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Space and time distribution of zooplankton in a Mediterranean lagoon (Etang de Berre)

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Abstract

In the Berre lagoon, a large brackish and shallow area near Marseille, the environmental factors (temperature, salinity, oxygen, suspended particulate matter and chlorophyll) generally display strong space and time variations. The rotifer *Brachionus plicatilis* and the copepod *Acartia tonsa* constitute the bulk of the zooplankton population during all the year. Their space and time distributions were studied in 23 stations distributed all over the lagoon, during four seasonal cruises (February, June, October, November), at surface and bottom layers. There is no marked difference in the horizontal and vertical distribution of the two species, (except in November when rotifers were prevailing in surface and copepods at depth) and in their time occurrence. When the four series of data are pooled, correlation analysis show that *A. tonsa* is positively correlated with temperature, salinity and seston and negatively to oxygen and chlorophyll. *B. plicatilis* is positively correlated with temperature and seston, but also with chlorophyll, while salinity has a negative effect. The specific eggs number of both species is chlorophyll dependent. Considering seasonal cruises separately, some differences appear in the sense or the significance of these different correlations. The respective distribution of the two species is only partly dependent on the variation of the environmental factors: most of the variance remains unexplained, as indicated by the result of a stepwise multiple regression analysis using the most significant factors (temperature, salinity and oxygen explain 33 to 42% of the variance in *Acartia*, while temperature and salinity explain 27 to 28% of the variance in *Brachionus*). Thus, internal behavioral factors could also play a role in the distribution of organisms, particularly in some cases of aggregations of organisms observed during this study. As the two species occupied the same space habitat most of the year, they are potentially in competition for food. A way to optimize the food utilization could be the time separation of their feeding activity, nocturnal in *Acartia* and diurnal in *Brachionus*. Another way could be selective feeding upon food particles depending on their size (*Brachionus* being able to use finer particles than *Acartia*) or their quality (*Brachionus* being more herbivorous than *Acartia*) as demonstrated in some grazing experiments carried out in parallell.

Introduction

Coastal lagoons generally display large space and time variations of their physical and chemical characteristics (Amanieu & Lasserre, 1982). Due to their shallowness, there is little damping effect of the water column and atmospheric temperature variations are transmitted to the whole water mass. Moreover, the salinity mainly depends on the antagonistic effect of the fresh water inflow by the rivers and evaporation, both highly time variable factors. These effects are magnified by the confined character of most of these ecosystems (Guelorget & Perthuisot, 1983).

In many cases, high phytoplankton biomass results from the eutrophic conditions created by the richness of nutrients from land run off. Zooplankton is also abundant, but its diversity is generally reduced due to contrasted ecological conditions, with only the most tolerant species surviving. This leads to simplified zooplankton assemblages which contain few species (Arfi *et al.*, 1990; Gaudy, 1984).

Among the most representative zooplanktonic lagoonal species, the estuarine copepods *Acartia* and the rotifer *Brachionus* are frequently observed (Jeffries, 1962; Castel & Courties, 1982; Arfi *et al.*, 1987). In the Berre lagoon, a large brackish semi-closed and shallow area near Marseille, zooplankton are dominated by *Acartia tonsa*, a species recently introduced in the Mediterranean basin where it is restricted only to this type of environment (Gaudy & Vinas, 1985), and by *Brachionus plicatilis*. As both species can potentially produce large populations, the problem is to examine if they occup different time or space ecological niches, of if they cohabit and thus eventually have to compete for food.

The adopted strategy to answer this question was to study, during four seasonal cruises (temporal variation), the distribution of the main zooplankton organisms, according to the environmental factors, in surface and near the bottom (vertical variation), at 24 stations located on the surface of the investigated area (horizontal variation).

Description of the site

The Berre lagoon is a large (155 km^2) and shallow (7 m average depth) semi-closed basin which communicates with the Mediterranean through the canal of Caronte in the south and receives freshwater mainly in its northern part, via the canal of Saint-Chamas power plant (deviation of the Durance river) and three small rivers (Fig. 1). The Saint-Chamas canal represents the main freshwater input (2 to 4 10^9 m^3 y^{-1}), which varies seasonally according to energy demand. Maximum inflows occur from November to June and minimum from July to October (Arfi, 1989). Because of these hydrological features, important salinity variations are noted, and stratification occurs seasonally, particularly in the southern part where marine waters are introduced in the bottom.

