

Seasonal variations of mixotrophic ciliates in the northwest Mediterranean Sea*

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ABSTRACT: The seasonal distribution of mixotrophic oligotrichous ciliates was compared to that of the strict heterotrophic oligotrichs and of the autotrophic haptorid *Mesodinium rubrum*, in surface coastal waters of the Ligurian Sea, from March 1988 to December 1989. The results show that (1) mixotrophic ciliates, which were observed year-round, average 51% of the overall biovolume (from 45% for cells 30 to 50 µm to 57% for cells > 50 µm); (2) mixotrophs dominate the ciliate populations in spring and in summer (average > 60%, maximum 100%); (3) pigmented ciliates, mixotrophic oligotrichs and *M. rubrum* dominate the biovolume of ciliates in the size ranges < 30 and > 50 µm; (4) besides numerous *Strombidium* spp., 5 mixotrophic species belonging to the genera *Tontonia*, *Laboea* and *Lohmaniella* were observed; and (5) a positive correlation was found between biovolume of pigmented ciliates and light and between biovolume of mixotrophic ciliates and biovolume of cyanobacteria.

KEY WORDS: Mixotrophy · Oligotrichs · *Mesodinium rubrum* · Seasonal distribution · NW Mediterranean

INTRODUCTION

Mixotrophy is a nutritional pathway which combines heterotrophy and autotrophy (Laval-Peuto et al. 1986, Jonsson 1987, Stoecker 1987), either simultaneously or alternately (amphitrophy — see review by Laval-Peuto 1992). Mixotrophy is known in several protistan phyla (Sanders 1991, Dolan 1992, Laval-Peuto 1992). In the Strombidiidae (Oligotrichida), mixotrophy is due either to plastid retention (Stoecker et al. 1987, Laval-Peuto 1992), or to purple non-sulphur bacteria symbiosis known in only *Strombidium purpureum* (Fenchel & Bernard 1993a, b).

Earlier studies of mixotrophic oligotrichs which harbour plastids focused on photosynthesis and respiration (McManus & Fuhrman 1986, Jonsson 1987, Putt 1990a, Stoecker & Michaels 1991) or on ultrastructural features (Laval-Peuto et al. 1986). These studies showed that products of photosynthesis are available

to the ciliates and could provide them with an advantage in heterogeneous and patchy environments such as oligotrophic ones (Laval-Peuto 1992). Mixotrophic oligotrichs have been recorded both in freshwater (Rogerson et al. 1989) and in seawater such as the Mediterranean Sea, the Atlantic Ocean, the Baltic proper, the Kattegat/Skagerrak, Norwegian fjords, the Antarctic and the Arctic (McManus & Fuhrman 1986, Jonsson 1987, Laval-Peuto & Rassoulzadegan 1988, Stoecker et al. 1989, Auf dem Venne 1990, Nielsen et al. 1990, Putt 1990b, Stoecker et al. 1992, Verity & Vernet 1992). Available data on the distribution of mixotrophic ciliates, except for an annual survey in the waters of Great Harbor, USA (Stoecker et al. 1987), deal with short periods. During their survey, Stoecker et al. (1987) found that the biomass of mixotrophic ciliates might range from 18 to 81% of the ciliate fauna.

The seasonal distribution of mixotrophic planktonic oligotrichs in the Mediterranean Sea was investigated over 21 mo with the aim of surveying their occurrence in oligo- to mesotrophic water. The seasonal distribution patterns were compared to those of strict heterotrophic oligotrichs and of the autotrophic Haptorida *Mesodinium rubrum* and also to parameters such as light intensity and autotrophic pico- and nanoplankton.

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MATERIAL AND METHODS

Surface seawater samples were collected (average of 2 times a week) with an acid-rinsed carboy at Point B, a standard oceanographic station at the mouth of the Bay of Villefranche, NW Mediterranean (43° 41' 10" N, 7° 19' 0" E) during the period March 1988 to December 1989. Samples were transported directly to the laboratory within 1 h after sampling.

