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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 nondiatom planktonic cells were studied in coastal ponds, which are areas traditionally used for fattening and greening table-sized 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 the French Atlantic coast near La Rochelle. The production of these microbiotas was determined in the summer period. The structure of plankton communities revealed the following observations: (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 colorless nanoflagellates. Diatoms were dominated by Naviculiineae. Dinoflagellates were dominated by Peridinales. Oligotrichida were predominant in the ciliate community. Protist biomass levels were nine times higher from April to August (summer period  $1033 \mu\text{g C L}^{-1}$ ) than from September to March (winter period  $114 \mu\text{g C L}^{-1}$ ). Whatever the season, nanoflagellates were dominant in the water column (66 and 53% of the entire protist biomass in the summer and winter periods, respectively). Nanoflagellates represented the highest production of nano–microplanktonic communities (76% of carbon protist production) in the coastal pond in summer and showed 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, first, 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. Overall, the system appeared to be more autotrophic than heterotrophic. Because inorganic nutrients are quickly exhausted in a semiclosed pond, pigmented flagellates dominated the carbon biomass, production and biomass of bacteria were high (thus, the microbial food web appeared to be active in this pond), and mixotrophy seemed to be an important trophic mode there.

### 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], whereas bacterioplankton have been occasionally studied [8, 9]. In semiclosed systems, such as ponds where nutrients are quickly exhausted, the development of microphytoplankton is limited [47]. 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 resuspension as a result of the lack of turbulence compared with the intertidal zone [4]. Microalgae, usually considered as the main food source of oysters, 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

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marine nanoplankton and microzooplankton in the microbial food web. Numerous studies have been made on the trophic link of microzooplankton and nanoplankton because they are preyed on 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 nanoplanktons are important grazers of bacteria [53].

In the Atlantic coastal ponds, 17–50% 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 dissolved organic matter into particles potentially available to upper trophic levels, such as nano–microzooplankton [1, 41]. In addition, bacterioplankton are not held by oysters, which retain particles between 5 and 100  $\mu\text{m}$  [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 with 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. The flat bottom is made up of thin layers of silt resulting from sedimentation of marine particles brought by turbid coastal waters and from destabilization of the banks surrounding it. The pond was small ( $\approx 200 \text{ m}^2$ ) and shallow ( $\approx 1 \text{ m}$ ).

Planktonic protist abundance and biomass were monitored over 1 year (12 sequestration cycles between February 1998 and February 1999) by weekly water samples. The first samples were taken 2 days after the pond water was replaced to decrease the turbidity levels. Coastal water was channeled into the pond at high spring tides. Seawater was held in the pond for 3–4 weeks, resulting in progressive modifications in the ecological conditions of

these semiclosed 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 with the use of 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 water column to estimate average values of microbiota abundance over its entire surface: the pond was divided into 12 squares (3 m wide), and one subsurface 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 was 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 by using the sampling method described above.

**Taxonomy and Enumeration of Protist Communities.** Taxonomic determination of protists present in the pond was carried out 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 by using a theoretical carbon/volume ratio of  $0.14 \text{ pg C } \mu\text{m}^{-3}$  [42].

For nanoplanktonic and microzooplanktonic cells, 40- 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 by using a theoretical carbon/volume ratio of  $0.14 \text{ pg C } \mu\text{m}^{-3}$  for nanoplankton (nanoflagellates) and  $0.17 \text{ pg C } \mu\text{m}^{-3}$  for microzooplankton (ciliates; [42]

corrected for glutaraldehyde fixative according to Leakey *et al.* [31]).

**Measurement of Growth Rates and Production of Planktonic Protists.** Production rates were estimated, for the summer period, from the growth rates, and biomass was measured for each group.

To estimate diatom, dinoflagellate, and ciliate growth rates in June 1999, organisms were fractionated by gravity filtration and reverse flow through nylon screens according to Ferrier-Pagès and colleagues [15, 16]. To remove different size classes of predators, a <145- $\mu\text{m}$  filter was used to remove copepods in water containing bacteria, nanoflagellates, diatoms, ciliates, and dinoflagellates; <45- $\mu\text{m}$  filter removed large ciliates and diatoms in water containing bacteria, nanoflagellates, diatoms, ciliates, and dinoflagellates. Nonfractionated seawater samples (entire population) were also incubated. Each size fraction was then transferred into three 1-L polycarbonate bottles that are closed at one end by a dialysis membrane (Spectra/Por 2, 12,000–14,000 Da). The bottles were incubated *in situ* in the subsurface 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 with the use of the dilution method [29] modified by Landry *et al.* [30]. One part of the water sample was filtered through a 1- $\mu\text{m}$  Nuclepore membrane. This filtered water, containing only bacteria, was then added to the unfiltered seawater; dilutions ranged from 1 to 20%. Two controls were taken—one with filtered seawater and the other with unfiltered water. The dilution and controls were transferred into three 1-L polycarbonate bottles that are closed as described 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

1998 and highest values in August 1998 (25°C; Fig. 1A). The annual mean was 15.2°C.

