Vol. 155: 89–101, 1997 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published August 28

Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods

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ABSTRACT: In May 1995, the planktonic ciliate community of the Ligurian Sea (NW Mediterranean) was dominated by 3 *Strombidium* species: a mixotroph 16 µm in length, a heterotrophic species 15 µm in length and a larger (26 µm) heterotrophic species. Growth rates of these oligotrichs and their consumption by copepods were examined in 3 shipboard experiments during the JGOFS-France DYNAPROC cruise. Growth rates were estimated by means of 24 h incubations in seawater samples filtered through a 64 µm mesh and apparent growth or disappearance rates were estimated in whole water samples and in incubated samples with copepods added. Ciliate community generation time ranged from 52 to 88 h. Copepod predation was highest on the larger heterotrophic ciliate and higher on the nano-sized heterotrophic species relative to mixotrophic nanociliate. The net growth rates of the mixotroph in 'predator-free' water ranged from 0.2 to 0.4 d^{-1} compared to rates of 0.9 to 1.0 d^{-1} in samples with copepods added. Net growth rates of heterotrophic species ranged from 0.2 to 0.5 d^{-1}. The higher mixotrophic growth rates when copepods were present was concomitant with the disappearance of heterotrophic microciliates (2.2 to 9.0 ml cleared of heterotrophic microciliates $copepod^{-1}$ h^{-1}, estimated clearance rates). While we found that mixotrophs, relative to heterotrophs, may be less subject to copepod predation, data and models suggests that mixotrophic oligotrichs have lower maximal growth rates than similar-sized heterotrophic species.

KEY WORDS: Mixotrophy · *Strombidium* Predation

INTRODUCTION

Marine planktonic ciliates are an ecologically important group; they dominate the microzooplankton in most marine systems (Beers et al. 1980) and serve as a trophic link between the microbial food web and metazoans, especially copepods (Sherr et al. 1986, Stoecker & Capuzzo 1990, Gifford 1991). It is now recognised that many planktonic oligotrich ciliates contain chloroplasts and are mixotrophic (Stoecker et al. 1987, Laval-Peuto & Rassoulzadegan 1988, Stoecker et al. 1989). Mixotrophic ciliates obtain energy from both photosynthesis and phagotrophic feeding; they represent a variable fraction of the ciliate fauna in different marine systems (Stoecker 1991). For example, in the NW Mediterranean during autumn and winter, an average of about 40% of the oligotrich species contain chloroplasts (Laval-Peuto & Rassoulzadegan 1988) and during the spring, mixotrophs can occasionally approach 100% of total ciliate biovolume (Bernard & Rassoulzadegan 1994). Despite the common occurrence of mixotrophs in estuarine and marine ecosystems, little is known about factors regulating their abundance or factors influencing their importance relative to heterotrophic species. Advantages of mixotrophy in food-poor or oligotrophic environments are obvious but there are likely to be some costs involved with mixotrophy given the fact that such forms rarely achieve complete dominance.

While the importance of oligotrichs in marine systems is recognised, very few field studies have provided estimates of oligotrich, either heterotrophic or mixotrophic, growth rates. To our knowledge, reports based on experimental studies of only 2 open-water

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marine systems are available: the North Atlantic (Verity et al. 1993) and the Peruvian upwelling system (Tumantseva & Kopylov 1985); none exist for relatively oligotrophic systems such as the NW Mediterranean.

In this report we present the results of 3 field experiments designed to provide estimates of oligotrich growth rates for the NW Mediterranean. We used these experiments to compare heterotrophic and mixotrophic growth rates and the relative susceptibility of the different oligotrich types to predation by copepods. We also examined apparent growth capacities of mixotrophic and heterotrophic oligotrich ciliates on the basis of maximum reported growth rates available in the literature and summarise existing data on copepod consumption of oligotrichs.

MATERIAL AND METHODS

Experiments were carried out onboard the 'Sûroit' during the JGOFS-France DYNAPROC cruise (Dynamics of Rapid Processes in the Water Column) in May 1995. Samples were taken at the JGOFS-France reference station DYFAMED (43° 25.2' N, 7° 51.8' E; NW Mediterranean) located approx. 50 km offshore from Nice, France. The water column depth of the station is about 2000 m. Ciliate growth rates and grazing losses were estimated by monitoring changes in cell concentrations in predator-free seawater, in whole water with *in situ* concentrations of copepods, and in water to which copepods were added.

Experimental protocol. Water samples were taken with Go-flo bottles at 20 m depth. This depth was chosen as previous studies had indicated that it would probably yield a ciliate community about evenly divided between mixotrophs and heterotrophs (Dolan & Marrasé 1995) After sampling, the following manipulations were performed to yield 3 distinct subsamples: 2 l was passed through a 64 µm nylon mesh to remove large zooplankton, 2 l remained untreated, and 2 l received the addition of 10 adult copepod females (*Centropages*) collected with a WP 2 plankton net. The treatments provided samples containing: (1) only small ciliates without copepods or large predacious ciliates; (2) whole water with approximately the *in situ* ciliate and copepod communities; (3) water with an increased concentration of copepods. Samples were assigned to 2 l polycarbonate bottles which were placed in a running seawater incubator with a neutral density screen removing 70% of incident illumination, corresponding roughly with the incident illumination at 20 m depth.

Samples for ciliate counts were taken at time zero and after 24 h (end of incubation). 500 ml was removed from each bottle and preserved in acid Lugol's (2% final concentration) which minimizes cells losses relative to aldehyde fixatives (Stoecker et al. 1994). We used 2% acid Lugol's because a volume-to-carbon conversion factor exists (Putt & Stoecker 1989). The principal disadvantage of acid Lugol's is that mixotrophic ciliates can be identified only from characteristics of gross morphology. To get round this problem a 1 l sample of whole water was taken prior to the experiments. 500 ml was preserved in acid Lugol's for the determination of distinct ciliate morphospecies and the remaining 500 ml fixed with 2% borate-buffered formaldehyde to identify by epifluorescence microscopy the mixotrophic forms among the morphospecies determined previously. At the end of the incubation after samples for ciliate counts were removed, the remaining water in the bottles with whole seawater and with added copepods was concentrated to 40 ml over a 20 µm nylon mesh and preserved with 2% acid Lugol's to allow estimation of copepod concentrations.

Experiments were run in triplicate for filtered and whole water samples and in duplicate for copepod additions. For each experiment, replicates represented consecutive repetitions of the entire procedure beginning with a new water bottle sample. Experiments were conducted on 3 dates: 11, 14 and 27 May 1995 and each time started in the morning between 07:30 and 08:40 h local time.

Sample processing and data analysis. For determination of trophic types, 500 ml subsamples, fixed with formaldehyde or acid Lugol's, were concentrated via sedimentation in 500 ml graduated glass cylinders. After 4 d the upper 400 ml of the sample was gently siphoned and the bottom concentrated 100 ml settled in a standard settling chamber. Both samples were examined in parallel with a Zeiss Axiovert 35 inverted microscope. Ciliates were identified to genus when possible according to Montagnes & Lynn (1991) from the acid Lugol's preserved sample. The determination of trophic type (mixotrophic or heterotrophic) was made by examining the aldehyde-fixed sample using epifluorescence microscopy.