Prior to plankton concentration, aliquots were used for microscopy: (1) 50 ml was fixed with acid Lugol's solution (1 to 2%) for Utermöhl counts of ciliates (Rassoulzadegan & Gostan 1976, Thronsen 1978), and (2) 10 ml was fixed with borax-buffered formalin at 2% (v/v) final concentration (Steedman 1976) for epifluorescence counts of autotrophic pico- and nanoplankton (Hobbie et al. 1977, Davis & Sieburth 1982). Cyanobacteria were counted during the whole period and plastidic pico- and nanoflagellates from November 1988 to December 1989. Samples used to assess the percentages of mixotrophic, strict heterotrophic and autotrophic ciliates were concentrated up to 500-fold on a 10 μm mesh net by a gentle reverse filtration technique (Sheldon & Rassoulzadegan 1987). Concentrates were then fixed with borax-buffered formalin at 3% (v/v) final concentration and settled in a 10 ml Utermöhl chamber. To avoid pigment degradation, Utermöhl sedimentation took place in the dark and at 4 °C. An average of 30 ciliates were examined under an epifluorescence microscope according to Rassoulzadegan et al. (1988), as modified by Bernard & Rassoulzadegan (1990).

To compare the relative importance of the different organisms studied, numerical abundances were normalized into biovolumes. The volumes of the ciliates were 4000, 21 500 and 47 000 μm^3 for cells < 30 μm ('small cells'), cells ranging from 30 to 50 μm ('medium cells') and cells > 50 μm ('large cells') respectively (Rassoulzadegan 1977, 1982). Other volumes were: 0.32 μm^3 for cyanobacteria (size \approx 0.84 μm ESD), 1.77 μm^3 for plastidic picoflagellates (size \approx 1.50 μm ESD) and 65.45 μm^3 for plastidic nanoflagellates (size \approx 5.00 μm ESD).

The data on seasonal changes in light intensity were obtained from the 'Centre de la Météorologie Nationale', Nice, France.

RESULTS

Biomass distribution

Fig. 1 shows that mixotrophic and strict heterotrophic oligotrichs occurred year-round in surface waters at Point B. Their respective biovolumes were of the same order of magnitude, ca $10^3 \mu\text{m}^3 \text{ml}^{-1}$ (Fig. 1D). In general, blooms occurred in spring and autumn. The