Material and methods

Samples were collected from 23 stations (Fig. 1) during daytime at four outings: 27–28 February, 15–16 June, 25–26 October and 28–29 November 1985. At each station, horizontal samples were taken from the surface and the deeper layer, about one meter from the bottom. Zooplankton were collected with a Clarke Bumpus type net (80 μm); temperature, salinity (salinograph YTECH), dissolved oxygen (polarographic probe), chlorophyll-a concentration (fluorimetric method) and seston (dry weight) were measured at the two levels. For each sample we determined: the number of individuals per cubic meter of the different zooplanktonic organisms (*Acartia tonsa* Dana, *Brachionus plicatilis* O. F. Muller, *Balanus* nauplii, *Podon polyphemoides* Leuckart, a few copepods species other than *Acartia tonsa*, and Polychaete larvae). In this work, we analyzed only *Acartia tonsa* and *Brachionus plicatilis* data, because these two species were clearly dominant. For the copepod *Acartia tonsa*, we measured total abundance, and also the number of eggs, nauplii, copepodites and adults males or females, and we calculated the eggs/female ratio. For the rotifer *Brachionus plicatilis* we counted the individuals and the eggs and also calculated the eggs/individual ratio.

For each series of samples, statistical analysis was performed on surface, deep water and both levels considered together. Comparison of abundance was made between the two water layers for each cruise and also for total of the four outings, using the Mann and Whitney non parametric method, because the distribution of samples was not normal. Correlations between zooplankton total, *Acartia tonsa*: (eggs, nauplii, copepodites, females, males, eggs/female) and *Brachionus plicatilis*: (individuals, eggs, eggs/individual) and environmental factors (temperature, salinity, oxygen,chlorophyll, seston) were calculated by using the Sperman non-parametric method (non-normal distribution). Multiple linear regression using the Stepwise variable selection procedure was also used to examine the relationship between zooplankton and one or more environment variables. This method allows to use a forward selection procedure for controlling the input of variable into the model. This model was linear, according to the following equation: $Z = a_0 + a_1 (^\circ C) + a_2(S‰) + a_3 (O_2) + a_4 (\text{Chlorophyll}) + a_5 (\text{seston})$. This method was only used in cases where significant correlations between zooplankton and environmental parameters were obtained.

Results

Distribution of environmental parameters

As a north–south gradient of most parameters was expected from the location of the main freshwater

