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Seasonal Variations in Planktonic Community Structure and Production in an Atlantic Coastal Pond: The Importance of Nanoflagellates

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Abstract:

The structure and summertime production of planktonic communities and the role of non-diatom planktonic cells were studied in coastal ponds, which are areas traditionally used for fattening and greening table-size oysters. The abundance and biomass of nano-microplanktonic protists were determined at weekly intervals between February 1998 and February 1999 in a coastal pond without oysters in French Atlantic coast near La Rochelle. The production of these microbiota were determined in summer period. The structure of plankton communities revealed that (1) microphytoplanktonic cells were mostly diatoms and dinoflagellates, (2) microzooplanktonic cells were mainly ciliates and (3) nanoplanktonic cells were represented by pigmented (80- 90 % of the nanoplankton biomass) and colourless nanoflagellates. Diatoms were dominated by Naviculiineae. Dinoflagellates were dominated by Peridiniales. Oligotrichida were predominant in the ciliate community. Protist biomass levels were 9 times higher from April to August (summer period: 1033 µg C L^{-1}) than from September to March (winter period: 114 µg C L^{-1}). Whatever the season, nanoflagellates were dominant in the water column (respectively 66 % and 53 % of the entire protist biomass in the summer and winter periods). Nanoflagellates represented the highest production of nano-microplanktonic communities (76 % of carbon protist production) in the coastal pond in summer as well as showing the shortest generation time (7.1 h). Dinoflagellates came after nanoflagellates in production (19.5 % of carbon protist production). Diatoms represented only a supplementary carbon resource available for higher trophic levels, whereas until now they were considered as the principal food of oysters in coastal ponds. Ciliates were a small source of carbon, but their growth rate was high. We suggest, firstly, that nanoflagellates represented the primary resource available in the pond and could constitute an important food resource for higher trophic levels, such as oysters, farmed in this type of pond. The system appeared to be more autotrophic than heterotrophic overall. Since inorganic nutrients are quickly exhausted in a semi-closed pond, pigmented flagellates dominated the carbon biomass, production and biomass of bacteria was high, so the microbial food web appeared to be active in this pond, and mixotrophy seemed to be an important trophic mode there.

Keywords: Coastal pond, nanoflagellates, microbial structure and production, food source.

Introduction

Oyster farming is an important activity in Charente-Maritime, on the French Atlantic coast in Europe. Studies on coastal ponds, traditionally used for fattening and greening table-sized oysters [28], began in 1980. Microphytoplanktonic and microphytobenthic communities have often been studied in coastal ponds [7, 46, 47, 60, 61] and bacterioplankton studied occasionally [8, 9]. In semi-closed systems such as ponds where nutrients are quickly exhausted, the development of microphytoplankton is limited [47]. And although the microphytobenthic biomass can reach up to 25 times the higher levels of phytoplankton biomass [47, 61] in the water column, it is unlikely that the microphytobenthos is a significant direct source because of its low level of re-suspension, due to the lack of turbulence in rather than an intertidal zone [4]. Microalgae, usually considered as oysters' main food source, cannot entirely account for their energy requirements in Atlantic coastal ponds [24].

In recent years, interest in the ecological role of marine planktonic protists has increased, particularly for marine nanoplankton and microzooplankton in the microbial food web. Numerous studies have been made on the trophic link of microzooplankton and nanoplankton since they are preyed upon by many sorts of zooplankton, particularly copepods [3, 19, 22, 25, 57], bivalve larvae [27], and suspension-feeding bivalves, such as oysters, *Crassostrea gigas* [11, 33]. Microzooplankton is considered to be an important grazer of nanoplankton [13] and bacterial production [49, 50]. Heterotrophic and mixotrophic nanoplankton are important grazers of bacteria [53].

In the Atlantic coastal ponds, 17 % to 50 % of the planktonic carbon biomass is made up of bacterioplankton [9, 17]. Such heterotrophic bacterioplankters, with typically high growth rates and efficiencies, represent a significant energy pathway by recycling DOM into particles potentially available to upper trophic levels, like nano-microzooplankton [1, 41]. In addition, bacterioplankton are not held by oysters which retain particles between 5 and 100 µm [2, 24, 44, 55]. Thus, in Atlantic coastal ponds, nano-microzooplankton may represent a trophic link between bacteria and the higher trophic levels in the benthos, especially oysters [11].

The aim of this study was to determine the structure and production of planktonic communities and to estimate the significance of microphytoplankton, compared to nano-microzooplankton, as a potential food source for oysters. Our experimental design was to monitor physical-hydrobiological parameters, abundance and biomass of phytoplanktonic and zooplanktonic communities in a coastal pond without oysters between February 1998 and February 1999 (12 cycles) on a weekly basis. Protist production was estimated in summer by incubation experiments as described by Landry and Hassett [29] and Ferrier-Pagès and Rassoulzadegan [15].

Materials and Methods

Study site

This study was performed in an experimental coastal pond without oysters called "Marais du Plomb" (L'Houmeau, near La Rochelle, French Atlantic coast). It was dug 15 years ago in clay sediment and the flat bottom is made up of thin layers of silt resulting from sedimentation of marine particles brought by turbid coastal waters, and destabilisation of the banks surrounding it. The pond was small (≈ 200 m²) and shallow (≈ 1 m).

Planktonic protist abundance and biomass were monitored over one year (12 sequestration cycles between February 1998 and February 1999), by weekly water samples. The first samples were taken two days after the pond's water was replaced to decrease the turbidity levels. Coastal water was channelled into the pond at high spring tides. Sea water

was held in the pond for 3 to 4 weeks, resulting in progressive modifications in the ecological conditions of these semi-closed systems. At the end of the sequestration period, the pond was emptied at ebb tide and filled again with new water during the following high tide.

Physical parameters

Hydrological data were recorded by the Aanderaa data logger using sensors (thermometer and conductivity meter). The hydrological sensors were cleaned every 30 min. The data were transferred every month via a portable computer to a magnetic disk in ASCII format.

Experimental procedure

Preliminary tests were performed to define an accurate sampling strategy for the pond's water column in order to estimate average values of microbiota abundance over its entire surface: the pond was divided into 12 squares (3 m wide) and 1 sub-surface water sample was taken from each square at each sampling date. These 12 samples were collected with a 2.5 L "Van Doorn" bottle (Wildco) and 500 ml from each sample was mixed in a single, opaque carboy and quickly taken to the laboratory. The final 6 L sample was assumed to represent a mean spatial estimate of water column parameters within the pond and sampling date.