Time zero and 24 h samples from the experiments (50 or 100 ml) were settled and the entire surface of the settling chamber examined at 200× with an inverted microscope. Ciliates of distinct morphospecies, determined using the double analysis, were counted. Copepod abundances were determined from the sample concentrated over 20 µm mesh Nitex. The concentrate was transferred into a settling chamber and the chamber surface was scanned at 100× with an inverted microscope. Preserved copepods were identified by Suzanne Nival (Station Zoologique).

Rates of ciliate growth and copepod grazing were calculated from ciliate counts following the system of equations of Frost (1972):

$$k = \ln(C_1/C_0)/(t_1 - t_0)$$

$$g = k - [\ln(C_1^*/C_0^*)/(t_1 - t_0)]$$

where k is the growth constant, C_1 and C_0 are ciliate concentrations (cells ml^{-1}) in the bottles without grazers at times t_1 and t_0 respectively, g is the grazing coefficient and C_1^* and C_0^* are ciliate concentrations in cells ml^{-1} at t_1 and t_0 in bottles with copepods.

RESULTS

Experimental conditions

Fig. 1 shows depth profiles of temperature, density, chlorophyll *a* (chl *a*) and ciliates on the 3 experimental dates. In May 1995, the water column was beginning to stratify with a weak density gradient and a considerable temperature gradient, ranging from 17.4 to 13.3°C on 11 May and from 16 to 13.3°C on 14 and 27 May. The different experimental conditions during the incubations are summarised in Table 1. Illumination was low due to cloud cover during incubations especially on 27 May (213.23 W m^{-2} h^{-1} average during daylight hours). Water temperature at 20 m ranged from 13.9°C (14 May) to 15.5°C (27 May) and chl *a* concentration, the most variable parameter, ranged from 0.28 µg l^{-1} on 11 May to 1.15 µg l^{-1} on 14 May. Similar to chlorophyll, cyanobacteria and nanoflagellates were less abundant on 27 May compared to 14 May. The highest chl *a* concentration at the sampling depth of 20 m on 14 May was due to strong winds on 13 May moving the chl a peak up from 30 to 20 m. Copepods in whole water were a mixture of approx. 50% *Oithona* sp. and 50% small calanoids (*Pseudocalanus* and *Clausocalanus* spp.).

Generation time and growth rates

Community generation times (Table 2) varied from 51.9 h on 14 May to 87.8 h on 27 May. On all 3 dates, the ciliate community was dominated by 3 *Strombidium* species with metabolic charac-

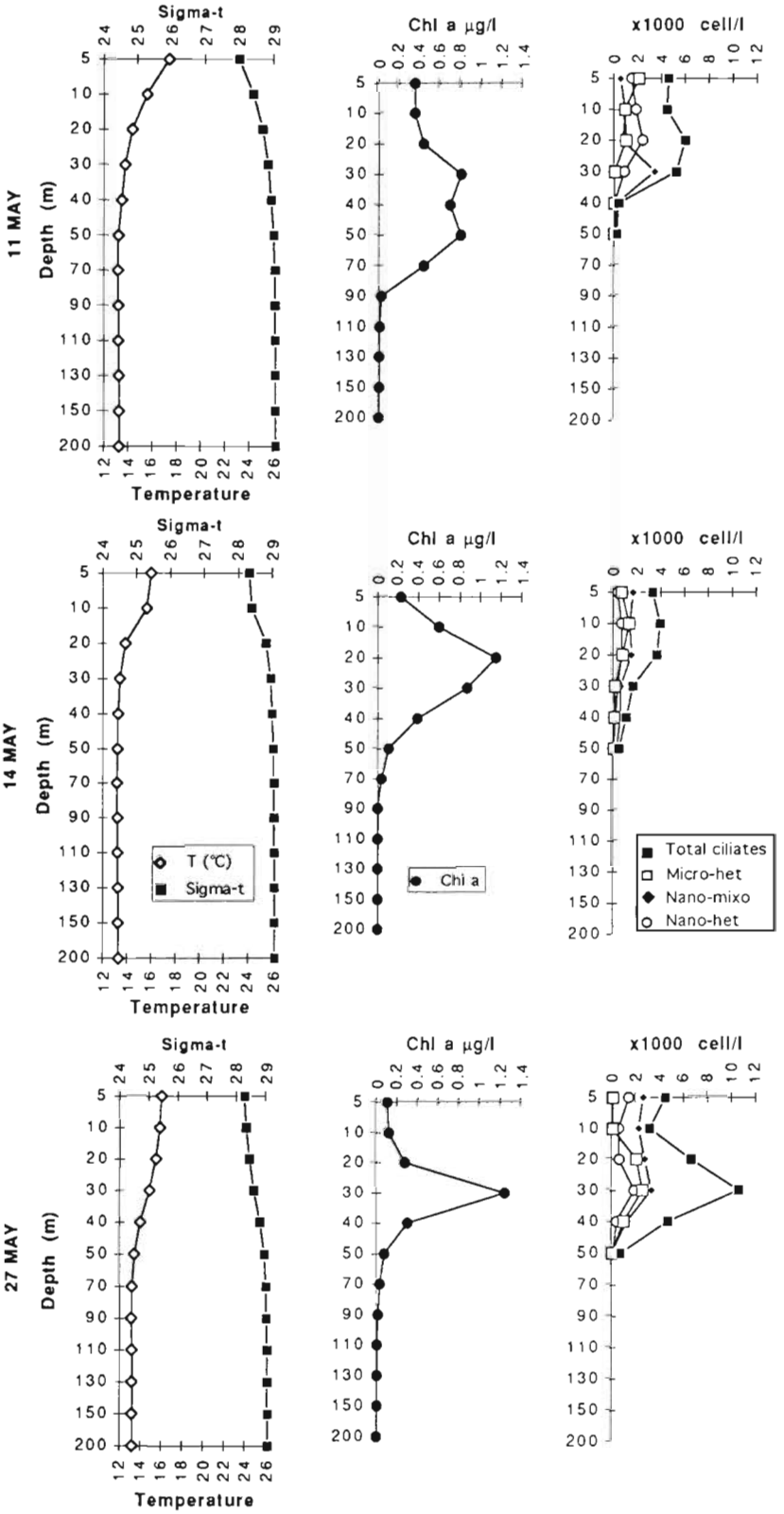

Fig. 1. Depth profiles of physical and biological parameters at the beginning of incubations on the 3 experimental dates in 1995. T: temperature; Chl *a*: chlorophyll *a* concentration

Table 1. Incubation experimental conditions Chlorophyll *a*, illumination and temperature values at 20 m at time zero. Averaged concentration (n = 3) in cells ml^{-1} of cyanobacteria, heterotrophic nanoflagellates (HNF), and autotrophic nanoflagellates (ANF) in the experimental bottles (whole water) at time zero

Date	Chl *a* ($\mu g\ l^{-1}$)	Illumination ($W\ m^{-2}\ h^{-1}$)	Temp. (°C)	Cyanobacteria (SD)	HNF (SD)	ANF (SD)
11 May	0.28	251.87	14.3	1.78×10^5 (2.90×10^4)	No data	No data
14 May	1.15	392.48	13.9	1.07×10^5 (3.62×10^4)	13.4×10^2 (5.64×10^2)	12.9×10^2 (6.49×10^2)
27 May	0.44	213.23	15.5	0.64×10^5 (2.05×10^4)	4.86×10^2 (1.11×10^2)	3.36×10^2 (1.33×10^2)

teristics and linear dimensions as given in Table 2. Figs. 2 & 3 show, respectively, the initial and final concentrations of ciliates and the growth rates of dominant species in different treatments during experiments.