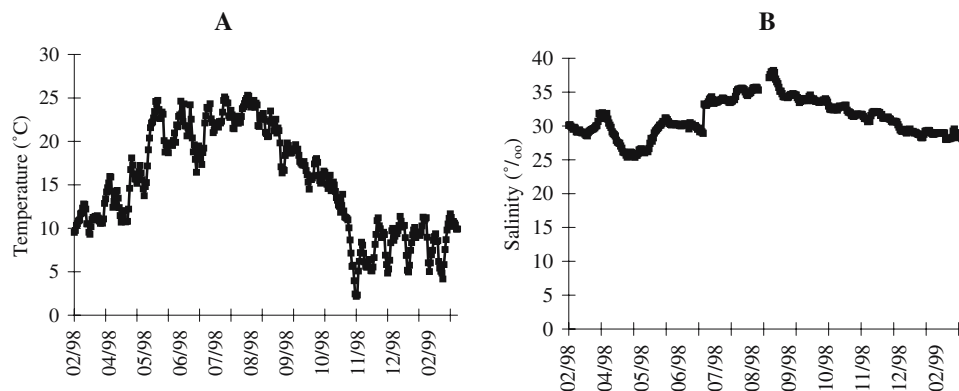
Salinity of the coastal pond waters varied with the season. The maximum occurred at the beginning of September 1998 (38.2) and the minimum in April 1998 with 25.4 (Fig. 1B). The annual mean was 31.

**Diversity and Standing Stocks of Protists.** The annual cycle was divided into two 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 two orders of diatoms (centric and pennate diatoms; Table 1) was recorded in the Atlantic coastal pond during the sampling period, ranging in length from 11 to 125  $\mu\text{m}$ . Diatoms were put into five suborders (Table 1), all of which were identified to genus level and a further two to species level.

The maximum number of taxa found during the 1-year study was 10 in July (data not shown). The suborder 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; Fig. 2A and B). Exceptionally, blooms of Coscinodiscineae (especially *Skeletonema costatum*) appeared in February, October, and December 1998 and in January 1999. The suborder 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.

Diatoms exhibited some degree of seasonal variability in population abundance and biomass: abundance was higher in spring ( $1100 \times 10^4$  cells  $\text{L}^{-1}$  in May), although the biomass was  $300 \mu\text{g C L}^{-1}$  at the same period (Fig. 3A and B). 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 September, diatom



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

**Table 1.** Taxonomic composition, sizes, and biovolumes of diatoms in the Atlantic coastal pond between February 1998 and February 1999

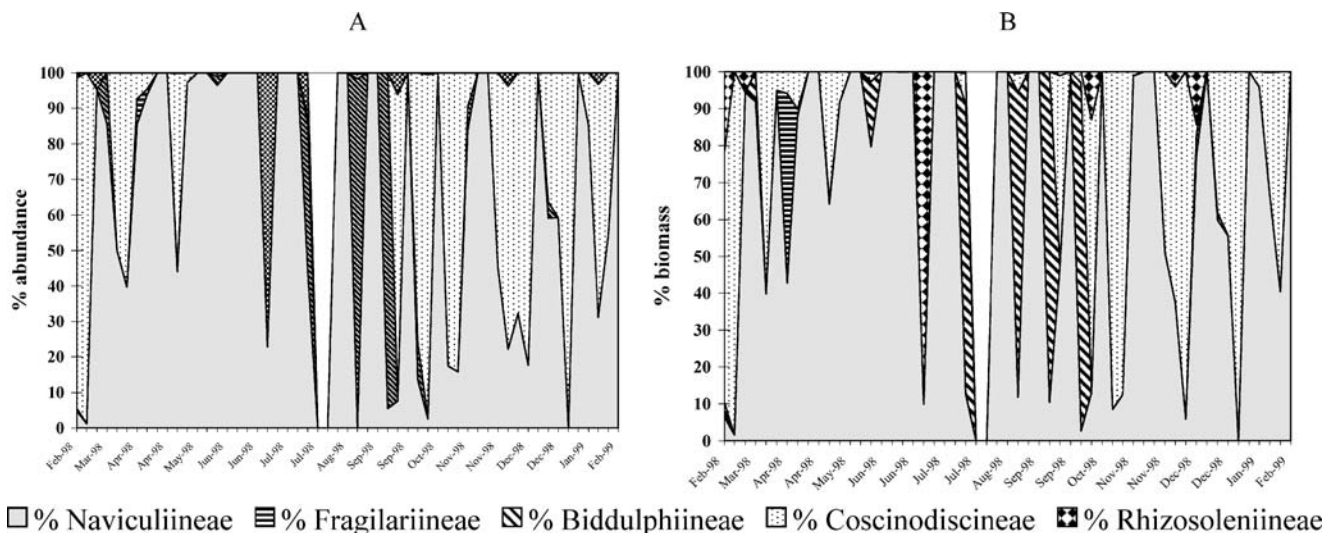
Order	Suborder	Family	Genus	Species	Cell length ( $\mu\text{m}$ )	Cell volume ( $\times 10^3 \mu\text{m}^3$ )
Centrales	Coscinodiscineae	Coscinodiscineae	<i>Coscinodiscus</i>	sp.	50	15.7
		Thalassiosiraceae	<i>Thalassiosira</i>	sp.	24	4.6
			<i>Skeletonema</i>	<i>costatum</i>	10	0.5
		Melosiraceae	<i>Melosira</i>	sp.	25	8.2
			<i>Podosira</i>	sp.	50	65.4
	Rhizosoleniineae	Rhizosoleniaceae	<i>Rhizosolenia</i>	sp.	92.5	9.2
		Leptocylindraceae	<i>Leptocylindrus</i>	sp.	30	1.2
	Biddulphiineae	Biddulphiaceae	<i>Biddulphia</i>	sp.	30	3
			<i>Cerataulina</i>	<i>pelagica</i>	60	117.8
		Eupodiscaceae	<i>Odontella</i>	sp.	15	1.2
		Chaetoceraeae	<i>Chaetoceros</i>	sp.	11	1.7
		Lithodesmiaceae	<i>Ditylum</i>	sp.	50	8.8
			<i>Lithodesmium</i>	sp.	45	18
	Pennales	Fragilariineae	Fragilariaceae	<i>Asterionella</i>	sp.	40
<i>Thalassionema</i>				sp.	15	0.4
			<i>Licmophora</i>	sp.		
Naviculiineae			Naviculaceae	<i>Diploneis</i>	sp.	55
		<i>Gyrosigma/Pleurosigma</i>		sp.	125	19.5
		<i>Navicula</i>		sp.	52	6.9
		Cymellaceae	<i>Amphora</i>	sp.	95	318.2
		Nitzshiaceae	<i>Cylindrotheca</i>	sp.	27	0.1
			<i>Nitzshia</i>	sp.	97	8.1