To estimate the production of planktonic protists in summer, pond water was collected in June 1999 using the sampling method described above.

Taxonomy and enumeration of protist communities

Taxonomic determination of protists present in the pond was done in accordance with systematic literature [26, 34, 37, 39, 43, 59].

For microphytoplanktonic cells (diatoms and dinoflagellates), a 20 mL triplicate aliquot from the 6 L pond water samples was fixed with formaldehyde (final concentration 1 %) and stained with alkaline lugol. Microphytoplanktonic cells were counted in Utermöhl settling chambers (Hydro-Bios combined plate chambers) under an inverted microscope. The cell sizes (length and width) were measured on at least 100 cells through a calibrated ocular micrometer. From cell size measurements, the mean cell volume of each 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 0.14 pg Carbon (C) μm^{-3} [42].

For nanoplanktonic and microzooplanktonic cells: 40 mL and 100 mL triplicate aliquots of the 6 L sample of pond water were fixed, stained and enumerated according to methods described by Haas [20], Caron [6] and Sherr et al. [54] as modified by Dupuy et al. [11]. From replicate cell size measurements of all protists, the mean cell volume of each group was calculated as above for at least 100 cells. The cell volume was converted into carbon units, using a theoretical carbon/volume ratio of 0.14 pg Carbon (C) μm^{-3} for nanoplankton (nanoflagellates) and 0.17 pg C μm^{-3} for microzooplankton (ciliates), ([42] corrected for glutaraldehyde fixative, according to Leakey et al. [31]).

Measurement of growth rates and productions of planktonic protists

Production rates were estimated for the summer period from the growth rates and biomass measured for each group.

To estimate diatom, dinoflagellate and ciliate growth rate in June 1999, organisms were fractionated by gravity filtration and reverse flow through nylon screens according to [15] and [16]. To remove different size classes of predators, < 145 µm filtering removed copepods in water containing bacteria, nanoflagellates, diatoms, ciliates and dinoflagellates, < 45 µm filtering removed large ciliates and diatoms in water containing bacteria, nanoflagellates, diatoms, ciliates and dinoflagellates. Non-fractionated seawater samples (entire population) were also incubated. Each size fraction was then transferred into 3

polycarbonate bottles of 1 L in volume, closed at one end by a dialysis membrane (Spectra/Por, 2, 12 000 to 14 000 Daltons). The bottles were incubated *in situ* in the sub-surface water for 24 h. The abundance of each protist group was determined at the beginning and end of incubation.

The nanoflagellate growth rate was estimated using the dilution method [29] modified by [30]. One part of the water sample was filtered through a 1 µm (Nuclepore) membrane. This filtered water, containing only bacteria, was then added to the unfiltered seawater: dilutions from 1 to 20 %. Two controls were taken: one with filtered seawater and the other one with unfiltered water. The dilution and controls were transferred into 3 one liter polycarbonate bottles, closed as above. Nanoflagellate abundance was determined at the beginning and end of incubation.

Results

Physical variables

Temperatures showed the expected seasonal pattern with lowest values (2 °C) in November 98 and highest values in August 98 (25 °C) (Fig. 1A). The annual mean was 15.2 °C.

Salinity of the coastal pond waters varied with the season. The maximum occurred at the beginning of September 98 (38.2) and the minimum in April 98 with 25.4 (Fig. 1B). The annual mean was 31.

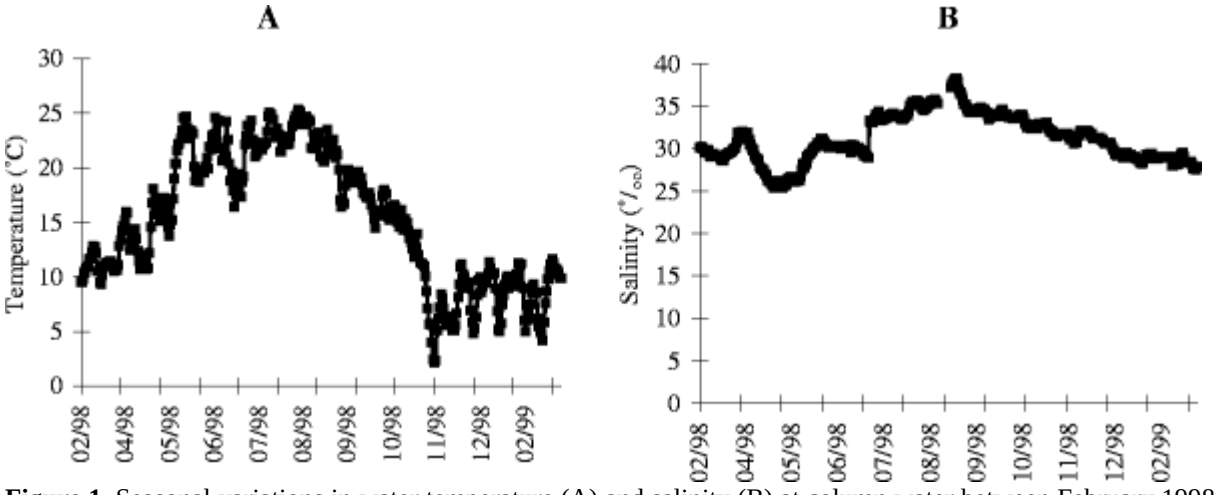

Figure 1. Seasonal variations in water temperature (A) and salinity (B) at column water between February 1998 and February 1999.

Diversity and standing stocks of protists

The annual cycle was divided into 2 periods, a winter period (from September to March) and a summer period (from April to August).

Diatoms

A total of 22 diatom taxa belonging to 2 orders of diatoms (centric and pennate diatoms, Table 1) was recorded in the Atlantic coastal pond during the sampling period, ranging in size from 11 to 125 µm in length. Diatoms were put into 5 suborders (Table 1), all of which were identified to genus and a further 2 to species level.

Table 1. Taxonomic composition, sizes, biovolumes of diatoms in the Atlantic coastal pond between February 1998 and February 1999. Classification according to Sournia [59].