The net growth rate of the mixotrophic nanociliate in the <64 µm fraction ranged from a negative rate during the first experiment (11 May) to 0.41 and 0.24 d^{-1} for the second and third experiments (14 and 27 May

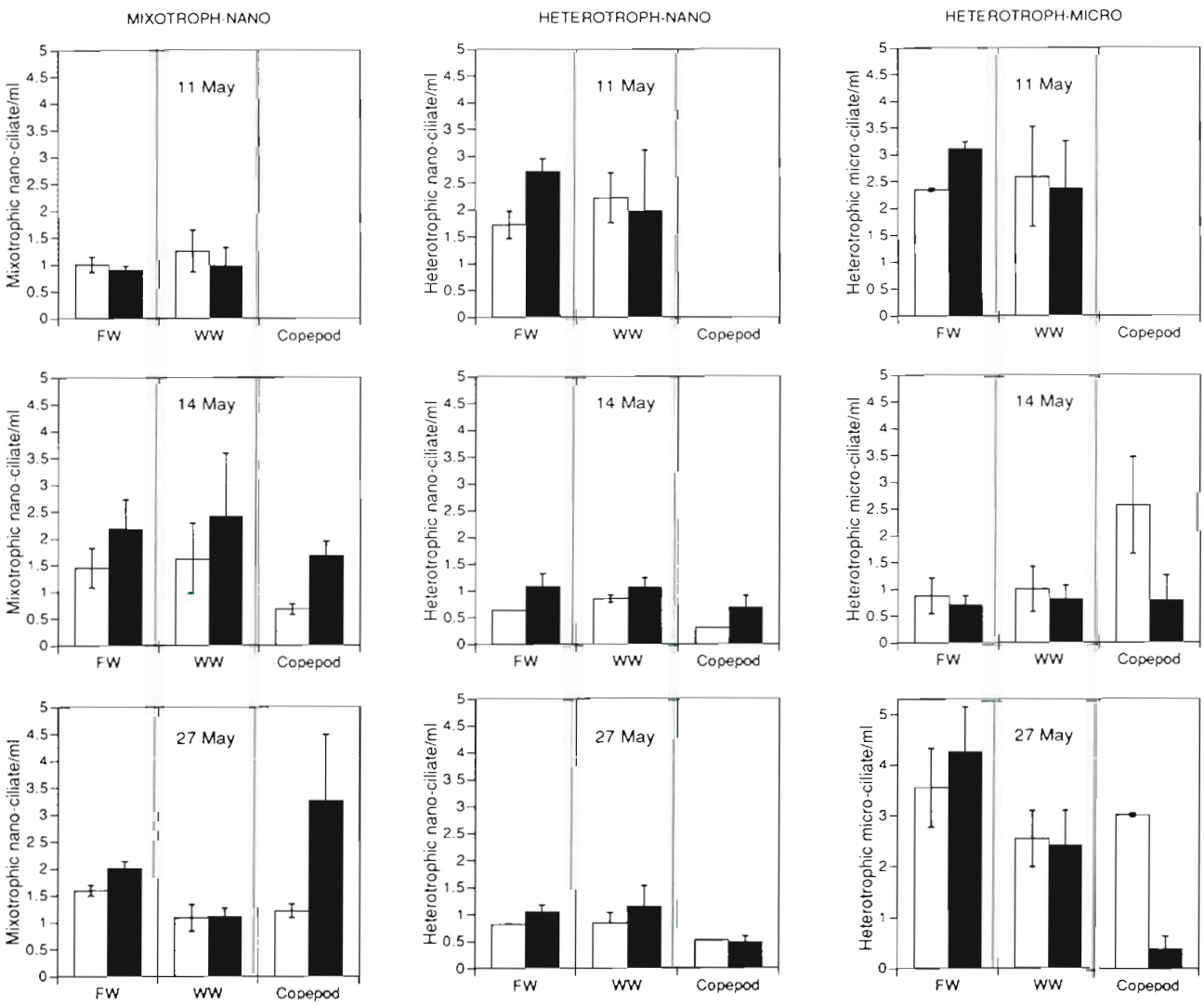

Fig. 2. Initial (open bars) and final (solid bars) ciliate concentrations in experimental bottles during incubations conducted on 11, 14 and 27 May. FW: water filtered through a 64 µm mesh; WW: whole water; Copepod: water with copepods added. Values are means of 3 replicates, except for Copepod (means of 2 replicates); error bars are standard deviation. Missing values for Copepod on 11 May correspond to missing samples on this date

Table 2. Community generation time (h) and dominant species growth rate (d^{-1}) and generation time (h) estimated in water filtered through a 64 µm mesh. T0: ciliate community concentration in cells ml^{-1} at time zero. L × W: length × width (µm)

Date	n	T0 (SD)	Community generation time (SD)	Dominant species	Metabolism	L × W	Growth rate (SD)	Generation time (SD)
11 May	2	5.25 (0.35)	69.7 (20.6)	*Strombidium* sp. a	Mixotrophic	16 × 10	No growth	No growth
	2			*Strombidium* sp. b	Heterotrophic	15 × 15	0.46 (0.23)	41.6 (21.2)
	2			*Strombidium* sp. c	Heterotrophic	26 × 18	0.22 (0.06)	80.5 (24.7)
14 May	3	3.11 (0.53)	51.9 (4.8)	*Strombidium* sp. a	Mixotrophic	16 × 10	0.41 (0.07)	41.2 (8.03)
	3			*Strombidium* sp. b	Heterotrophic	15 × 15	0.52 (0.21)	36.0 (15.0)
	3			*Strombidium* sp. c	Heterotrophic	26 × 18	No growth	No growth
27 May	3	6.64 (0.66)	87.8 (38.8)	*Strombidium* sp. a	Mixotrophic	16 × 10	0.24 (0.005)	69.8 (1.48)
	3			*Strombidium* sp. b	Heterotrophic	15 × 15	0.26 (0.14)	76.5 (33.2)
	3			*Strombidium* sp. c	Heterotrophic	26 × 18	0.19 (0.18)	87.5 (92.4)

respectively). Net growth rates of mixotrophs in whole water ranged from a negative rate on 11 May to 0.38 and 0.03 d^{-1} on 14 and 27 May, respectively. For the 2 heterotrophic species, net growth rate in filtered seawater was between 0.26 and 0.46 d^{-1} for nanociliate and between 0.19 and 0.22 d^{-1} for the microciliate. The growth rate of the heterotrophic nanociliate in whole water was negative on 11 May and ranged from 0.20 to 0.30 d^{-1} on 14 and 27 May respectively. Heterotrophic microciliates did not grow in whole water. The highest net growth rates for nanociliates (both mixo- and heterotrophic) in filtered water were found on 14 May, coinciding with no growth of the heterotrophic micro-sized oligotrich.