Classification according to Sournia [59].

abundance was low ( $6.6 \times 10^4$  cells  $\text{L}^{-1}$ ) and biomass was maximal ( $514 \mu\text{g C L}^{-1}$ ) as a result of a moderate bloom of *Amphora* sp. (Naviculiineae) with high biovolume ( $318.2 \times 10^3 \mu\text{m}^3$ ). In winter, abundance and biomass were lower ( $1600$  cells  $\text{L}^{-1}$  and  $0.2 \mu\text{g C L}^{-1}$ , respectively, in January 1999). The mean abundance and biomass of diatoms were  $1.2 \times 10^6$  cells  $\text{L}^{-1}$  and  $39 \mu\text{g C L}^{-1}$ , respectively, in the summer period (from April to August)

and  $6.2 \times 10^4$  cells  $\text{L}^{-1}$  and  $27 \mu\text{g C L}^{-1}$ , respectively, in the winter period (from September to March).

**Dinoflagellates.** A total of 14 dinoflagellate taxa, ranging in size from 23- to 70- $\mu\text{m}$  length, was recorded in this Atlantic coastal pond waters during the sampling period (Table 2). Twelve of these taxa were identified to genus and a further two to species level (Table 2).



**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.



**Table 2.** Taxonomic composition, sizes, and biovolumes of dinoflagellates in the Atlantic coastal pond between January 1998 and February 1999

Order	Family	Genus	Species	Cell length ( $\mu\text{m}$ )	Cell volume ( $\times 10^3 \mu\text{m}^3$ )
Peridinales	Peridiniaceae	Unidentified		24	15.1
		Unidentified		30	9.5
		<i>Scropsiella</i>	spp.	29	8.4
		<i>Protoperidinium</i>	spp.	27	5.3
		<i>Minuscula</i>	sp.	15	1.7
		<i>Amphidoma</i>	sp.	23	1.8
Gymnodiniales	Gymnodiniaceae	<i>Cochlodinium</i>	spp.	46	12.6
		<i>Amphidinium</i>	spp.	19	1.3
		<i>Gyrodinium</i>	spp.	40	7.6
		<i>Gymnodinium</i>	spp.	25	1
		<i>Gymnodinium</i>	<i>splendens</i>	70	55.6
		Prorocentrales	Prorocentraceae	<i>Prorocentrum</i>	spp.
Dinophysiales	Dinophysiaceae	<i>Dinophysis</i>	spp.	51	17
Ebriales	Chrysophyceae	<i>Ebria</i>	<i>tripartita</i>	32	5.2

Classification according to Sournia [59].

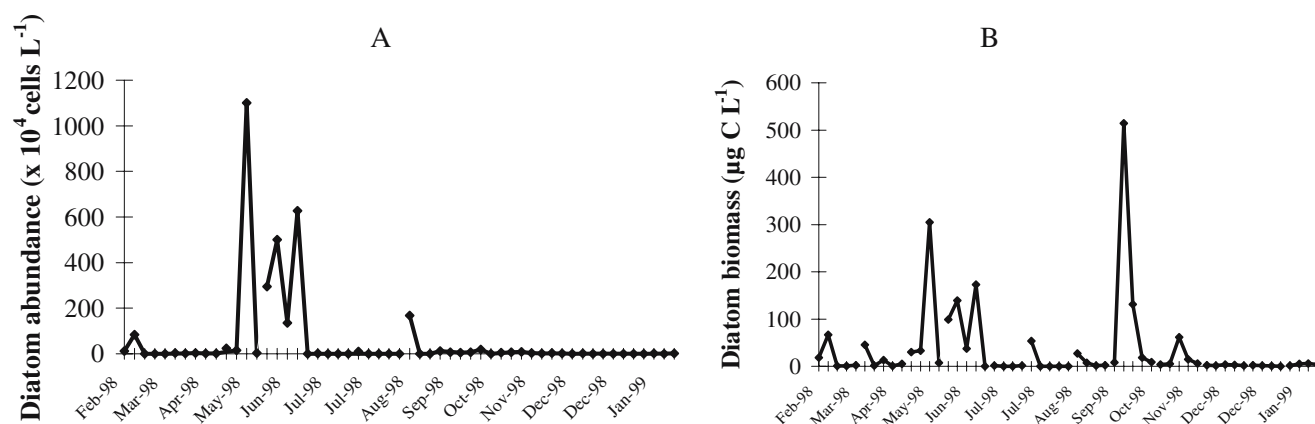
The maximum number of taxa found together was nine in July, August, September, and October (data not shown). The minimum was one taxon in March, April, and May. The Peridinales (especially *Scropsiella* sp.) dominated the dinoflagellate community throughout the year in terms of abundance (69% of abundance) and biomass (66% of biomass; Fig. 4A and B). Prorocentrales appeared during spring (in April and May, 100% of abundance and biomass) and in July (98% of abundance and biomass). The order 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 (Fig. 4A and B).