Order	Suborder	Family	Genus	Species	Cell length (µm)	Cell volume (x 10^3µm^3)
Centrales						
	Coscinodiscineae	Coscinodiscaceae				
			Coscinodiscus	sp.	50	15.7
		Thalassiosiraceae				
			Thalassiosira	sp.	24	4.6
			Skeletonema	*costatum*	10	0.5
		Melosiraceae				
			Melosira	sp.	25	8.2
			Podosira	sp.	50	65.4
	Rhizosoleniineae	Rhizosoleniaceae				
			Rhizosolenia	sp.	92.5	9.2
		Leptocylindraceae				
			Leptocylindrus	sp.	30	1.2
	Biddulphiineae	Biddulphiaceae				
			Biddulphia	sp.	30	3
			Cerataulina	*pelagica*	60	117.8
		Eupodiscaceae				
			Odontella	sp.	15	1.2
		Chaetoceraceae				
			Chaetoceros	sp.	11	1.7
		Lithodesmiaceae				
			Ditylum	sp.	50	8.8
			Lithodesmium	sp.	45	18
Pennales						
	Fragilariineae	Fragilariaceae				
			Asterionella	sp.	40	3.1
			Thalassionema	sp.	15	0.4
			Licmophora	sp.		
	Naviculiineae	Naviculaceae				
			Diploneis	sp.	55	17.5
			Gyrosigma/Pleurosigma	sp.	125	19.5
			Navicula	sp.	52	6.9
		Cymbellaceae				
			Amphora	sp.	95	318.2
		Nitzschiaceae				
			Cylindrotheca	sp.	27	0.1
			Nitzschia	sp.	97	8.1

The maximum number of taxa found during the one-year study was 10 in July (data not shown). The suborder of Naviculiineae (especially *Cylindrotheca* sp.) was mainly dominant throughout the follow-up in terms of abundance (63 % of diatom abundance) and biomass (65 % of diatom biomass) (Figs. 2A and 2B). Exceptionally, blooms of Coscinodiscineae (especially *Skeletonema costatum*) appeared in February, October and December 98 and in January 99. The suborder of Biddulphiineae (especially *Cerataulina* sp.) was seen in summer and at the beginning of autumn: in that period, they represented on average 78 % of the population's abundance and 86 % of the population's biomass of diatoms.

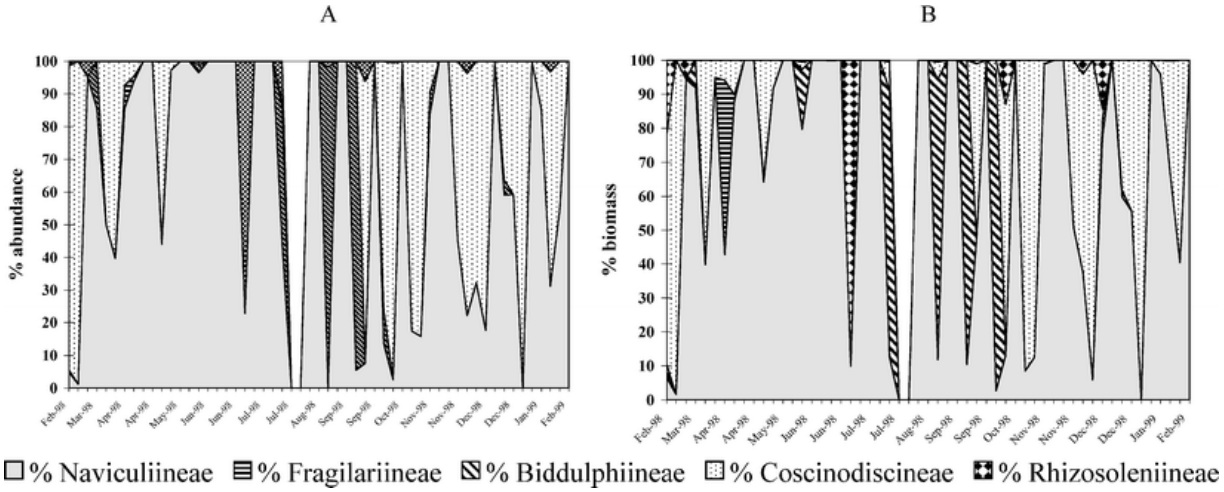

Figure 2. Diatom abundance and biomass in Atlantic coastal pond waters between February 98 and February 99: (A) mean percentage abundance of diatom groups (B) mean percentage biomass of diatom groups. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the water and the last point of cycle is the end of the sequestration period.

Diatoms exhibited some degree of seasonal variability in population abundance and biomass: abundance was higher in spring (1100 x 10^4 cells L^{-1} in May) even though the biomass was 300 µg C L^{-1} at the same period (Figs. 2C and 2D). The individual biovolumes of diatoms fluctuated greatly (Table 1). As a consequence of these fluctuations in biovolumes, and thus in biomass, taxa did not tend to reflect variations in abundance: on 29th September, diatom abundance was low, 6.6 x 10^4 cells L^{-1} and biomass was maximal, 514 µg C L^{-1} due to a moderate bloom of *Amphora* sp. (Naviculiineae) with high biovolume (318.2 x 10^3 µm^3). In winter, abundance and biomass were lower (1600 cells L^{-1} and 0.2 µg C L^{-1}, in January 99). The mean abundance and biomass of diatoms were 1.2 x 10^6 cells L^{-1} and 39 µg C L^{-1} respectively in the summer period (from April to August), and 6.2 x 10^4 cells L^{-1} and 27 µg C L^{-1} respectively in the winter period (from September to March).

Dinoflagellates

A total of 14 dinoflagellate taxa was recorded in this Atlantic coastal pond's waters during the sampling period (Table 2) ranging in size from 23 µm to 70 µm length, 12 of which were identified to genus and a further 2 to species level (Table 2).

Table 2: Taxonomic composition, sizes, biovolumes of dinoflagellates in the Atlantic coastal pond between January 1998 and February 1999. Classification according to Sournia [59].