The highest growth rates for both of the nano-sized oligotrichs were estimated from samples with increased copepod concentrations (Fig. 3). On 14 May the average of the apparent growth rate for the mixotrophic form in samples with added copepods was 0.93 d^{-1}, 2-fold greater than the 0.41 d^{-1} found without added copepods. For the heterotrophic nanociliate growth rate ranged from 0.52 d^{-1} without copepods to 0.86 d^{-1} in bottles with copepods added. On 27 May the average apparent growth rate of mixotrophic ciliates was 1.03 d^{-1} in samples with copepods added relative to 0.24 d^{-1} in filtered samples. In both cases, increase in apparent growth rate was concomitant with the disappearance of microheterotrophic species in the bottles.

Copepod grazing

A surprising result was that copepod grazing rates were higher on the heterotrophic species, whether micro- or nano-sized (Table 3). Although some positive filtration rates on the nano-sized mixotroph were recorded, they were always less than those estimated on heterotrophic oligotrichs. For example, for the May 11 experiment a filtration rate of 0.54 ml $copepod^{-1}$ h^{-1} was estimated for mixotrophic nanociliates from whole water samples, compared to 1.89 and 1.26 ml $copepod^{-1}$ h^{-1} on the nano- and microheterotrophs, respectively. Unfortunately, for this first experiment we have

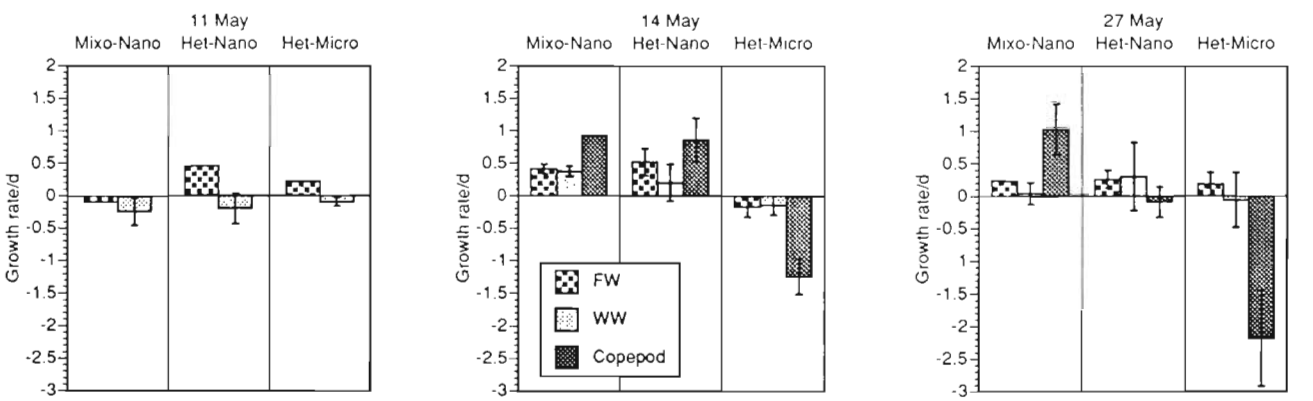

Fig. 3. Growth rate per day of different ciliate categories, estimated in water filtered through a 64 µm mesh (FW) and in bottles with grazers [whole water (WW) and water with copepods added (Copepod)], during the experiments conducted on 11, 14 and 27 May. Values are means of 3 replicates, except for Copepod (means of 2 replicates); error bars are standard deviation. Missing values for Copepod on 11 May correspond to missing samples on this date

Table 3. Summary data of copepod grazing experiment. μ: ciliate growth rate in control bottles (filtered water). G (grazing rate) and F (filtration rate in ml copepod^{-1} h^{-1}) were estimated in both kind of grazer bottles: whole water and water with copepods added. Rep: replicate number. n: number of nauplii or copepods l^{-1}. nf: no filtration. –: samples lacking

Expt	Ciliate category	Rep	Control (FW)	Grazer (whole water)			Grazer (copepod)		
			μ (h^{-1})	G (h^{-1})	n	F	G (h^{-1})	n	F
11 May	Mixotroph-Nano	1	–	–	–	–	–	–	–
		2	No growth	No grazing	5.5/4.5	nf	–	–	–
		3	0.0022	0.0108	9/11	0.54	–	–	–
	Heterotroph-Nano	1	–	–	–	–	–	–	–
		2	0.0261	0.0191	5.5/4.5	1.91	–	–	–
		3	0.0123	0.0372	9/11	1.86	–	–	–
	Heterotroph-Micro	1	–	–	–	–	–	–	–
		2	0.0110	0.0250	5.5/4.5	2.50	–	–	–
		3	0.0071	0.0004	9/11	0.02	–	–	–
14 May	Mixotroph-Nano	1	0.0187	0.0038	9/6	0.25	No grazing	9/11	nf
		2	0.0191	No grazing	12/8	nf	No grazing	12/13	nf
		3	0.0137	0.0004	9.5/3.5	0.03	–	–	–
	Heterotroph-Nano	1	0.0207	0.0254	9/6	1.69	No grazing	9/11	nf
		2	0.0132	No grazing	12/8	nf	No grazing	12/13	nf
		3	0.0308	No grazing	9.5/3.5	nf	–	–	–
	Heterotroph-Micro	1	No growth	No grazing	9/6	nf	0.0542	9/11	2.71
		2	No growth	0.0456	12/8	2.28	0.0423	12/13	1.69
		3	No growth	0.0006	9.5/3.5	0.05	–	–	–
27 May	Mixotroph-Nano	1	0.0097	0.0142	5/1	2.37	No grazing	5/6	nf
		2	0.0101	0.0008	4/2	0.13	No grazing	4/7	nf
		3	0.0099	0.0096	6.6/1.2	1.23	–	–	–
	Heterotroph-Nano	1	0.0066	No grazing	5/1	nf	0.0175	5/6	1.59
		2	0.0082	0.0163	4/2	2.72	0.0052	4/7	0.47
		3	0.0172	0.0035	6.6/1.2	0.45	–	–	–
	Heterotroph-Micro	1	0.0002	No grazing	5/1	nf	0.1131	5/6	10.3
		2	0.0152	0.0375	4/2	6.25	0.0849	4/7	7.72
		3	0.0079	0.0187	6.6/1.2	2.40	–	–	–

no data from bottles with copepods added due to loss of samples.