Dinoflagellates exhibited real seasonal variability in population abundance and biomass. They were widely present during the summer (Fig. 5A and B) and remained scarce during the rest of the year. Maximum abundance and biomass were found in July ( $2.6 \times 10^6$  cells  $\text{L}^{-1}$  and

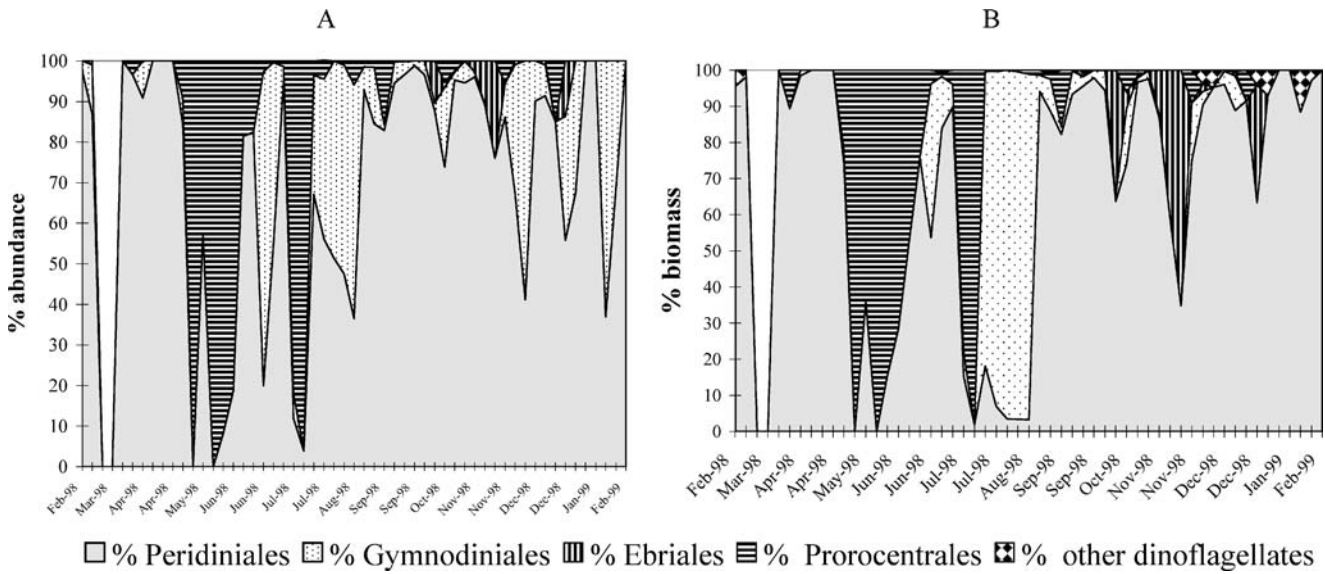
$2054 \mu\text{g C L}^{-1}$ , respectively). The mean abundance and biomass of dinoflagellates were  $2.4 \times 10^5$  cells  $\text{L}^{-1}$  and  $286 \mu\text{g C L}^{-1}$ , respectively, in summer and  $3.8 \times 10^4$  cells  $\text{L}^{-1}$  and  $11 \mu\text{g C L}^{-1}$ , respectively, in the winter period.

**Euglenophyceae.** The Euglenophyceae were represented exclusively by the order Eutrepsiales. They often appeared during the 1-year study (data not shown) but brought little carbon (maximal value of  $5.6 \mu\text{g C L}^{-1}$  in February and September and on average  $0.5 \mu\text{g C L}^{-1}$ ).

**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 from colorless nanoflagellates [6].



**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.



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

A total of 27 different nanoflagellate forms was recorded in the pond waters during the sampling period, ranging in length from 3 to 19  $\mu\text{m}$ . The maximum number of different nanoflagellates found together was 23 in July and 24 in September (data not shown). The minimum was five different nanoflagellate forms in March.

During the 1-year study, pigmented nanoflagellates dominated the population (80–90% of population

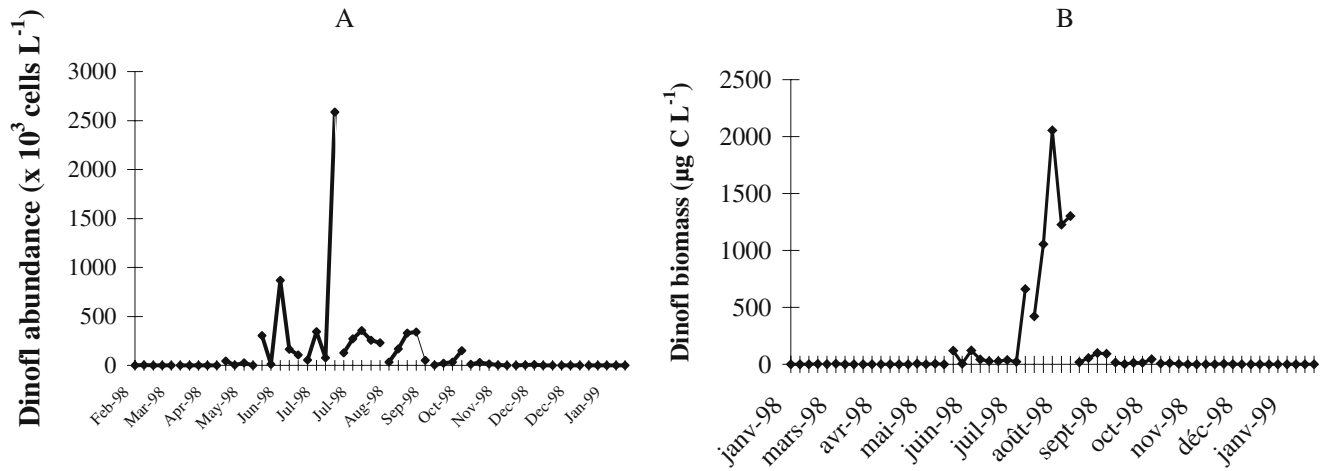
abundance and biomass; Fig. 6A and B) except in April where colorless nanoflagellates constituted 60% of their abundance and 50% of their biomass in June and July 1998 and January 1999.