Order	Family	Genus	Species	Cell length (µm)	Cell volume (x 10^3 µm^3)
Peridiniales		unidentified		24	15.1
		unidentified		30	9.5
	Peridiniaceae				
		Scripsiella	spp.	29	8.4
		Protoperidinium	spp.	27	5.3
		Minuscula	sp.	15	1.7
	Gonyaulacaceae				
		Amphidoma	sp.	23	1.8
Gymnodiniales	*Gymnodiniaceae*				
		Cochlodinium	spp.	46	12.6
		Amphidinium	spp.	19	1.3
		Gyrodinium	spp.	40	7.6
		Gymnodinium	spp.	25	1
		Gymnodinium	*splendens*	70	55.6
Prorocentrales	*Prorocentraceae*				
		Prorocentrum	spp.	35	11.2
Dinophysiales	*Dinophysiaceae*				
		Dinophysis	spp.	51	17
Ebriales	*Chrysophyceae*				
		Ebria	*tripartita*	32	5.2

The maximum number of taxa found together was 9 in July, August, September and October (data not shown). The minimum was 1 taxon in March, April and May. The Peridiniales (especially *Scripsiella* sp.) dominated the dinoflagellate community throughout the year in terms of abundance (69 % of abundance) and biomass (66 % of biomass): (Figs. 3A and 3B). Prorocentales appeared during spring (in April and May, 100 % of abundance and biomass) and in July (98 % of abundance and biomass). The order of Gymnodiniales was hardly present, except at the end of July and in August, where *Gymnodinium splendens* represented on average 43 % of dinoflagellate abundance and 91 % of dinoflagellate biomass (Figs. 3A and 3B).

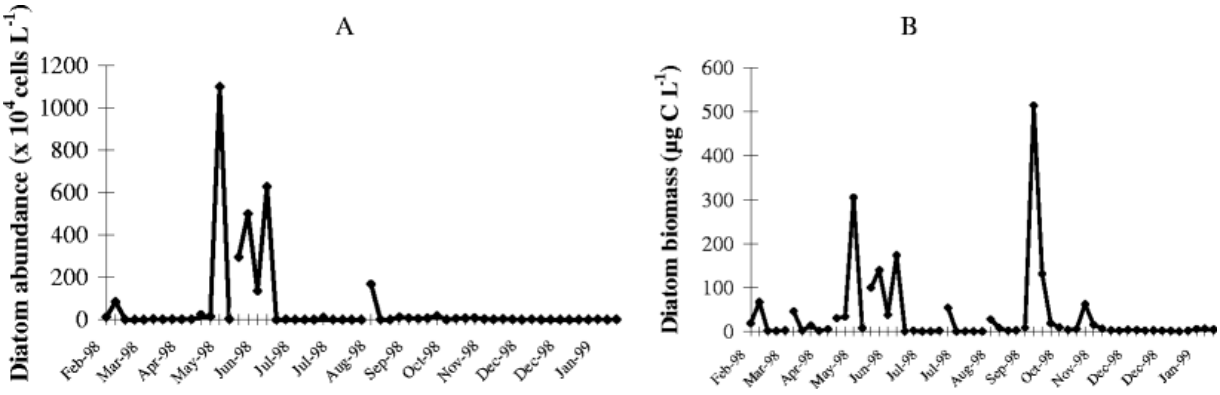

Figure 3 Diatom abundance and biomass in Atlantic coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of diatoms. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the water and the last point of cycle is the end of the sequestration period.

Dinoflagellates exhibited real seasonal variability in population abundance and biomass. They were widely present during the summer (Figs. 3C and 3D) and remained scarce during the rest of the year. Maximum abundance and biomass were found in July (2.6 x 10^6 cells L^{-1} and 2054 µg C L^{-1}). The mean abundance and biomass of dinoflagellates were 2.4 x 10^5 cells L^{-1} and 286 µg C L^{-1} respectively in summer and 3.8 x 10^4 cells L^{-1} and 11 µg C L^{-1} respectively in the winter period.

Euglenophyceae

The euglenophyceae were represented exclusively by the order of Eutrepsiales (Table 2). They often appeared during the one-year study (data not shown) but brought little carbon (maximal value of 5.6 µg C L^{-1} in February and September and on average 0.5 µg C L^{-1}).

Nanoflagellates

The nanoflagellate enumeration method used, with a black Nuclepore filter, prevented their taxonomic determination. Only the size and the cell outlines of nanoflagellates were estimated. Moreover, the method allowed us to distinguish pigmented nanoflagellates from colourless ones (Caron 1983).

A total of 27 different nanoflagellate forms was recorded in the pond waters during the sampling period, ranging in size from 3 to 19 µm in length. The maximum number of different nanoflagellates found together was 23 in July and 24 in September (data not shown). The minimum was 5 different nanoflagellate forms in March.

During the one-year study, pigmented nanoflagellates dominated the population (80 to 90 % of population abundance and biomass, Figs. 4A and 4B) except in April where colourless nanoflagellates constituted 60 % of their abundance and 50 % of their biomass in June, July and January 99.

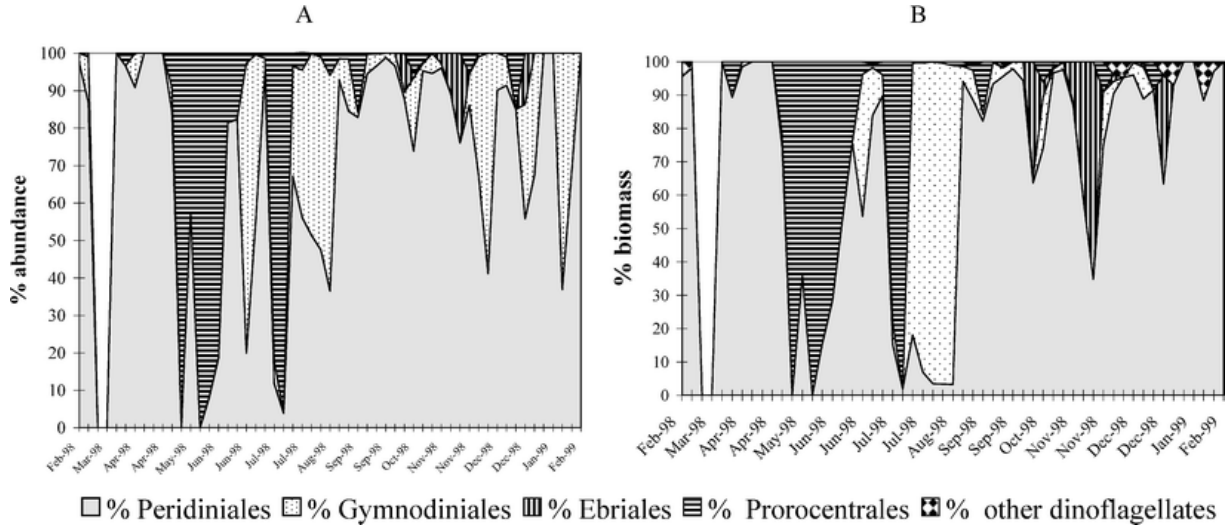

Figure 4 Dinoflagellate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of dinoflagellate groups (B) mean perecentage biomass of dinoflagellate groups.