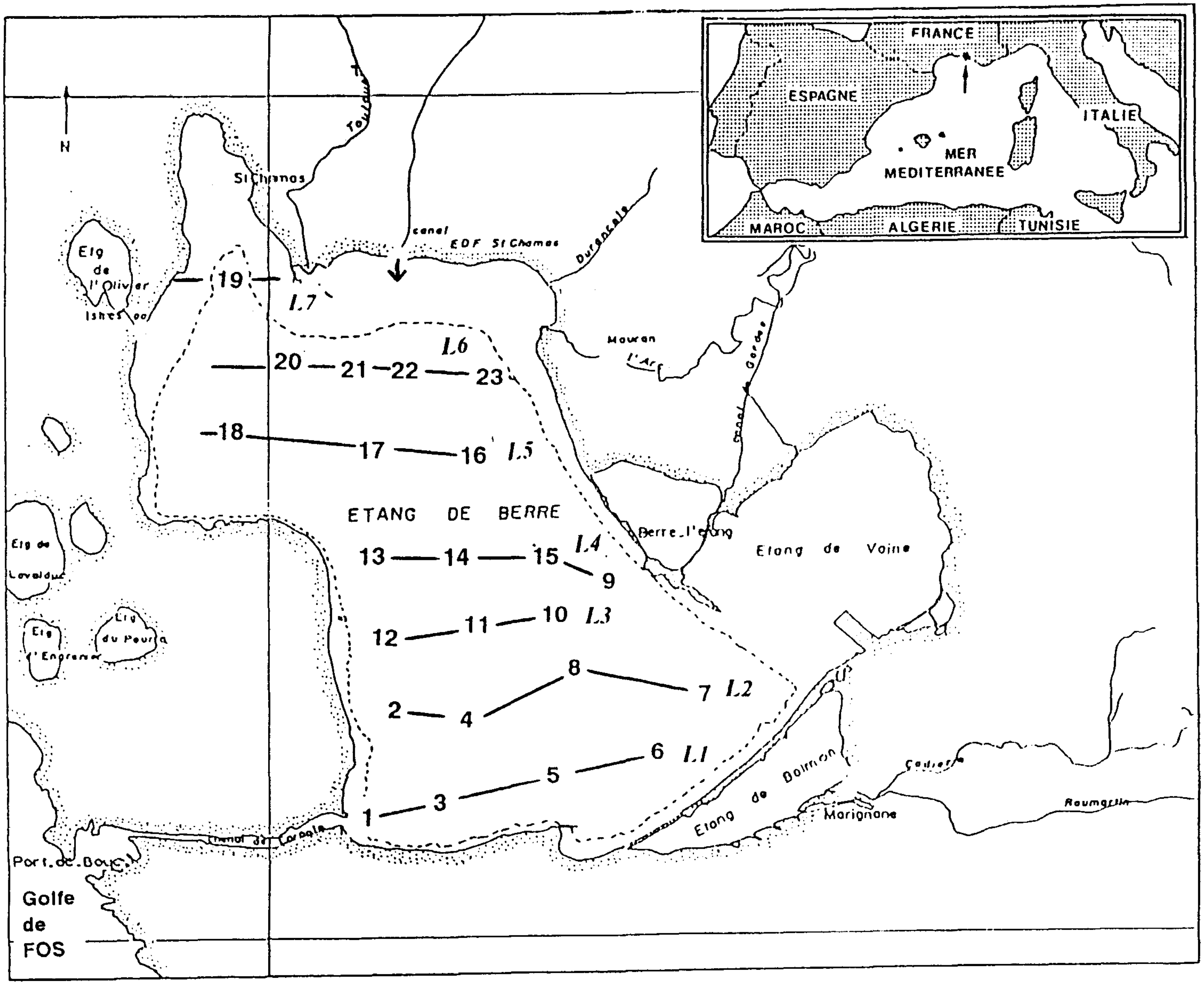


Fig. 1. Map of the Etang de Berre and position of the sampling stations (numbers), grouped according to latitudinal lines (1 to 7).

(North) and marine (South) influences, values obtained in stations located on each of the 7 latitudinally espaced west-east lines were averaged to allow a clearer graphic representation of the results (Fig. 2). Temperature was relatively homogeneous, with slight gradients caused by the difference of temperature of incoming marine or fresh water. Salinity generally showed highest values in the south, mainly in depth where marine water, introduced via the Caronte canal accumulated. At this level, strong south-north gradients appeared in February and June. In October, surface waters were homogeneous because the power plant did not operate during summer, and, consequently, little or no freshwater was introduced. The gradient observed in deep water corresponded to the accumulation of marine water coming from the south instead of the north fresh water influence. In November, saline water was still accumulated at depth, but surface water showed a salinity gradient caused by the operating of the plant.

Oxygen values were generally stable in surface, without a marked gradient, but in October a minimum was noted at lines 2 and 3. In depth, low concentrations were found at the south (line 6), and a NS gradient was noted. November conditions were different because no low values were found.

Chlorophyll concentration depended greatly on season, with high values in February and low values in November. Its space distribution was irregular, for example in February, a minimum was noted in the surface at line 3 while a maximum was observed at the same line in the surface. In June a gradient was observed at depth, an inverse relationship with salinity, but not in the surface. In October, a similar gradient was noted in the surface, but with depth, minimal values were observed at intermediate NS position as for oxygen. In November, the maximum was noted in the middle of the lagoon at the surface, and an isolated peak appeared at depth, in the southern part of the lagoon.

The highest values of seston were found in the southern part, at depth, while, in the surface, the gradient was less marked (February, October) or absent (June, November).

Spatial and seasonal variations of zooplankton abundance

Figure 3 show the horizontal distribution of *Acartia* and *Brachionus* in surface and at depth, for the four cruises. It can be observed that both species were present all over the lagoon, with an abundance variable according to the different stations. Their abundance showed a tendency to increase towards the North in June, but no clear distribution pattern was observed for other cruises. Some cases of patchy distribution appeared in October and November, the organisms of one or both species being considerably more abundant in some stations in comparison with adjacent ones.

Maximum density of zooplankton was found in June (103 ind.l^{-1} mean for the two levels) and minimum, in November (19 ind. l^{-1}). In February, the deep value greatly exceeded the surface one. Rotifers were minimum in October and maximum in June. They were generally the most numerous zooplankter, except in October when *Acartia tonsa* exceeded their abundance.

Comparison of the abundance of organisms between surface and bottom

For total zooplankton, no difference was observed when the four set of data were considered together. For seasonal samples (Table 1), a significant difference was noted only in February with more individuals in the bottom (most of them being rotifers).