Nanoflagellate abundance and biomass varied according to the season (Fig. 7A and B): the high values were found during spring ( $2500 \times 10^5 \text{ cells L}^{-1}$  and  $1700 \mu\text{g C L}^{-1}$ , respectively) and summer ( $3.2 \times 10^8 \text{ cells L}^{-1}$  and

**Table 3.** Taxonomic composition, sizes, and biovolumes of the ciliate community in the Atlantic coastal pond between January 1998 and February 1999

Subclass	Order	Suborder	Family	Genus	Species	Length ( $\mu\text{m}$ )	Cell volume ( $\times 10^3 \mu\text{m}^3$ )	
Choreotrichia	Choreotrichida	Tintinnina	Codonellidae	<i>Tintinnopsis</i>	sp. 1	53	38	
				<i>Tintinnopsis</i>	sp. 2	60	18.3	
				<i>Tintinnopsis</i>	sp. 3	97	136.4	
				Unidentified		46	207.4	
			Codonellopsidae	<i>Stenosemella</i>	sp.	38	15.9	
				Tintinnidae	<i>Eutintinnus</i>	sp.	110	54
			Strobilidiina	Strobilidiidae	<i>Lohmaniella</i>	sp.	37	33.4
					<i>Strobilidium</i>	sp.	40	14.6
					<i>Strombidium</i>	sp.	46	24.9
			Oligotrichida	Strombidiidae	<i>Strombidium</i>	<i>conicum</i>	68	47.9
		Halteriidae			<i>Halteria</i>	sp.	34	8.6
		Haptorida	Haptorida	Mesodiniidae	<i>Askenasia</i>	sp.	49	96
					<i>Mesodinium</i>	sp.	26	5.7
					<i>Mesodinium</i>	<i>pulex</i>	18	1.3
					<i>Mesodinium</i>	<i>rubrum</i>	38	9.3
<i>Didinium</i>	sp.				49	37		
Hymenostomatia	Scuticociliatida				Unidentified		44	27.9
					Phylasterina	Uronematidae	<i>Uronema</i>	sp.
Hypotrichia	Unidentified	Sporadotrichina	Oxytrichidae	Unidentified		44	16	
							81	17.3
Karyorelictea	Protostomatida	Unidentified				15	0.7	
							93	129.9
Unidentified aloriccate ciliates								

Classification according to Lee *et al.* [34].



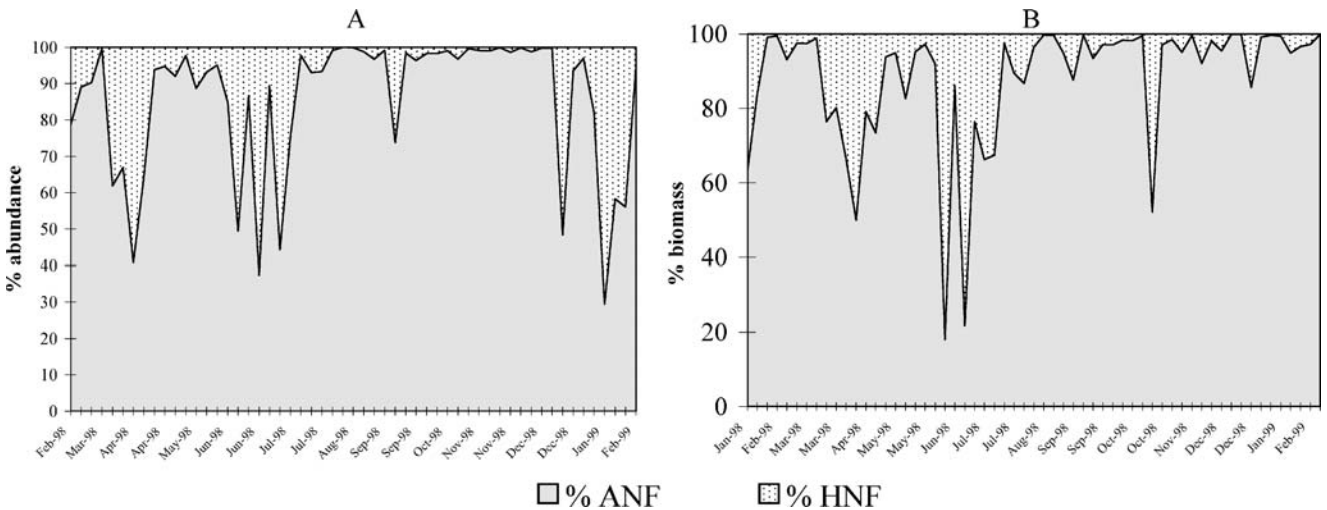
**Figure 5.** Dinoflagellate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of dinoflagellates. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of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

1650  $\mu\text{g C L}^{-1}$ , respectively). During the winter, nanoflagellate abundance and biomass were generally low, except in December, where a moderate bloom of nanoflagellates was seen ( $1.5 \times 10^7$  cells  $\text{L}^{-1}$  and  $700 \mu\text{g C L}^{-1}$ , respectively). The mean abundance and biomass of nanoflagellates were  $7.7 \times 10^7$  cells  $\text{L}^{-1}$  and  $681 \mu\text{g C L}^{-1}$ , respectively, in the summer period and  $6.9 \times 10^6$  cells  $\text{L}^{-1}$  and  $61 \mu\text{g C L}^{-1}$ , respectively, in winter.