Nanoflagellate abundance and biomass varied according to the season (Figs. 4C and 4D): the high values were found during spring (2500 x 10^5 cells l^{-1} and 1700 µg C l^{-1}) and summer (3.2 x 10^8 cells L^{-1} and 1650 µg C L^{-1}). During the winter, nanoflagellate abundance and biomass were generally low, except in December, where a moderate bloom of nanoflagellates was seen (1.5 x 10^7 cells L^{-1} and 700 µg C L^{-1}). The mean abundance and biomass of nanoflagellates were 7.7 x10^7 cells L^{-1} and 681 µg C L^{-1} respectively in the summer period and 6.9 x10^6 cells L^{-1} and 61 µg C L^{-1} respectively in winter.

Ciliates

A total of 21 ciliate taxa was recorded in the Atlantic coastal pond waters during the one-year study, 16 of which were identified to genus and a further 3 to species level (Table 3).

Table 3: Taxonomic composition, sizes, biovolumes of the ciliate community in the Atlantic coastal pond between January 1998 and February 1999. Classification according to Lee et al. [34].

Sub-class	Order	Suborder	Family	Genus	Species	length (µm)	Cell volume (x 10^3µm^3)
Choreotrichia							
	Choreotrichida	Tintinnina	Codonellidae				
				Tintinnopsis	sp. 1	53	38
				Tintinnopsis	sp. 2	60	18.3
				Tintinnopsis	sp. 3	97	136.4
				unidentified		46	207.4
			Codonellopsidae				
				Stenosemella	sp.	38	15.9
			Tintinnidae				
				Eutintinnus	sp.	110	54
		Strobilidiina	Strobilidiidae				
				Lohmaniella	sp.	37	33.4
				Strobilidium	sp.	40	14.6
	Oligotrichida		Strombidiidae				
				Strombidium	sp.	46	24.9
				Strombidium	*conicum*	68	47.9
			Halteriidae				
				Halteria	sp.	34	8.6
	Haptorida		Mesodiniidae				
				Askenasia	sp.	49	96
				Mesodinium	sp.	26	5.7
				Mesodinium	*pulex*	18	1.3
				Mesodinium	*rubrum*	38	9.3
			Didinnidae				
				Didinium	sp.	49	37
Hymenostomatia							
	Scuticociliatida	unidentified				44	27.9
		Phylasterina	Uronematidae				
				Uronema	sp.	34	3.7
Hypotrichia							
	unidentified					44	16
	Stichotrichia	Sporadotrichina	Oxytrichidae				
				unidentified		81	17.3
Karyorelictea							
	Protostomatida	unidentified				15	0.7
Unidentified aloricate ciliates						93	129.9

The length of ciliates ranged from 15 to 110 µm. The greatest number of taxa was 14 in February (data not shown). The minimum was 2 taxa in July and August. Ciliates were members of Choreotrichia with the suborder of Tintinnina (loricate cells) and aloricate forms such as Oligotrichida (Table 3). Aloricate ciliates dominated the population abundance and biomass during most months, comprising up to 100 % of the abundance and biomass (Figs. 5A and 5B). In aloricate ciliates, Oligotrichids (especially *Strombidium* sp.) were the commonest taxonomic group (Figs. 5A and 5B). Tintinnids (loricate ciliates) were the second most present group, except in June, July and all autumn, when they represented 70 % of population abundance and 74 % of population biomass (Figs. 5A and 5B). Haptorida were present during the one-year study with peaks in April (95 % of population abundance and biomass), June and September (≈ 100 % of population abundance and biomass in September). The order of Strobilidiina remained scarce, except in December, when they represented 50% of population biomass. The sub-classes of Hypotrichs, Scuticociliatida and Oxytrichia, more characteristic of benthic environments, were only present on a few occasions.

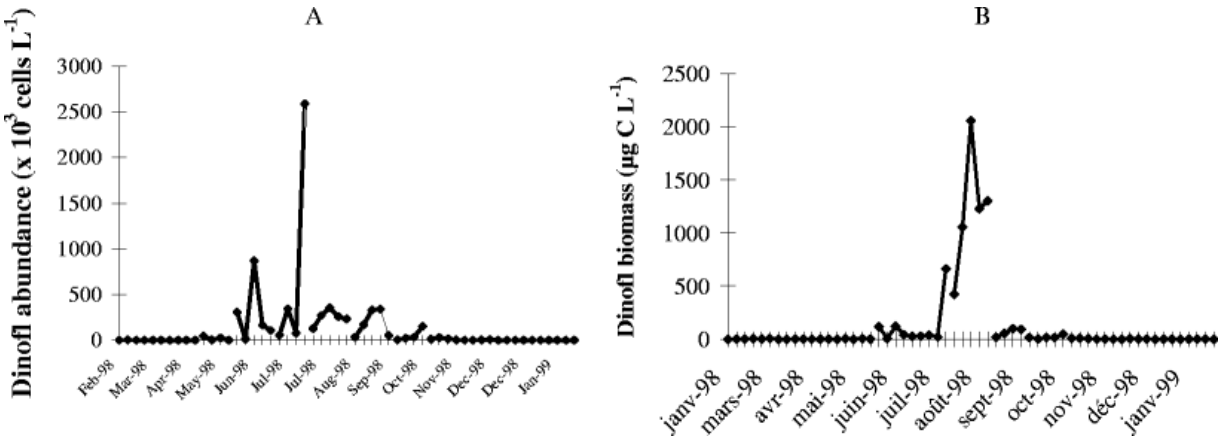

Figure 5 Dinoflagellate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of dinoflagellates. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the seawater and the last point cycle is the end of the sequestrastion period. Dinofl = dinoflagellates

Ciliates exhibited some degree of seasonal variability in population abundance and biomass. The biomass of ciliates tended to reflect variations in abundance. Ciliates were present during the one-year study (Figs. 5C and 5D) with peaks in spring, summer (in July, 1.45 x 10^5 cells L^{-1} and 142 µg C L^{-1}) and autumn. During the winter, ciliates were not often present or were absent in February, July and November 98 and January 99. The mean abundance and biomass of ciliates were 32 x 10^3 cells L^{-1} and 27 µg C L^{-1} respectively in summer period and 13 x 10^3 cells L^{-1} and 13 µg C L^{-1} respectively in winter period.