For *Acartia tonsa*, females, males, copepodites nauplii and eggs were more abundant in the deep layer when considering the total data, and also for November samples. No differences were found in other cases except for males which were more numerous in depth in June. Females were absent in February.

For *Brachionus plicatilis*, no significant difference in their vertical distribution was found when all data or June and October samples were considered, but a difference was noted in February (more animals in the bottom) and in November (more animals in the surface).

Correlation between organisms

Table 2 shows that *Brachionus* and *Acartia* (at different ages or sexes) were positively correlated when the data of the four cruises were considered. For seasonal data, all significant correlations were also positive, but *Brachionus* was only correlated with *Acartia* nauplii in February and with copepodites in June and October. Thus, in most cases, direct competition between these organisms could be expected.

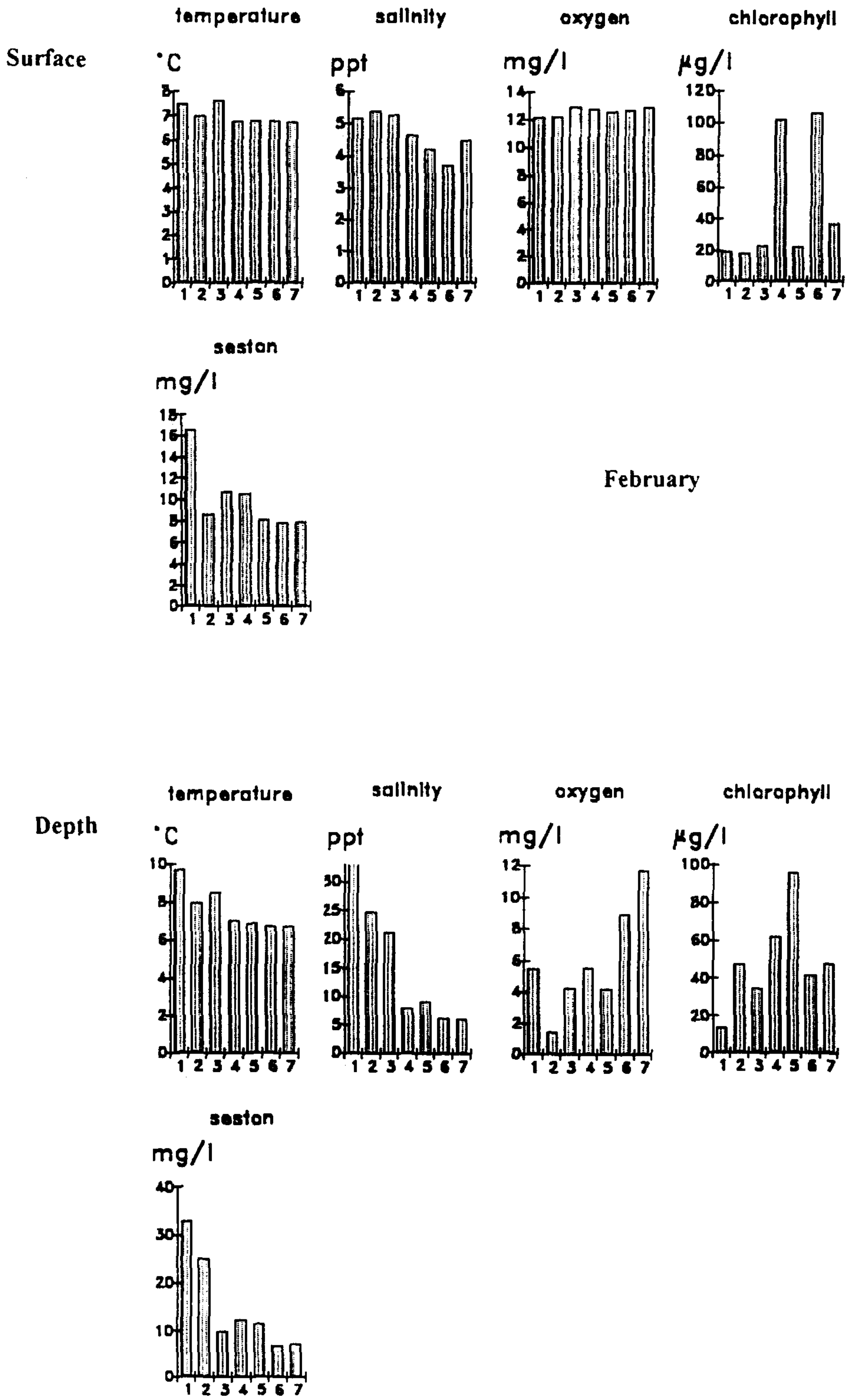


Fig. 2 A. Distribution of temperature, salinity, oxygen, chlorophyll and seston values according to latitudinal lines (1 to 7), at surface and at depth, for the four seasonal cruises (February, June, October, November).