**Ciliates.** A total of 21 ciliate taxa were recorded in the Atlantic coastal pond waters during the 1-year study, 16 of which were identified to genus level and a further 3 to species level (Table 3).

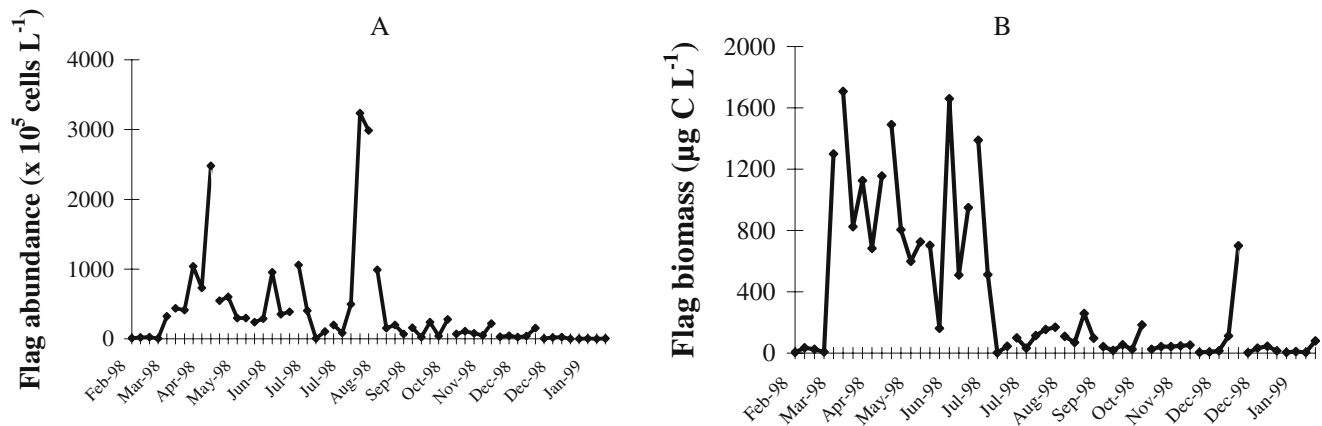
The length of ciliates ranged from 15 to 110  $\mu\text{m}$ . The greatest number of taxa was 14 in February (data not shown). The minimum was two taxa in July and August.

Ciliates were members of Choreotrichia with the suborder 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 (Fig. 8A and B). In aloricate ciliates, Oligotrichids (especially *Strombidium* sp.) were the most common taxonomic group (Fig. 8A and B). 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 (Fig. 8A and B). Haptorida were present during the 1-year study with peaks in April (95% of population abundance and biomass), June, and September ( $\approx 100\%$  of population abundance and biomass in September). The order Strobilidiina remained scarce, except in



**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.





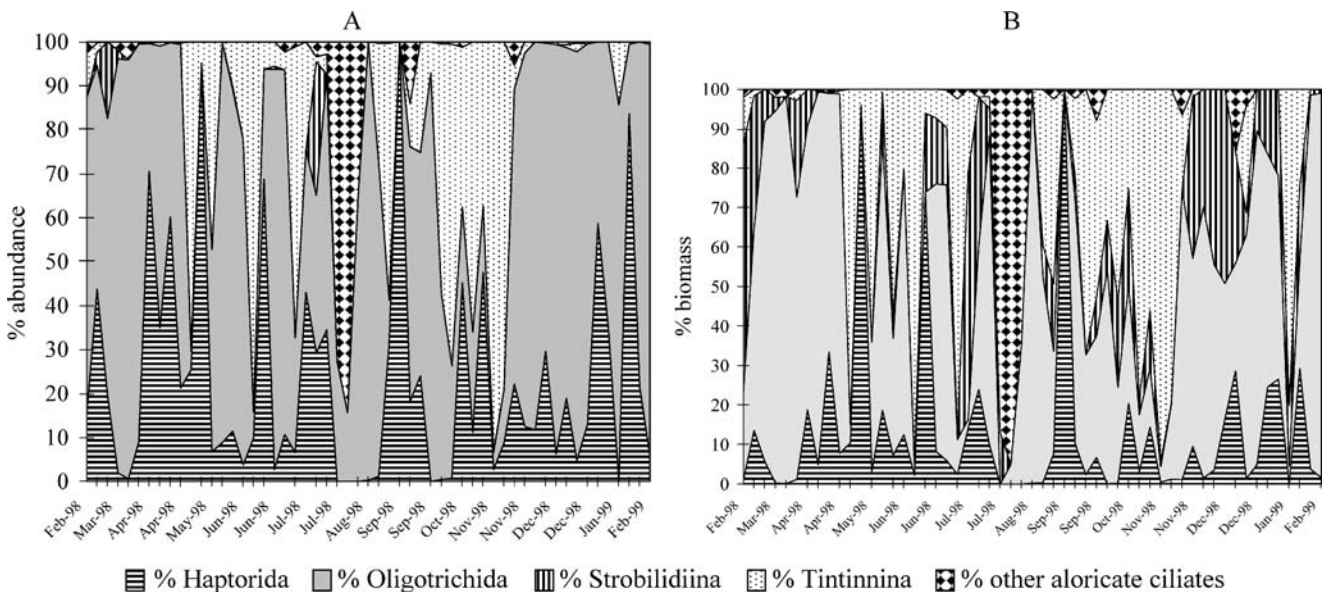
**Figure 7.** Nanoflagellates abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of nanoflagellates. Breaks in curves corresponds to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival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