On 14 May, estimated filtration rates on mixotrophic and heterotrophic nanociliates from whole water were 0.14 and 1.69 ml copepod^{-1} h^{-1}, respectively. Grazing on these species was not detected in bottles with copepods added. In contrast, average filtration rates of 1.17 and 2.20 ml copepod^{-1} h^{-1} were calculated on heterotrophic microciliates from bottles with whole water and with increased copepod concentrations, respectively.

For the May 27 experiment, average filtration rate of 1.24 ml copepod^{-1} h^{-1} was calculated on mixotrophic nanociliates with natural copepod concentrations and no filtration was detected in water with increased copepod concentrations. Declines in heterotrophic nanociliates gave average filtration rate estimates of 1.60 ml copepod^{-1} h^{-1} with natural copepod concentrations and 1.03 ml copepod^{-1} h^{-1} with increased copepod concentrations. Changes in heterotrophic microciliate concentrations indicated lower copepod filtration rates in whole water relative to water with copepods added, from 4.33 to 9.01 ml copepod^{-1} h^{-1}, respectively.

DISCUSSION

Ciliate growth rates estimated from *in situ* incubations are not exempt from artefacts due to containment effects, accumulation of waste products, food depletion or excesses (Leakey et al. 1994). Fractionation, used to eliminate large predators, may cause cell damage and alter ciliate growth or decrease ciliate concentration relative to their food (reviewed in Landry 1994). In our experiments, ciliate community concentrations at time zero did not significantly differ between the filtered sample and the untreated sample (*t*-test), but we were not able to assess the physiological state of cells after fractionation. Some of our data suggest that fractionation may have injured some species. For example, the autotrophic ciliate *Mesodinium rubrum*, present during the 27 May incubation, did not grow in the fractionated sample but we found an average growth rate of 0.59 d^{-1} in whole water during this experiment. While this indicates that our growth estimates based on water filtered through a 64 µm mesh may be underestimates, the rates estimated from whole water and samples to which copepods were added should not have been affected.

Ciliate community generation time in the NW Mediterranean during May ranged from 52 to 88 h. These growth rates are somewhat higher than the generation time of 80 h estimated for Catalan Sea ciliates in June, based on simple considerations of chl *a* concentration and temperature (Dolan & Marrasé 1995), but somewhat lower than recent estimates for other marine systems, based on ciliate growth in size-fractionated samples. For example, the ciliate community generation time in Plymouth Sound, UK (Leakey et al. 1994), ranged from 29 to 52 h depending on the size of the mesh used. Ciliate community generation time in the North Atlantic during the spring bloom ranged from 18.5 to 55.4 h (Verity et al. 1993). Water temperature was roughly similar in all 3 studies considered (13 to 16°C), but in our experiments, chlorophyll concentrations averaged about 0.5 µg l^{-1} (Table 1) compared to 2.5 µg l^{-1} in the North Atlantic study (Verity et al. 1993) or 1.5 µg l^{-1} in the Plymouth Sound experiments (Leakey et al. 1994). Thus, our values for community generation times (Table 2) appear reasonable considering water temperature and chl *a* concentrations. In our incubations, the shortest generation time was found on 14 May when chl *a* concentration and illumination were highest.

We found that the mixotrophic nanociliate grew at rates similar to the heterotrophic nanociliate species, 0.41 and 0.52 d^{-1}, respectively, on 14 May and 0.24 and 0.26 d^{-1}, respectively, on 27 May, and in general faster than the larger heterotrophic microciliate species. Nevertheless, there was no net growth of the mixotroph during the first incubation. Net growth rates of the mixotrophic nanociliate in water filtered through a 64 µm mesh were higher for experiments in which chl *a* concentrations were higher, while net growth of heterotrophic microciliates was lower. In addition, growth rates of mixotrophic ciliates seemed to be higher when copepods were added; we obtained net growth rates 2-fold higher than in the filtered sample (Fig. 3). While fractionation may lower growth rate estimates because it damages cells, increases in net growth rates in samples to which copepods were added, relative to untreated water, are probably due to the effects of copepods. We do not know if such effects were direct (e.g. ammonium excretion) or indirect (e.g. predation on a competitor). However, it is noteworthy that mixotrophic growth occurred when the density of heterotrophic microciliates was greatly reduced, and that corresponded with an increased presence of copepods. Our observations support a hypothesis of competition between mixo- and heterotrophic species in experimental bottles that is balanced by copepod grazing which is higher on the heterotrophic forms.

Estimated filtration rates on heterotrophic microciliates from bottles with increased copepod concentrations (range 2.20 to 9.01 ml copepod^{-1} h^{-1}) were similar to rates calculated for copepods in bottles with natural copepod concentrations (range 1.17 to 4.33 ml copepod^{-1} h^{-1}). The rates estimated correspond with most previous reports for small calanoid copepods feeding on ciliates (Table 4). Clearance rates on heterotrophic nanociliates were lower (1.03 and 1.73 ml copepod^{-1} h^{-1} with natural and increased copepod concentrations, respectively) but still in the range reported by Gifford & Dagg (1988) for small oligotrichs. The somewhat higher clearance rate estimates for the bottles to which adult copepods were added are probably due to a reduction in the relative importance of naupliar stages in the 'copepods added' bottles as clearance rates for naupliar stages can be up to 2 orders of magnitude lower relative to adults (Berggreen et al. 1988).

In our experiments, copepod grazing on the mixotrophic nanociliate was low with natural copepod concentrations (avg. of 0.75 ml copepod^{-1} h^{-1}) and undetectable with increased copepod concentrations. As filtration rates of calanoid copepods are related to prey size (e.g. Frost 1972, Tiselius 1989) one explanation could be its small size but there was significant grazing on the similar-sized heterotrophic nanociliate. The particle size corresponding to 100% filtration efficiency for adult *Centropages* is 20 µm (Nival & Nival 1973). Based purely on considerations of size alone, for both the mixotrophic and heterotrophic nanociliates present in our study, the filtration efficiency was probably around 80 to 90%, based on the data of Nival & Nival (1973) for *C. typicus*. On this basis, we could explain the lower filtration rates estimated on heterotrophic nanociliates relative to heterotrophic microciliates. However, size considerations do not explain the differences in predation losses suffered by the heterotrophic nano-oligotrich compared to the mixotrophic nano-oligotrich.