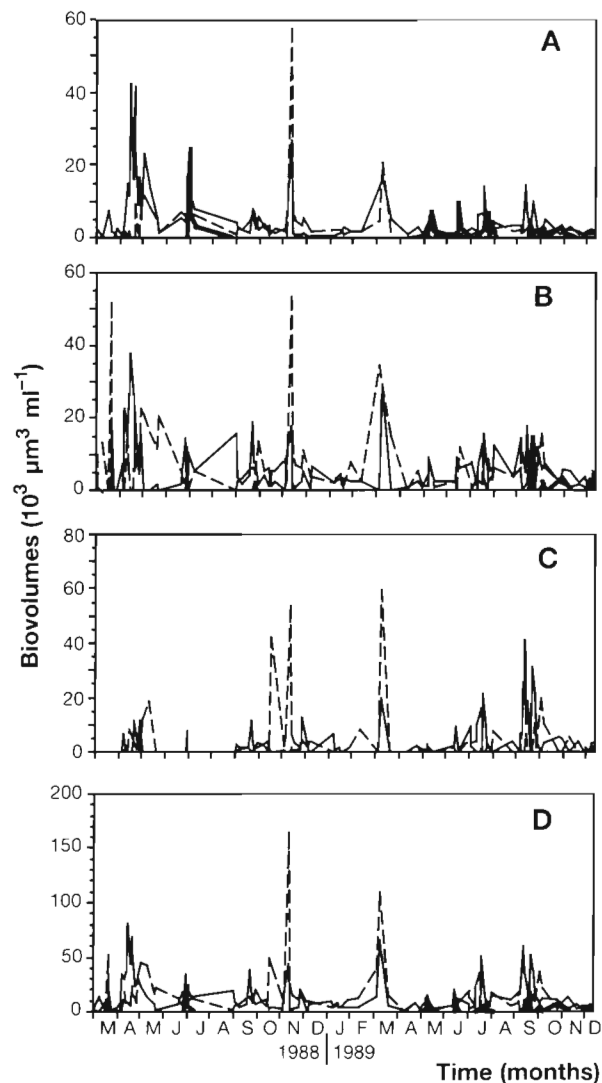


Fig. 1 Seasonal distribution of the biovolumes of oligotrichs (— strict heterotrophs, --- mixotrophs) and of *Mesodinium rubrum* (—) at the surface of Point B from March 1988 to December 1989. (A) Ciliates < 30 μm , (B) ciliates 30 to 50 μm , (C) > 50 μm , (D) all sizes together

highest global (total of 3 size classes) values were in April 1988 ($80 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) for the mixotrophs and in November 1988 ($165 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) for the strict heterotrophs. The autotroph *Mesodinium rubrum* was observed only during a few months each year, with blooms occurring in summer (maximum of $25 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in July) (Fig. 1D).

With an annual average biovolume of $6 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$, mixotrophs were dominated by medium-sized cells. They displayed spring blooms with biovolume maxima of $40 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in April 1988 and $20 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in March 1989 for the small and medium-sized cells (Fig. 1A, B). These 2 groups also exhibited autumnal blooms with values reaching $30 \times 10^3 \mu\text{m}^3$

ml⁻¹ in November 1988 and $15 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in September 1989 (Fig. 1A, B). Large mixotrophs were less present than the above groups. Their biovolume maxima reached values of $12 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in March, April and November 1988, and $31 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in September 1989. For all the mixotrophs, secondary blooms were observed in July. All the blooms were synchronized in the 3 size categories. Minimal values were observed in winter (Fig. 1).

Strict heterotrophic ciliates also displayed spring and autumnal blooms with highest values observed in November 1988 ($58 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) and in March 1989 ($54 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) for the small and medium-sized ciliates respectively (Fig. 1A, B). With an annual average of $4 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$, biovolumes of the large cell class were in general lower than those of the 2 other size classes (Fig. 1C).

Mesodinium rubrum was observed from April 1988 to December 1989. Only the small and medium-sized classes were represented. Maximal values of biovolumes for the small-sized cells were reached in summer: $25 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in early July 1988 and $10 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in mid-June 1989 (Fig. 1A). For medium-sized cells, the highest value was observed in September 1989 ($15 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) (Fig. 1B).

Relative percentages of frequency

Total mixotrophs comprised on average 51% of the total ciliate biovolume, but approached 100% especially in spring (Fig. 2D). Considered separately, the small, medium and large-sized mixotrophs represented 49, 45 and 57% respectively of the total ciliate biovolume in their size category (Fig. 2A to C). Large mixotrophs were absent for long periods in spring and summer 1988 but less frequently the rest of the year (Fig. 2C). With an annual average of 15% of the biovolume of small-sized ciliates, *Mesodinium rubrum* highest biovolume values were 53, 75 and 79% in July 1988, May 1988 and June 1989, respectively (Fig. 2A). The medium-sized cells were only represented in autumn (maximum of 74% in September 1989) (Fig. 2B).

Occurrence of the main mixotrophic oligotrichous species

Four genera were observed: *Strombidium*, *Tontonia*, *Laboea* and *Lohmaniella*. *Strombidium* was the only genus observed year-round and in all 3 size classes (Table 1). Small and medium-sized cells of *Lohmaniella* were observed but the medium-sized ones only sporadically. Three species of *Tontonia* were identified: *T. appendiculariformis* (only in 1989), *T. gra-*