December, when they represented 50% of population biomass. The subclasses Hypotrichs, Scuticociliatida, and Oxytrichia, more characteristic of benthic environments, were only present on a few occasions.

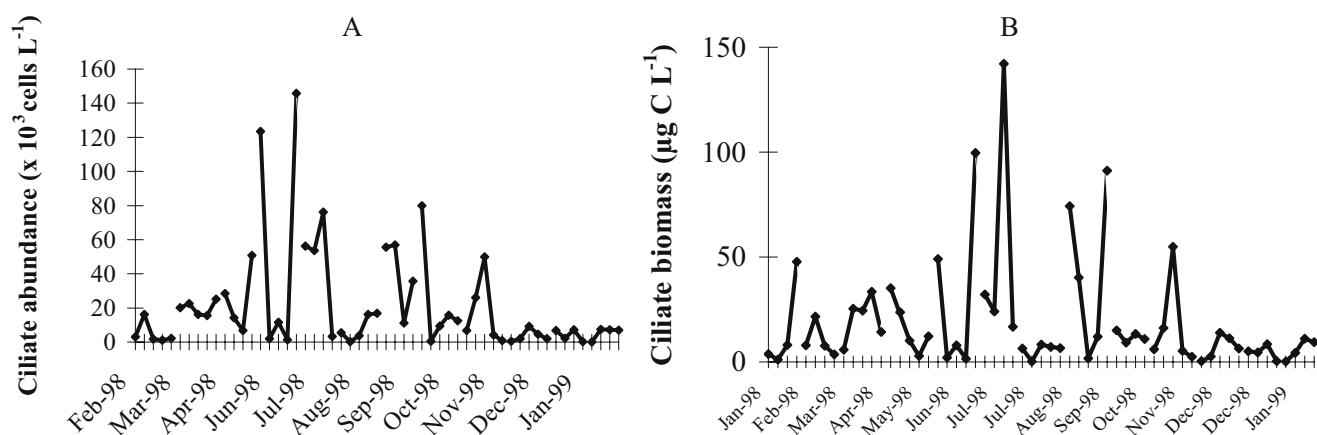
Ciliates exhibited some degree of seasonal variability in population abundance and biomass. The biomass of ciliates tended to reflect variations in abundance. Ciliates were present during the 1-year study (Fig. 9A and B) with peaks in spring, summer (in July,  $1.45 \times 10^5$  cells  $L^{-1}$  and  $142 \mu g C L^{-1}$ ), and autumn. During the winter, ciliates were not often present or were absent in February, July, and November 1998 and in January 1999. The mean abundance and biomass of ciliates were  $32 \times 10^3$  cells  $L^{-1}$  and  $27 \mu g C L^{-1}$ , respectively, in the summer period and

$13 \times 10^3$  cells  $L^{-1}$  and  $13 \mu g C L^{-1}$ , respectively, in the winter period.

The available biomass of major protists present in coastal pond waters was assessed (Fig. 10). In the summer period (from April to August), nanoflagellates were predominant in the water column ( $681 \mu g C L^{-1}$ ). The estimated biomass of other microbes was lower, with  $286 \mu g C L^{-1}$  for dinoflagellates,  $39 \mu g C L^{-1}$  for diatoms, and  $27 \mu g C L^{-1}$  for ciliates (Fig. 10). In the winter period (from September to March), nanoflagellates were always most predominant in the water column ( $61 \mu g C L^{-1}$ ). The estimated biomass of other microbes was lower, with  $27 \mu g C L^{-1}$  for diatoms,  $13 \mu g C L^{-1}$  for ciliates, and  $11 \mu g C L^{-1}$  for dinoflagellates (Fig. 10). The biomass of protist carbon



**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.



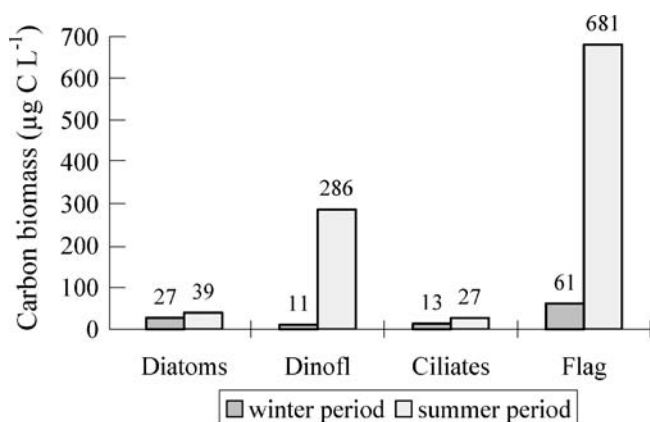
**Figure 9.** Ciliate abundance and biomass in coastal pond waters between February 98 and February 99: (A) mean abundance and (B) mean biomass of ciliates. Breaks in curves correspond to 12 sequestration cycles. The first point of cycle is the first sampling 2 days after the arrival of the seawater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

available in the pond waters was nine times lower in winter than in summer.