A possible explanation for the difference in mortality rates between the mixotrophic and heterotrophic species of a similar size is a difference in swimming pattern or higher swimming speeds. Jonsson & Tiselius (1990) reported that the autotrophic *Mesodinium rubrum* was cleared more than 6 times less efficiently than *Strombidium spiralis* because of its swimming behaviour (rapid short jumps after immobility). As rapid jumps are known to be very expensive metabolically (Gilbert 1994), this suggests that exploiting photosynthesis allows costly predation-resistant behaviour. Crawford (1992) noted that many fast swimming ciliates harbour algal endosymbionts or retain plastids. Furthermore, among oligotrich species studied by Buskey et al. (1993), the highest swimming speeds corresponded to 2 mixotrophic forms (*Laboea strobila* and *S. conicum*). However, it

Table 4. Copepod filtration rates on ciliates. [C]: ciliate concentration (ml^{-1}). V: prey volume (10^3 µm^3). F: filtration rate (ml copepod^{-1} h^{-1}). Copepods are adult individuals otherwise indicated. Ciliate species in bold characters are mixotrophic or phototrophic

Copepod species	Prey	[C]	V	F	Source
Marine calanoid copepods					
Acartia clausi	*Favella tarakaensis*	0.30	736.5[a]	1.97	Ayukai (1987)
	Helicosomella fusiformis	0.77–7.52	34.5[a]	0.30–0.90	Ayukai (1987)
	Natural assemblage	0.20–0.80	–	1.15–2.19	Tiselius (1989)
	Strombidium sulcatum	3.3	13.9	1.43–26.3	Wiadnyana & Rassoulzadegan (1989)
	Natural assemblage	1.73	–	0.41–0.44	Turner & Granéli (1992)
A. hudsonica	*Eutintinnus pectinus*	6.6–8.3	118[b]	0.19–0.38	Turner & Anderson (1983)
A. tonsa	*Favella panamensis*	0.25–1.0	1575.0	4.44	Robertson (1983)
	Tintinnopsis tubulosa	0.25–2.0	140.4	3.96–12.0	Robertson (1983)
	Favella sp.	1.0–4.0	195	2.8	Stoecker & Sanders (1985)
	Strombidium sp.	3.8–4.1	16.3[b]	2.54–3.08	Stoecker & Egloff (1987)
	Strobilidium sp.	1.7	47.4[b]	1.92	Stoecker & Egloff (1987)
	Favella sp.	0.2–2.5	195	0.29–10.4	Stoecker & Egloff (1987)
	Tintinnopsis sp.	2.3–2.8	52.3[b]	1.21–2.79	Stoecker & Egloff (1987)
	Balanion sp.	5.0–4.6	9.5[b]	4.21–4.42	Stoecker & Egloff (1987)
	Natural assemblage	3.7–21.8	–	1–7	Gifford & Dagg (1988)
	Strobilidium spiralis	0.5–1.0	150	3.58[c]	Jonsson & Tiselius (1990)
	Strombidium reticulatum	2.0–4.0	16	1.96[c]	Jonsson & Tiselius (1990)
	Mesodinium rubrum	1.0–2.0	30	0.625[c]	Jonsson & Tiselius (1990)
	Ciliates >10 µm	3.36–20.36	–	1.1–1.0	Gifford & Dagg (1991)
(Nauplius–post naupliar)	Natural assemblage	0.40–30.3	–	0.03–0.97	Dolan (1991)
	S. sulcatum	25	14	~4[d]	Kiørboe et al. (1996)
Acartia spp.	Natural assemblage	~0.13–20	–	1.04–12.5[d]	Londsdale et al. (1996)
Calanus pacificus	Natural assemblage	4.81	–	12.6–32.4	Fessenden & Cowles (1994)
C. finmarchicus	Natural assemblage	2.4–11.0	–	7–24.5[d]	Ohman & Runge (1994)
	Ciliates >30 µm	–	–	20.8[c]	Nejstgaard et al. (1997)
	Ciliates <30 µm	–	–	7.5[c]	Nejstgaard et al. (1997)
C. simillimus (CIII–CVI)	Natural assemblage	5.5	1.4	0.78–3.55[d]	Atkinson (1996)
Centropages hamatus	Natural assemblage	1.73	–	0.46–0.81	Turner & Granéli (1992)
	Natural assemblage	0.20–0.80	–	1.35–5.21	Tiselius (1989)
C. abdominalis	Natural assemblage	1.2–1.7	–	1.2–7.1	Fessenden & Cowles (1994)
C. typicus	*S. sulcatum*	3.3	13.9	5.36–58.1	Wiadnyana & Rassoulzadegan (1989)
Eucalanus pileatus (CIII–CIV)	Natural assemblage	56.7	1.3	5.4	Verity & Paffenhofer (1996)
	Natural assemblage	41.7	2.4	5.3	Verity & Paffenhöfer (1996)
Neocalanus tonsus (CV)	Natural assemblage	5.5	1.4	4.58[d]	Atkinson (1996)
N. plumchrus	Ciliates >5 µm	1.06–2.59	–	15.6–39.0	Gifford & Dagg (1991)
Pseudocalanus sp.	Natural assemblage	7.37	–	4.8–7.4	Fessenden & Cowles (1994)
Temora longicornis	*S. acuminatum*	~14.6	72.03[a]	3.85	Hansen et al. (1996)
	S. elegans	~46.2	22.76[a]	1.38	Hansen et al. (1996)
Marine cyclopoid copepods					
Oithona spp. (CIV–CVI)	Natural assemblage	5.5	1.4	0.13[d]	Atkinson (1996)
Freshwater calanoid copepods					
Acanthodiaptomus denticornis	*Paramecium aurelia*	1.62–6.87	103.4	0.87–2.62	Hartmann et al. (1993)
	P. caudatum	1.84–9.18	154.8	1.29–2.93	Hartmann et al. (1993)
	Loxodes sp.	1.95	403.0	0.55–0.30	Hartmann et al. (1993)
Diaptomus pygmaeus (N5–N6)	*Strobilidium velox*	1.9–5.2	46	2.08–2.25[d]	Burns & Gilbert (1993)
	Strob. velox	5.2	46	0.25	Burns & Gilbert (1993)
(N5–N6)	*Strombidium* sp.	0.7	3.76[b]	0.55	Burns & Gilbert (1993)
Diaptomus minutus (N5–N6)	*Strob. velox*	0.7–5.2	46	0.5–2.38[d]	Burns & Gilbert (1993)
	Strob. velox	5.2	46	0.27	Burns & Gilbert (1993)
(N5–N6)	*Strombidium* sp.	0.7	3.76[b]	0.51	Burns & Gilbert (1993)
(CII–CIII)	*Strobilidium* sp. 1	0.6	2.63[b]	0.97	Burns & Gilbert (1993)
Epischura lacustris	*Strob. velox*	0.8–1.9	46	6.25–19.1[d]	Burns & Gilbert (1993)
Freshwater cyclopoid copepods					
Cyclops abyssorum	***Askenasia volvox***	2	–	1.25[cd]	Wickham (1995)
	Coleps hirtus	2	–	0.7[cd]	Wickham (1995)
	Halteria grandinella	5	–	0.20[cd]	Wickham (1995)
	Stokesia vernalis	2	–	0.8[cd]	Wickham (1995)
	Strob. velox	2	–	1.7[cd]	Wickham (1995)
C. kolensis	***A. volvox***	2	–	3.12[cd]	Wickham (1995)
	C. hirtus	2	–	0.55[cd]	Wickham (1995)
	H. grandinella	10	–	0.37[cd]	Wickham (1995)
	S. vernalis	2	–	20[cd]	Wickham (1995)
	Strob. velox	2	–	9[cd]	Wickham (1995)

[a]Estimated from linear dimensions; [b]calculated from carbon biomass; [c]maximal filtration rates; [d]data from a figure

should be noted that swimming with rapid jumps is not exclusively found among mixotrophic oligotrichs and that in general swimming speeds increase with cell size.