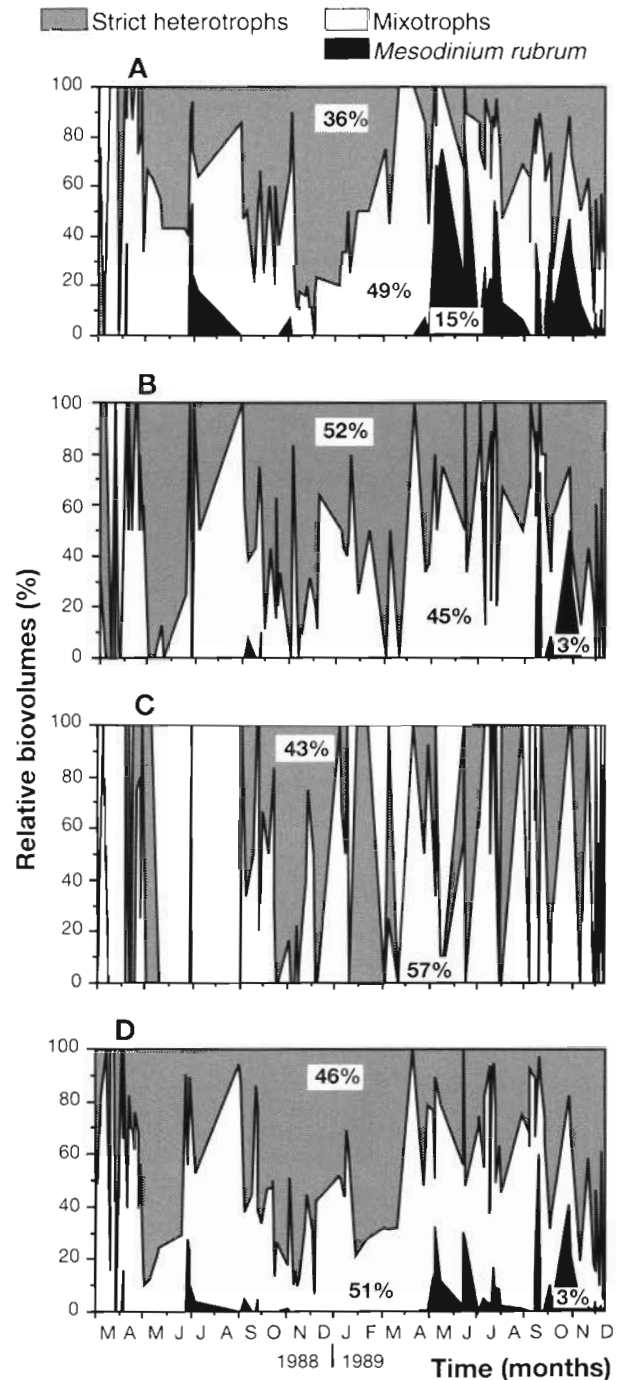


Fig. 2. Seasonal distribution of the relative biovolumes of oligotrichs (strict heterotrophs and mixotrophs) and of *Mesodinium rubrum* at the surface of Point B from March 1988 to December 1989. (A) Ciliates $< 30 \mu\text{m}$, (B) ciliates 30 to $50 \mu\text{m}$, (C) $> 50 \mu\text{m}$, (D) all sizes together

cillima (except in spring) and *T. ovalis* (in summer and autumn 1989). Medium-sized cells of *Laboea strobila* were observed sporadically in autumn 1988 and in winter 1989; large-sized cells were only sampled in spring and autumn 1989.

Table 1. Presence (+) or absence (-) of the different species of fluorescent ciliates (mixotrophic oligotrichs and *Mesodinium rubrum*) in different seasons at the surface of Point B from March 1988 to December 1989

Species	Size class (µm)	Winter	Spring	Summer	Autumn
Mixotrophs					
<i>Strombidium</i> spp.	<30	+	+	+	+
	30–50	+	+	+	+
	>50	+	+	+	+
<i>Lohmaniella</i> sp.	<30	-	-	+	+
	30–50	-	+	-	-
<i>Tontonia appendiculariformis</i>	30–50	-	-	+	-
	>50	+	+	+	+
<i>Tontonia gracillima</i>	30–50	+	-	+	+
	>50	+	-	+	+
<i>Tontonia ovalis</i>	<30	-	-	+	+
	30–50	-	-	+	+
<i>Laboea strobila</i>	30–50	+	-	-	+
	>50	+	+	-	+
Autotroph					
<i>Mesodinium rubrum</i>	<30	-	+	+	+
	30–50	-	-	-	+