#### Estimation of Growth Rates and Production 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,  $0.098 \text{ h}^{-1}$ , compared with  $0.026 \text{ h}^{-1}$  for ciliates,  $0.07 \text{ h}^{-1}$  for diatoms, and  $0.06 \text{ h}^{-1}$  for dinoflagellates. The protist communities multiplied between one and seven times per day in the coastal pond waters.

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



**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). Dinofl = dinoflagellates, Flag = nanoflagellates.

## Discussion

**Qualitative Protist Composition of the Water Column in the Atlantic Coastal Pond.** The microphytoplanktonic cells present were mostly diatoms and dinoflagellates, whereas the microzooplanktonic cells were ciliates. Nanoplanktonic cells were represented by pigmented and colorless nanoflagellates.

For diatoms, the suborder Naviculiineae was mainly dominant (Fig. 2) with blooms of *Skeletonema costatum* (Coscinodoscineae) in spring and a bloom of *Amphora* sp. in autumn. Peridinales dominated the dinoflagellates (Fig. 4). 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 (80–90% of the total nanoflagellate biomass; Fig. 6). Crottereau [8] found a high fraction of chlorophyll *a*, which were cells  $>20 \mu\text{m}$  in size, during annual monitoring (1996–1997) in the same coastal pond near La Rochelle. Ciliates belonging to the Choreotrichs subclass were usually the predominant planktonic ciliates in most environments [5, 10, 48, 51, 52]. Oligotrichids were the most common taxonomic group found during monitoring (Fig. 8).

#### Quantitative Protist Composition of the Water Column in Coastal Pond.

Our estimations of planktonic diatom abundance throughout the year 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  $0.3 \mu\text{g C L}^{-1}$  in January 1998, a value similar to that in the pond ( $0.59 \mu\text{g C L}^{-1}$ ). In February 1998, the

**Table 4. Growth rates ( $h^{-1}$ ) and generation time (h) obtained for different groups during the incubation experiments**

	Growth rate ( $h^{-1}$ )	Generation time (h)	Biomass ( $\mu g C L^{-1}$ )	Production ( $\mu g C L^{-1} day^{-1}$ )
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

Estimated productions ( $\mu g C L^{-1} day^{-1}$ ) were calculated by multiplying the biomass ( $\mu g C L^{-1}$ ) of each group by their respective growth rate ( $h^{-1}$ ).

dinoflagellate biomass in the Antioche Pertuis was higher than in the pond ( $12.4 \mu g C L^{-1}$  in the pertuis versus  $1.6 \mu g C L^{-1}$  in the pond). This phenomenon could be a result of the lower temperature in the pond in February 1998 ( $6.9^{\circ}C$ ; Fig. 1), which did not allow the development of dinoflagellates, compared with 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 1996 (Robin, pers. comm.; 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 (Denmark) [23].

Marine planktonic ciliates were recently shown to be abundant in Atlantic ponds: the compartment repre-

sented  $63.5 \mu g C L^{-1}$  during June 1997 [11]. In the same Atlantic pond, from April to July 1996, Robin (pers. comm.) found similar values, from 50 to  $60 \mu g C L^{-1}$ . 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).

The study in the Antioche Pertuis area showed that in January 1998, the ciliate biomass was in the same range as that of the coastal pond (2 versus  $3.8 \mu g C L^{-1}$ ); however, in February 1998, the biomass in open water was higher than in the semiclosed pond (21 versus  $10.3 \mu g C L^{-1}$ ). 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. 10). 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 nanomicrozooplankton 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.

**Table 5. Comparison of abundance (cells  $L^{-1}$ ) and biomass ( $\mu g C L^{-1}$ ) with other bays and estuaries**

Groups	Site	Authors
<b>Diatoms</b>		
Abundance (cells $L^{-1}$ )		
1E+05	Bourgneuf Bay	Robert [47]
6.3E+05	Atlantic coastal pond	Our study
Biomass ( $\mu g C L^{-1}$ )		
200–500	Chesapeake Bay	Malone and Ducklow [36]
33	Atlantic coastal pond	Our study
<b>Dinoflagellates</b>		
Abundance (cells $L^{-1}$ )		
9.7E+03	Buzzards Bay	Pierce and Turner [40]
1.4E+05	Atlantic coastal pond	Our study
<b>Nanoflagellates</b>		
Abundance (cells $L^{-1}$ )		
3.8E+06	Saint-Lawrence Estuary	Lovejoy <i>et al.</i> [35]
4.2E+07	Atlantic coastal pond	Our study
Biomass ( $\mu g C L^{-1}$ )		
40	Atlantic coastal pond	Robin, comm. pers.
90	Aarhus Bay	Havskum and Riemann [23]
371	Atlantic coastal pond	Our study
<b>Ciliates</b>		
Biomass ( $\mu g C L^{-1}$ )		
0.4–14	Cobb Seamount	Sime Ngando <i>et al.</i> [56]
0.23–51.6	Saint-Lawrence Estuary	Sime Ngando <i>et al.</i> [57]
0.1–1.2	Northern Arabian Sea	Leakey <i>et al.</i> [32]
20	Atlantic coastal pond	Our study

*Production of Microbiota in the Water Column in the Coastal Pond for the 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 (47–70%) [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 because 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]. Because inorganic nutrients are quickly exhausted in a semiclosed coastal pond, 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 of the bacterial production was grazed by planktons in higher trophic 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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