The available biomass of major protists present in coastal pond waters was assessed (Fig. 6). In the summer period (from April to August), nanoflagellates were predominant in the water column (681 µg C L^{-1}). The estimated biomass of other microbes was lower, with 286 µg C L^{-1} for dinoflagellates, 39 µg C L^{-1} for diatoms and 27 µg C l^{-1} for ciliates. In the winter period (from September to March), nanoflagellates were always most predominant in the water column (61 µg C L^{-1}). The estimated biomass of other microbes was lower, with 27 µg C L^{-1} for diatoms, 13 µg C L^{-1} for ciliates and 11 µg C L^{-1} for dinoflagellates. The biomass of protist carbon available in the pond waters was 9 times lower in winter than in the summer period.

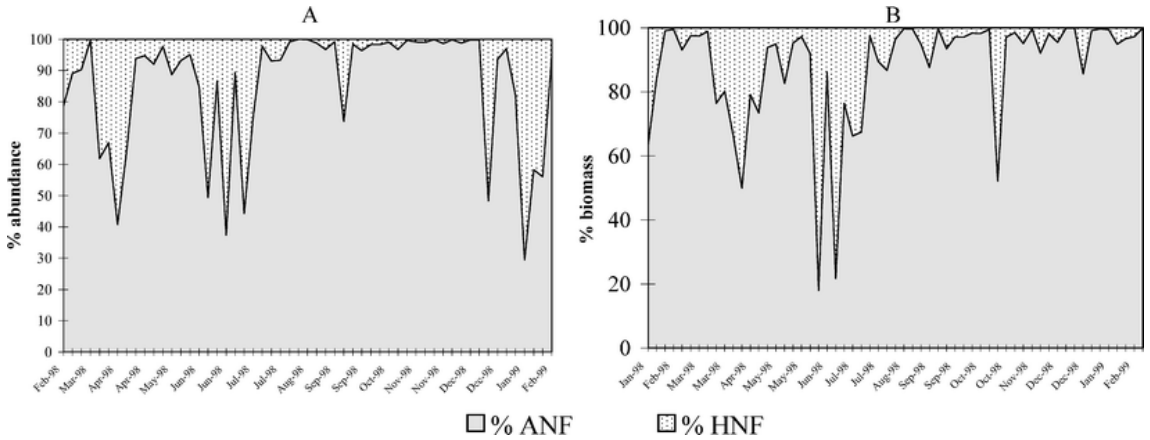

Figure 6 Nanoflagellates abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean percentage abundance of nanoflagellate groups (B) mean percentage biomass of nanoflagellate groups. ANF: Autotrophic nanoflagellates, HNF: Heterotrophic nanoflagellates.

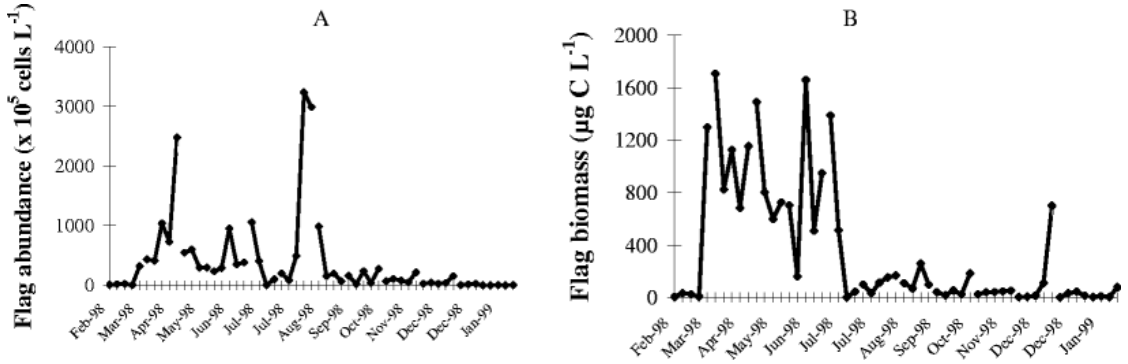

Figure 7 Nanoflagellates abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of nanoflagellates. Breaks in curves corresponds to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the seawater and the last point of cycle is the end of the sequestration period. Flag=nanoflagellates.

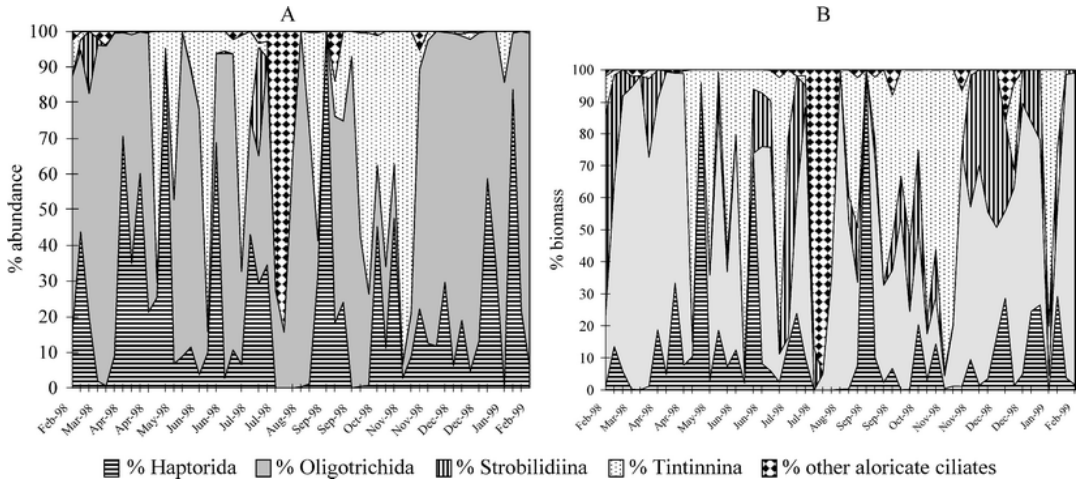

Figure 8 Ciliate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean percentage abundance of ciliate groups, (B) mean percentage biomass of ciliate groups. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the seawater and the last point of cycle is the end of the sequestration period.