Other parameters

The seasonal distribution of cyanobacteria was similar during the 2 years: maximal biovolumes in spring ($40 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in 1988 and $33 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$ in 1989) and minimal ones in winter. Secondary blooms

($< 20 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) developed in summer and autumn (Fig. 3A). Autotrophic picoflagellates bloomed twice: the main bloom in winter ($5 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) and a minor one in summer ($1 \times 10^3 \mu\text{m}^3 \text{ml}^{-1}$) (Fig. 3B). The autotrophic nanoflagellates also displayed 2 blooms, in late winter ($17 \times 10^4 \mu\text{m}^3 \text{ml}^{-1}$) and in summer ($19 \times 10^4 \mu\text{m}^3 \text{ml}^{-1}$) (Fig. 3C).

The average light intensity was 803 J cm^{-2} , with minimal values in winter and maximal ones in spring and summer (1450 J cm^{-2}) (Fig. 4).

DISCUSSION

Marine oligotrichs and the haptorid *Mesodinium rubrum* generally dominate the populations of pelagic ciliates (Rasoulzadegan 1975, Smetacek 1981, Stoecker et al. 1987, 1989, Sherr et al. 1988, Nöthig & von Bodungen 1989, Putt 1990b, Verity & Vernet 1992). Except for a few cases (e.g. Stoecker et al. 1987, 1989, Putt 1990b,

Verity & Vernet 1992), ecological studies do not generally take into account either the size or the trophic types of the oligotrichs, which may display both strict heterotrophy and mixotrophy (see Laval-Peuto 1992).

In this study, we use the term mixotrophy to mean a 'symbiosis' with plastid retention, implying the coexis-