At present, while data on copepod grazing on heterotrophic ciliates is considerable, data on grazing on mixotrophic species is sparse, and largely consists of recent studies on freshwater forms. These studies have concerned cyclopoid copepods and grazing rates did not appear to markedly differ between mixotrophs and heterotrophs. Wickham (1995) reported maximum filtration rates by cyclopoid copepods on 2 freshwater mixotrophic ciliates (*Askenasia volvox* and *Stokesia vernalis*) intermediate to rates estimated for heterotrophic species in the same experiments. Similarly, the mixotrophic *Strombidium viridae* was grazed at intermediate rates, relative to those recorded based on the disappearance of heterotrophic ciliates, by *Diacyclops thomasi* (Dobberfuhl et al. 1997). The lack of distinct differences between capture rates may be due to the fact that cyclopoid copepods are exclusively raptorial feeders. Data for marine organisms appears to be limited to a single study and concerns the mixotrophic oligotrich *Strombidium reticulatum* (Table 4). The maximum filtration rate of *Acartia tonsa* estimated on this ciliate by Jonsson & Tiselius (1990) was about half the filtration rate on the heterotrophic ciliate used in the experiments but the heterotrophic ciliate was considerably larger

Although further investigation is clearly needed, our data suggests that copepod grazing may have a considerable effect on ciliate community composition (mixotrophy vs heterotrophy). However, the effect may be species specific and thus very difficult to predict. Copepod capture rates vary with the size and mobility of the prey, and these characteristics may vary inconsistently with the trophic type of ciliate. Furthermore, the relative importance of such differences in prey characteristics or qualities probably varies with the feeding strategy employed by the copepod, i.e. filter or raptorial feeding, which can in turn vary with abiotic factors such as turbulence in some species of copepod (e.g. Kiørboe et al. 1996).

Concerning the growth capacities of oligotrich ciliates, we expected a difference between heterotrophic and mixotrophic ciliates because one trophic type would be at a disadvantage under a given set of circumstances. However, roughly similar net growth rates were estimated for the similar-sized nanomixotroph and nanoheterotroph in our experiments. Another manner of investigating this question is to consider maximum growth rates. Mixotrophic oligotrichs may profit from both phagotrophy and photosynthesis to survive in food-poor conditions at the price of forsaking rapid growth under food-rich conditions.

To investigate this question we compared the maximum observed growth rates given in the literature for mixotrophic and heterotrophic oligotrich ciliates (Table 5, Fig. 4). We used multiple regression analysis where growth rate is a function of temperature and volume using a model of this type: $\ln \mu = a \ln T + b \ln V + c$ (Fenchel 1968, Finlay 1977, Montagnes et al. 1988, Müller & Geller 1993, Montagnes 1996). Results of the analysis are given in Table 6; for both mixotrophic and heterotrophic oligotrichs, maximum observed growth rates were highly correlated with temperature and relatively weakly with cell volume. We compared the multiple regression equations of heterotrophs and mixotrophs following Zar (1984). First, we tested if the 2 regression equations came from the same statistical population, and the *F*-test indicated that the regression equations differ significantly (F_{obs} = 4.58, $p < 0.01$, df 3,34). To determine the origin of these differences, we tested the parallelism of planes defined by the multiple regression coefficients *a* and *b* corresponding to the terms associated with temperature and cell volume; the *F*-test indicated insignificant differences (F_{obs} = 1.64, df 1,34). We then examined the differences in the *c* coefficient of hetero- and mixotrophs and the *F*-test of elevation was highly significant (F_{obs} = 12.2, p <

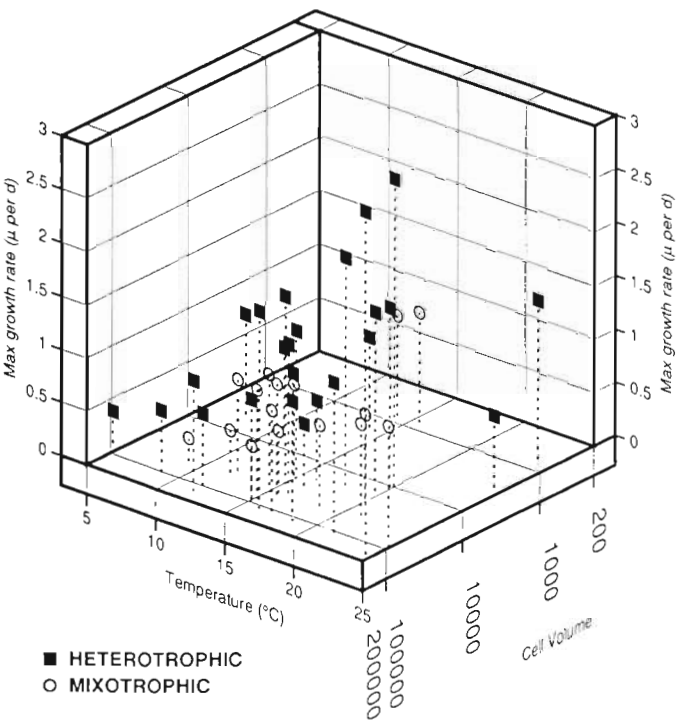

Fig. 4. Influence of temperature and cell volume on maximum observed growth rates of mixotrophs and heterotrophs. Data from Table 5

0.01, df 1,36), indicating that the elevations of planes, defined by coefficient *c*, are significantly different for mixotrophs and heterotrophs. Consequently, the effects of cell size and temperature are indistinguishable among mixotrophs and heterotrophs but lower maximum growth rates are predicted for mixotrophic oligotrichs.

The magnitude of the differences are shown in Fig. 5 in which maximum growth rates are plotted as a function of cell size at 15°C; regardless of cell volume, mixotrophs appear to have a maximum growth rate of about 0.5 generations d^{-1} less than similar-sized heterotrophic oligotrichs. Our analysis suggests that mixotrophic growth is inherently limited by their metabolism, although temperature and cell volume effects are exerted in the same way as in heterotrophic oligotrichs. Thus, the price of mixotrophy may be about 0.5 generations d^{-1} in food-rich conditions. This may explain the incomplete dominance of mixotrophs, especially in food-rich environments.