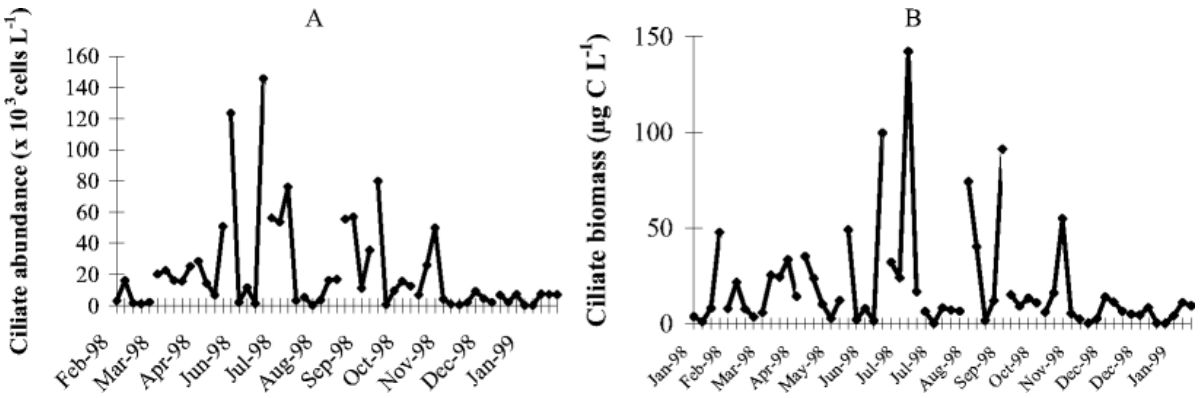

Figure 9 Ciliate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of ciliates. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the seawater and the last point of cycle is the end of the sequestration period.

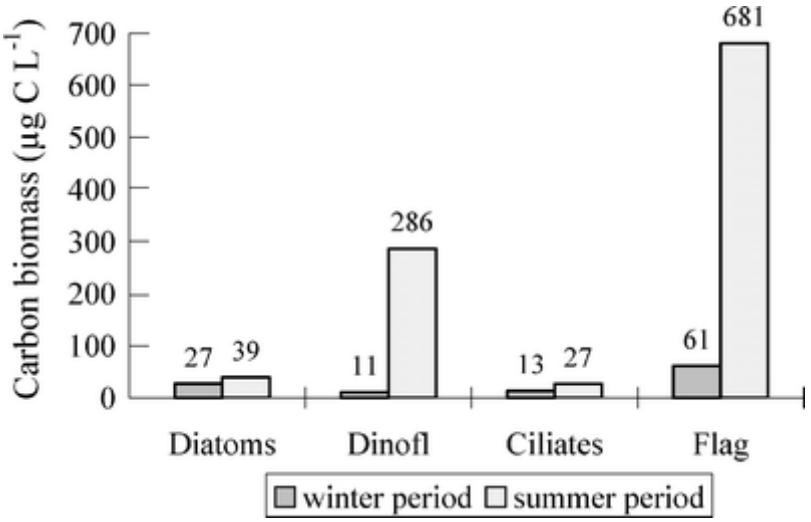

Figure 10 Mean biomass of major taxonomic groups in the column water pond between February 98 and February 99 at two different periods, in winter (from September to MArch) and in summer (from April to August). Donofl=dinoflagellates, Flag=nanoflagellates.

Estimation of growth rates and productions of various planktonic protist communities for the summer period

Growth rates varied from one taxonomic group to another (Table 4). Nanoflagellates exhibited the highest growth rate: 0.098 h^{-1} compared to 0.026 h^{-1} for ciliates, 0.07 h^{-1} for diatoms and 0.06 h^{-1} for dinoflagellates. The protist communities multiplied between 1 to 7 times per day in the coastal pond waters.

Table 4: Growth rates (h^{-1}) and generation time (h) obtained for different groups during incubation experiments in the summer period. Estimated productions (µg C L^{-1} day^{-1}) were calculated to multiply the biomass (µg C L^{-1}) of each group by this respective growth rate (h^{-1}).

	Growth rate (h^{-1})	Generation time (h)	Biomass (µg C L^{-1})	Production (µg C L^{-1} day^{-1})
Diatoms	0.07	9.9	39	66
Dinoflagellates	0.06	11.6	286	412
Ciliates	0.026	26.7	27	17
Flagellates	0.098	7.1	681	1602
Sum			1033	2096

In term of production, nanoflagellates showed the highest production in summer period with 1602 µg C L^{-1} day^{-1} (Table 4) against 412 µg C L^{-1} day^{-1} for dinoflagellates, 66 µg C L^{-1} day^{-1} for diatoms and 17 µg C L^{-1} day^{-1} for ciliates.

Discussion

Qualitative protist composition of the water column in the Atlantic coastal pond

The microphytoplanktonic cells present were mostly diatoms and dinoflagellates and the microzooplanktonic cells were ciliates. Nanoplanktonic cells were represented by pigmented and colourless nanoflagellates.

For diatoms, the suborder of Naviculiineae was mainly dominant (Fig. 2) with blooms of *Skeletonema costatum* (Coscinodoscineae) in spring and a bloom of *Amphora* sp. in autumn. Peridiniales dominated the dinoflagellates (Fig. 3). In the available published data on coastal ponds, similar qualitative composition and population dynamics of microphytoplankton were seen in the Bay of Bourgneuf [45, 47]. Nanoflagellates were dominated by pigmented cells (80 to 90 % of the total nanoflagellate biomass) (Fig. 4). Crottereau [8] found a high fraction of chlorophyll a, which were cells less than 20 µm in size, during annual monitoring (1996-1997) in the same coastal pond near la Rochelle. Ciliates belonging to the Choreotrichs sub-class were usually the predominant planktonic ciliates in most environments [5, 10, 48, 51, 52]. Oligotrichids were the commonest taxonomic group found during monitoring (Fig. 5).