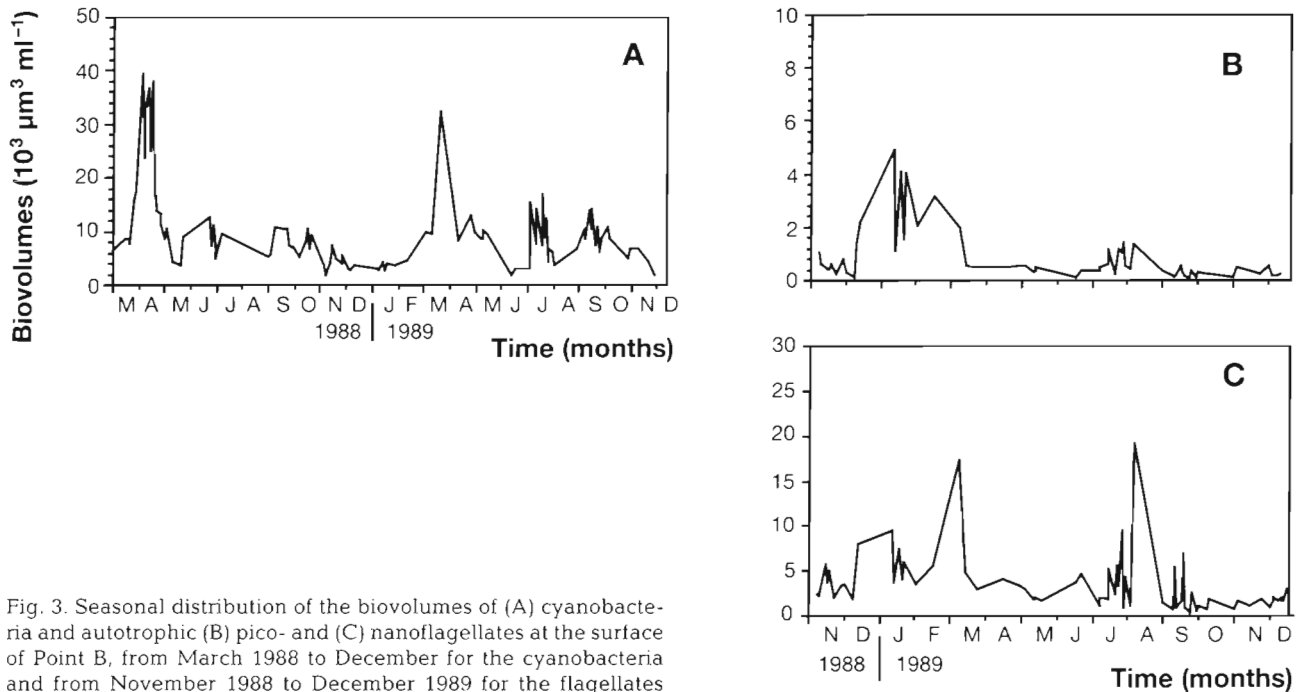


Fig. 3. Seasonal distribution of the biovolumes of (A) cyanobacteria and autotrophic (B) pico- and (C) nanoflagellates at the surface of Point B, from March 1988 to December for the cyanobacteria and from November 1988 to December 1989 for the flagellates

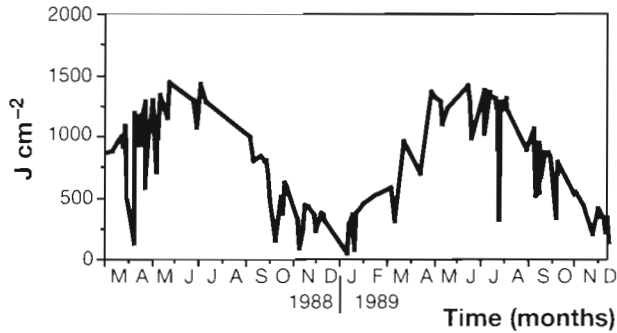


Fig. 4. Light intensity measured at the surface of Point B from March 1988 to December 1989

tence of heterotrophy and autotrophy (see Laval-Peuto 1992 and references therein). We consider that all the ciliates displaying a general fluorescence are mixotrophs, whatever the origin of the fluorescence (plastids or algae). No phagotrophic behaviour is known in *Mesodinium rubrum* (Lindholm et al. 1988) and we did not observe any prey in the cells during the 2 yr of this study.

The 4 genera of oligotrichs reported in this study, *Strombidium*, *Tontonia*, *Laboea* and *Lohmaniella* (Table 1), include mixotrophic species (Laval-Peuto & Rassoulzadegan 1988, Laval-Peuto 1992). Identification at the species level in *Strombidium* and *Lohmaniella* was uncertain with the investigating technique used here; thus we have assigned organisms to genera, only then taking their sizes into account (Table 1). Species were often found in 2 size classes, due to the variation in size of the cells throughout the cellular cycle. *Laboea strobila* is a widespread oligotrich (McManus & Fuhrman 1986, Dale 1987, Stoecker et al. 1987, 1989, Gifford 1988, Laval-Peuto & Rassoulzadegan 1988). While sporadically observed in autumn and in winter (Laval-Peuto & Rassoulzadegan 1988), in our study it was mostly present in spring 1989, but totally absent in summer. In the Atlantic Ocean, it has mostly been found in summer and in autumn (Blackbourn et al. 1973, McManus & Fuhrman 1986), and in late spring in Norwegian fjords (Verity & Vernet 1992). In the Mediterranean, its occurrence does not seem to be coupled with that of *Mesodinium rubrum*, (Table 1) as it is in the Atlantic (McManus & Fuhrman 1986). The length of *M. rubrum* is reported as varying from 20 to 60 μm (Lindholm & Mörk 1990). Only small and medium-sized cells were observed during our survey and they were sampled at different periods, exclusively in autumn for the medium-sized cells and from May to November for the small-sized ones (cf. McManus & Fuhrman 1986, Dale 1987). Two varieties of *M. rubrum*, one small and one large, have also been observed in Southampton Water, UK (Leakey et al. 1993). *M. rubrum* could therefore be a complex of species.