Table 5. Maximum observed growth rates (μ_{max}) of hetero- and mixotrophic oligotrichs from the literature. $\mu_{15°C}$: estimated maximum growth rate at 15°C using the multiple regression equations we established for hetero- and mixotrophic ciliates. Volume: live volume

Species	Volume (μm^3)	Temp. (°C)	μ_{max} (d^{-1})	$\mu_{15°C}$ (d^{-1})	Source	Location
Heterotrophic oligotrichs						
Halteria gradinella	17 736	20	1.73	1.20	Taylor (1978)	Ontario
L. spiralis	93 400[a]	18	1.06	1.05	Sheldon et al. (1986)	Mediterranean
L. spiralis	150 000	12	1.06	1.01	Jonsson (1986)	Laboratory
Strobilidium spiralis	11 494	20	1.7[b]	1.24	Verity (1991)	Laboratory
Strobilidium sp.	800[a]	24.3	1.55	1.54	Dolan (1991)	Chesapeake Bay
Strobilidium lacustris	113 000	5.5	0.43	1.03	Müller & Geller (1993)	Laboratory
	113 000	9	0.60	1.03		
	113 000	12	0.70	1.03		
	113 000	15.5	0.99	1.03		
	113 000	18.5	1.38	1.03		
	113 000	21.5	1.42	1.03		
Strobilidium neptuni	110 000	16	1.84	1.04	Montagnes (1996)	Laboratory
Strobilidium venilae	19 635	16	0.73	1.19	Montagnes (1996)	Laboratory
Strombidinopsis cheshiri	45 815	16	0.99	1.11	Montagnes et al. (1996)	Laboratory
Strombidium sp.	4 800[a]	10.2	0.75	1.33	Dolan (1991)	Chesapeake Bay
	4 800[a]	7.4	0.94	1.33		
Strombidium sp.	24 017	20	2.71	1.17	Ohman & Snyder (1991)	Laboratory
	24 017	15	1.38	1.17		
Strombidium sp. b	1 722	13.9	0.86	1.44	This study	Ligurian Sea
Strombidium B	–	–	1.2	–	Verity et al. (1993)	North Atlantic
S. acuminatum	393 300	25	0.74	0.77	Tumantseva & Kopylov (1985)	Peru
S. siculum	28 575	16	0.57	1.15	Montagnes (1996)	Laboratory
S. sulcatum	33 500	15	1.75	1.14	Rivier et al. (1985)	Laboratory
S. sulcatum	10 000	20	2.88	1.25	Fenchel & Jonsson (1988)	Laboratory
S. sulcatum	19 000	18	2.16	1.19	Allali et al. (1994)	Laboratory
Mixotrophic oligotrichs						
Laboea strobila	78 000	15	~1	0.72	Stoecker et al. (1988)	Laboratory
L. strobila	91 000	15	0.5	0.71	Putt & Stoecker (1989)	Laboratory
L. strobila	134 000[c]	17.4[b]	1.0[b]	0.69	Nielsen & Kiørboe (1994)	Kattegat
Pelagostrombidium fallax	50 000	9	0.21	0.74	Müller & Geller (1993)	Laboratory
	50 000	12	0.42	0.74		
	50 000	15.5	0.57	0.74		
	50 000	18.5	0.76	0.74		
	50 000	21.5	0.90	0.74		
Strombidium sp. a	740[a]	15.5	1.03	1.04	This study	Ligurian Sea
	740[a]	13.9	0.93	1.04		
Strombidium A	–	–	1.1	–	Verity et al. (1993)	North Atlantic
S. capitatum	54 199[c]	15	1.09	0.74	Stoecker & Silver (1990)	Laboratory
	64 140	16	1.07	0.73	Montagnes (1996)	Laboratory
S. conicum	92 800	25	1.13	0.71	Tumantseva & Kopylov (1985)	Laboratory
	25 550	15	0.88	0.79	Putt & Stoecker (1989)	Laboratory
S. oculatum	48 800[a]	–	0.65	–	Jonsson (1994)	St. Malo Bay
S. reticulatum	40 000	12	0.86	0.76	Jonsson (1986)	Laboratory
Tontonia gracillima	150 100	24.5	1.30	0.68	Tumantseva & Kopylov (1985)	Laboratory

[a]Volume estimated from reported linear dimensions and corrected from shrinkage following Ohman & Snyder (1991)
[b]Data from a figure; [c]Mean of several volumes reported for this species in the literature

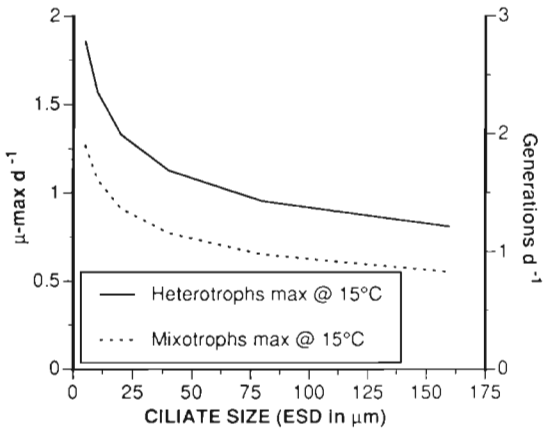

Fig. 5. Maximum growth rate (μ-max) of mixo- and heterotrophic ciliates calculated at 15°C as a function of cell size using the multiple regression equations shown in Table 6. Note that calculated maximum growth rates for mixotrophic oligotrichs are about 0.5 generations d^{-1} lower than those estimated for heterotrophic oligotrichs

Table 6. Multiple regression analysis of data presented in Table 5 and Fig. 4, using the model $\ln \mu = a \ln T + b \ln V + c$. n: number of data used. p: probability associated to constants a and b and to R^2 a and b coefficients for heterotrophs and mixotrophs were not significantly different: $F_{parallelism} = 1.64$ (df 1,34); but c coefficients were significantly different: $F_{elevation} = 12.2$ (df 1,36) $p < 0.01$

Group	n	R^2	a	b	c
Mixotrophs	16	0.58	1.4	−0.08	−3.22
p		0.0035	0.001	0.1552	
Heterotrophs	24	0.45	0.85	−0.08	−1.34
p		0.0018	0.0009	0.0984	
All groups	40	0.39	0.94	−0.08	−1.79
p		0.0001	0.0001	0.0639	

Acknowledgements. The work reported is part of the doctoral dissertation of M.T.P. We are indebted to V. Andersen for organising the DYNAPROC Cruise Program, P. Nival for supplying copepods, S. Nival for identifying copepods, F. Vidussi for generously providing chl *a* concentrations, L. Prieur and J. Raunet for providing CTD data, and the captain and crew of the 'Sûroit' for ship operations. Financial support was provided by the C.N.R.S., the Commission of the European Communities through the contract 'MEDEA' (MAS3 CT95-0016) and a Eusko Jaurlaritza (Basque government) grant to M.T.P. We are indebted to the reviewers of previous versions of this paper and Dr Stoecker; the manuscript was greatly improved as a result of their comments.

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Manuscript received: November 30, 1996
Revised version accepted: June 10, 1997