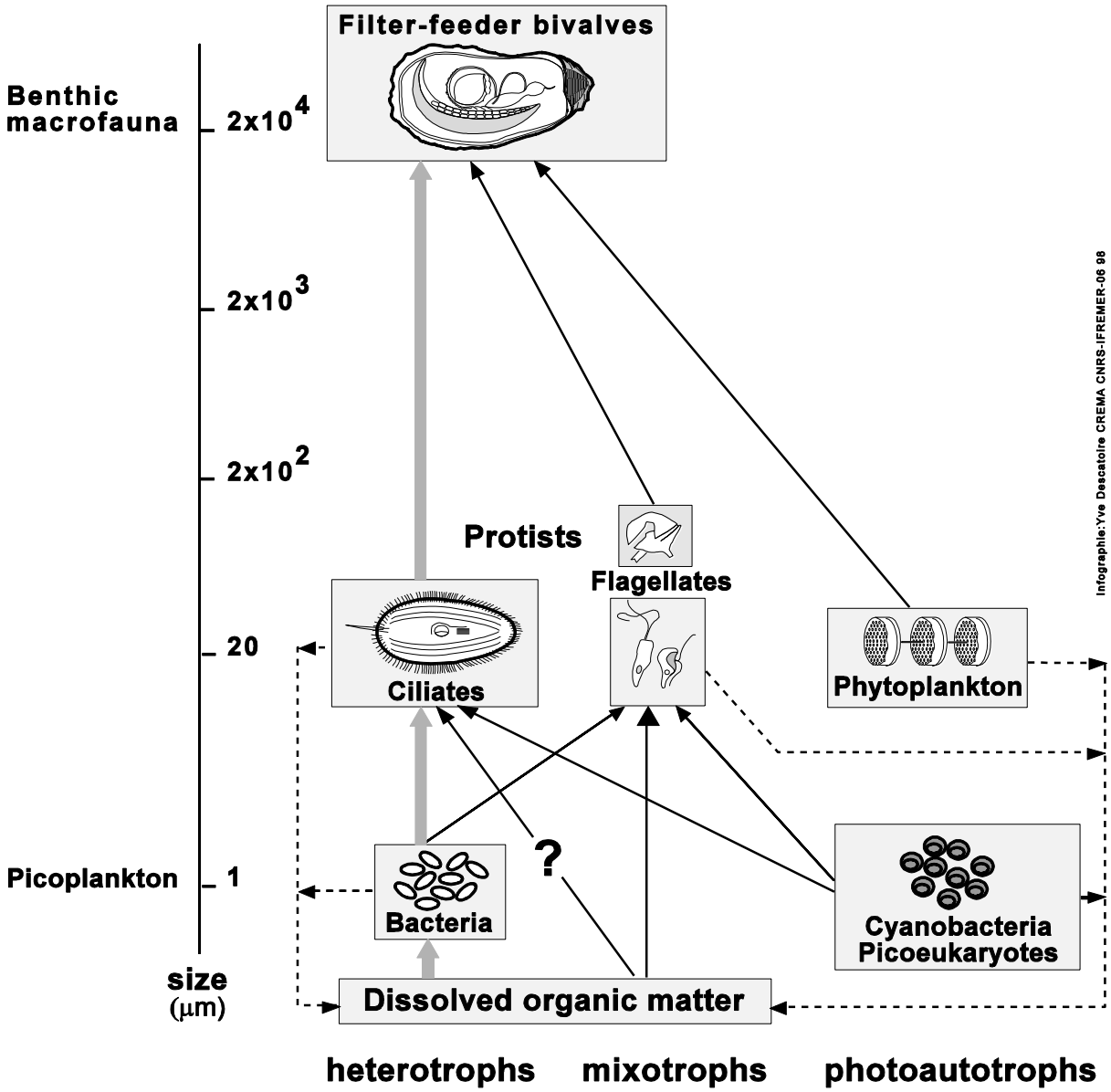


Figure 4: Hypothetical microbial food web in an oyster growing area

(modified from Le Gall et al., 1997)