Biovolumes of the mixotrophs and of the strict heterotrophs were of the same order of magnitude as those observed in the Atlantic Ocean, at least in summer (Stoecker et al. 1987). The domination of ciliate populations in the Mediterranean by medium-sized cells has been described earlier, but without taking into account the trophic type (Rassoulzadegan 1982). Average biovolume of the small-sized mixotrophs was almost equivalent to that of the medium-sized ones and average biovolume of the small-sized *Mesodinium rubrum* was higher than that of the medium ones. This confirms the need to pay more attention to populations of small-sized ciliates in future studies (Sherr et al. 1986).

Mixotrophs constituted the greater part of the biovolume of all oligotrichs with 51% (Fig. 2D) but mostly of the large (57%) and the small-sized (49%) cells (Fig. 2C, B). If we add to the latter the 15% represented by the small-sized autotroph *Mesodinium rubrum*, then small-sized pigmented ciliates largely dominated their size class. Mixotrophs sometimes represented 100% of the total biovolume in spring and summer (Fig. 2). Stoecker et al. (1989) also observed in coastal areas in summer that more than 90% of the ciliates were mixotrophic. Low percentages of mixotrophic ciliates have been found in rich environments like Chesapeake Bay, USA (5%; Dolan & Coats 1990) or the Clyde Estuary, UK (<5%; Laybourn-Parry et al. 1992). This might support the idea that mixotrophy is more emphasized in oligo- to meso-oligotrophic waters. Mixotrophs represented less than 10% of ciliates in late spring in Norwegian fjords (Verity & Vernet 1992). Although in the minority in autumn and in winter, mixotrophs were never absent (Fig. 2). In Atlantic coastal waters, they constituted ca 10% of ciliates in the cold seasons (Stoecker et al. 1987).

There are no up-to-date studies on the role of light in the occurrence and the distribution of the different trophic types of ciliates. Indeed, in periods of high light intensities (Fig. 4), the percentage of mixotrophic ciliates and the diversity of species were higher (Fig. 2, Table 1). A positive correlation was found between the biovolumes of mixotrophs and light (Table 2). The biovolume of mixotrophic ciliates was also positively correlated to that of cyanobacteria (Table 2). This may be explained by the same light requirement in cyanobacteria (positive correlation between cyanobacteria and light; data not shown) and mixotrophic ciliates. In effect, phycoerythrin pigments are present both in cyanobacteria (White et al. 1977) and in some mixotrophs (cf. *Laboea strobila*; McManus & Fuhrman 1986). It might well be that the relationship between mixotrophic ciliates and cyanobacteria is that of predator and prey, as is certainly the case for the relationship between strict heterotrophs and autotrophic nano-

Table 2. Correlation coefficients of the positive relations found between the biovolumes of the different ciliates, light and the biovolumes of cyanobacteria and nanoflagellates (n = 110). Significant correlation coefficients are indicated in **bold** type

	Strict heterotrophic oligotrichs	Mixotrophic oligotrichs	<i>Mesodinium rubrum</i> < 30 µm
Light	0.02 (p = 0.88)	0.20 (p = 0.05)	0.28 (p = 0.01)
Cyanobacteria	0.02 (p = 0.87)	0.44 (p = 0.01)	0.04 (p = 0.66)
Autotrophic nanoflagellates	0.32 (p = 0.01)	0.06 (p = 0.64)	0.10 (p = 0.69)

flagellates (Table 2). The present lack of correlation between the biovolume of flagellates and that of mixotrophic ciliates suggests that predation is not regular on this type of prey, which might be explained by the necessity of renewing the plastids only from time to time.

The physiological advantages of the symbiosis with plastids have been discussed elsewhere (Laval-Peuto & Febvre 1986, Laval-Peuto 1992). These ciliates should have an advantage over the strict heterotrophic ones because they might modulate their source of carbon. Mixotrophic ciliates seem particularly well adapted to oligotrophic environments which are poor in nutrients and heterogeneous particles (Jonsson 1987) but with good light conditions, as in the Mediterranean. A better understanding of the energetic and material transfers through the mixotrophic ciliates would result in a better overview of the microbial food web.

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