Quantitative protist composition of the water column in coastal pond

Our estimations of planktonic diatom abundance throughout the year (Fig. 2) were within the abundance range found by Robert [47] (Table 5). Our biomass measurements were lower than in Chesapeake Bay [36].

Our dinoflagellate abundance was higher than in Buzzards Bay (Massachusetts) [40] (Table 5). A study made in the Antioche pertuis area (near La Rochelle on the French Atlantic coast) showed that the dinoflagellate biomass was 0.3 µg C L^{-1} in January 98, a value similar to that in the pond (0.59 µg C L^{-1}). In February 98, the dinoflagellate biomass in the Antioche pertuis was higher than in the pond (12.4 µg C L^{-1} in the pertuis *versus* 1.6 µg C L^{-1} in the pond). This phenomenon could be due to the lower temperature in the pond in February 98 (6.9°C, Fig. 1), which did not allow the development of dinoflagellates, compared to a moderate temperature in open water.

In this study, the abundance and biomass of nanoflagellates were higher than in the same coastal pond in April and July 96 (Robin, comm.pers.) (Table 5). In comparison with distant estuaries and bays, nanoflagellates were always higher than in the Saint-Lawrence estuary [35] and than at the surface in the summer period of Aarhus Bay (Danemark), [23].

Marine planktonic ciliates were recently shown to be abundant in Atlantic ponds: the compartment represented 63.5 µg C L^{-1} during June 1997 [11]. In the same Atlantic pond, from April to July 1996, Robin (com. pers.) found similar values, from 50 to 60 µg C L^{-1}. The ciliate biomass was higher than that observed for other coastal and estuarine localities: in Cobb Seamount [56], in the Saint-Lawrence estuary, [57] and in the Northern Arabian Sea [32] (Table 5).

Table 5: Comparison of abundance (cells L^{-1}) and biomass (µg C L^{-1}) with other Bays and Estuaries

Groups			
Diatoms	Abundance (Cells L^{-1})	Site	Authors
	1,E+05	Bourgneuf bay	Robert (1983)
	6,3E+05	Atlantic coastal pond	Our study
	Biomass (µg C L^{-1})	Site	Authors
	200-500	Chesapeake bay	Malone & Ducklow (1990)
	33	Atlantic coastal pond	Our study
Dinoflagellates	Abundance (Cells L^{-1})	Site	Authors
	9,7E+03	Buzzards bay	Pierce & Turner (1994)
	1,4E+05	Atlantic coastal pond	Our study
Nanoflagellates	Abundance (Cells L^{-1})	Site	Authors
	3,8E+06	Saint-Lawrence estuary	Lovejoy et al (1993)
	4,2E+07	Atlantic coastal pond	Our study
	Biomass (µg C L^{-1})	Site	Authors
	40	Atlantic coastal pond	Robin, comm.pers.
	90	Aarhus Bay	Havskum & Riemann (1996)
	371	Atlantic coastal pond	Our study
Ciliates	Biomass (µg C L^{-1})	Site	Authors
	0.4 to 14	Cobb Seamount	Sime-Ngando et al (1992)
	0.23 to 51.6	Saint-Lawrence estuary	Sime Ngando et al (1995)
	0.1 to 1.2	Northern Arabian Sea	Leakey et al (1996)
	20	Atlantic coastal pond	Our study

The study in the Antioche Pertuis area showed that in January 98, the ciliate biomass was in the same range as that of the coastal pond (2 µg C L^{-1} *versus* 3.8 µg C L^{-1}), but in February 98, the biomass in open water was higher than in the semi-closed pond (21 µg C L^{-1} versus 10.3 µg C L^{-1}). The same assessment, as already mentioned above for dinoflagellates, can also be reliable for ciliates: the low temperature (Fig. 1) limited the development of ciliates in the coastal pond.

To summarize, pigmented nanoflagellates were the primary resource available in the water column (60 % of the total protist biomass) (Fig. 6). The second carbon resource was that of dinoflagellates (28 % of the total protist biomass). Diatoms and ciliates represented supplementary carbon resources available in the water column. In the absence of published data on nano-microzooplankton in a coastal pond, we are the first to report, here, that pigmented nanoflagellates represent the highest food source available for higher trophic levels, such as oysters. Diatoms, considered as the principal food of oysters, represent only a complementary carbon resource in the Atlantic pond.

Production of microbiota in the water column in the coastal pond for summer period

Nanoflagellates dominated the planktonic protist production (76 % of total carbon protist production) in the pond (Table 4). Dinoflagellates represented the second highest yield

in the coastal pond (20 % of total carbon protist production). Our results confirm the previous results reported by Robert [47] in a coastal pond. The ciliate production was the lowest (1 % of total carbon protist production), but the growth yield of this compartment was high (47 to 70 %, [14, 38, 50, 62]. Therefore, the loss of energy is minimal at the moment of transfer from bacteria to the higher trophic level of ciliates.

During our monitoring, the system appeared to be more autotrophic than heterotrophic, since heterotrophic cells were less abundant and productive than autotrophic cells. However, mixotrophy was extensive in planktonic protists, under conditions of inorganic nutrient limitation [58]. In coastal marine environments, phytoflagellates may account for > 50 % of the flagellate bacterivory in summer and somewhat less in winter [12, 21, 23]. For dinoflagellates, mixotrophy was also widespread [58]. It is estimated that approximately half of the known species of living dinoflagellates are obligate heterotrophs [18], and for most of them, the relative importance of photosynthesis, uptake of dissolved inorganic nutrients and feeding are all unknown [58]. Since in a semi-closed coastal pond, inorganic nutrients are quickly exhausted, planktonic pigmented cells dominate the carbon biomass and production and bacteria are numerous, we could believe that mixotrophy was apparently the significant trophic mode in the coastal pond. Previous studies over the same summer period showed that all bacterial production was grazed by higher trophic planktonic levels [8]. Thus the microbial food web appeared to be active in the coastal pond, channeling the energy from the pool of dissolved matter to higher trophic levels. In future studies, it will be important to obtain information about the mixotrophy of phytoflagellates and dinoflagellates and we will need to quantify the functional relationships between the phototrophy/phagotrophy of phytoflagellates and dinoflagellates.

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