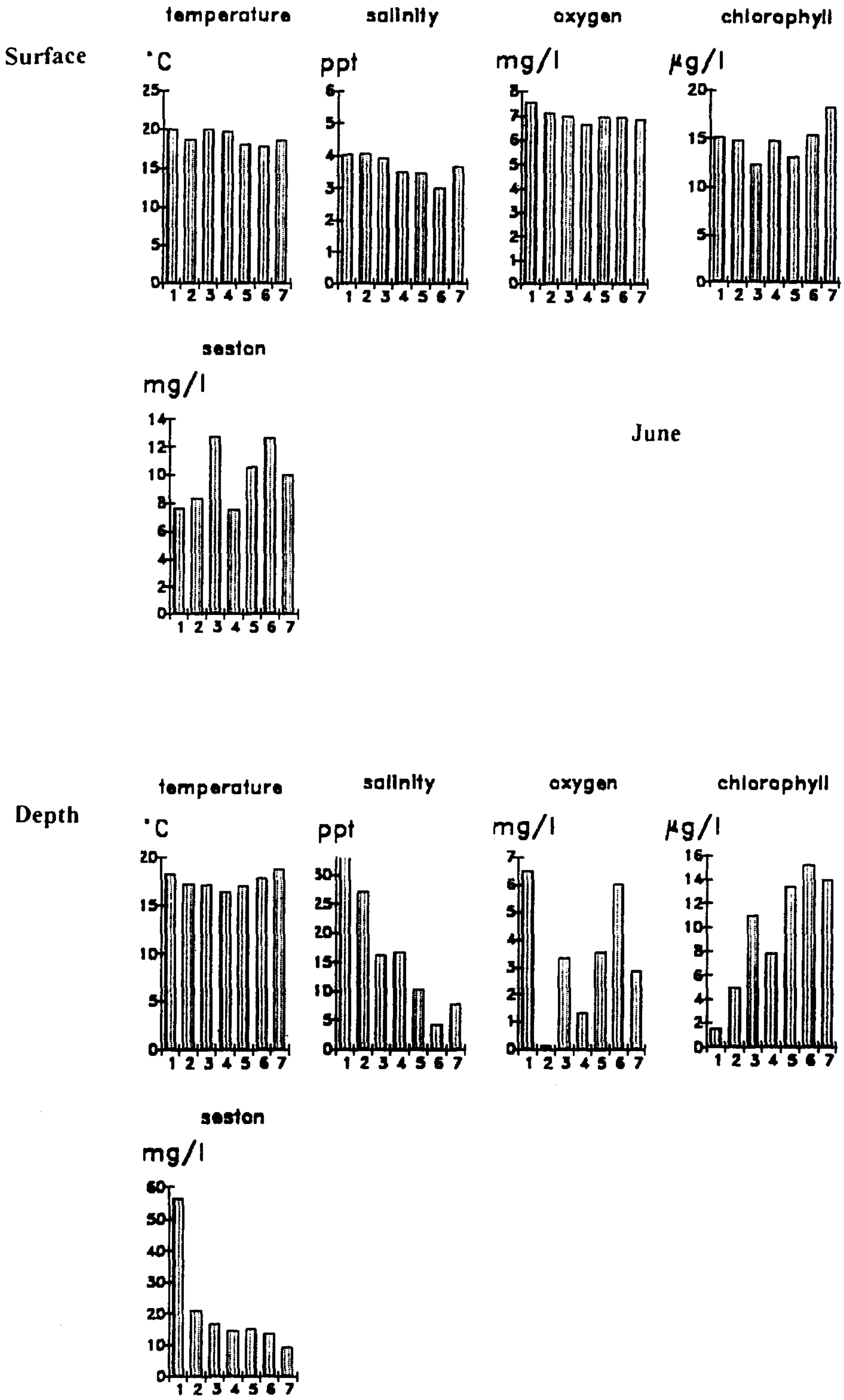

Surface
temperature
°C
salinity
ppt
oxygen
mg/l
chlorophyll
µg/l
seston
mg/l
June
Depth
temperature
°C
salinity
ppt
oxygen
mg/l
chlorophyll
µg/l
seston
mg/l
1 2 3 4 5 6 7

Fig. 2 B.

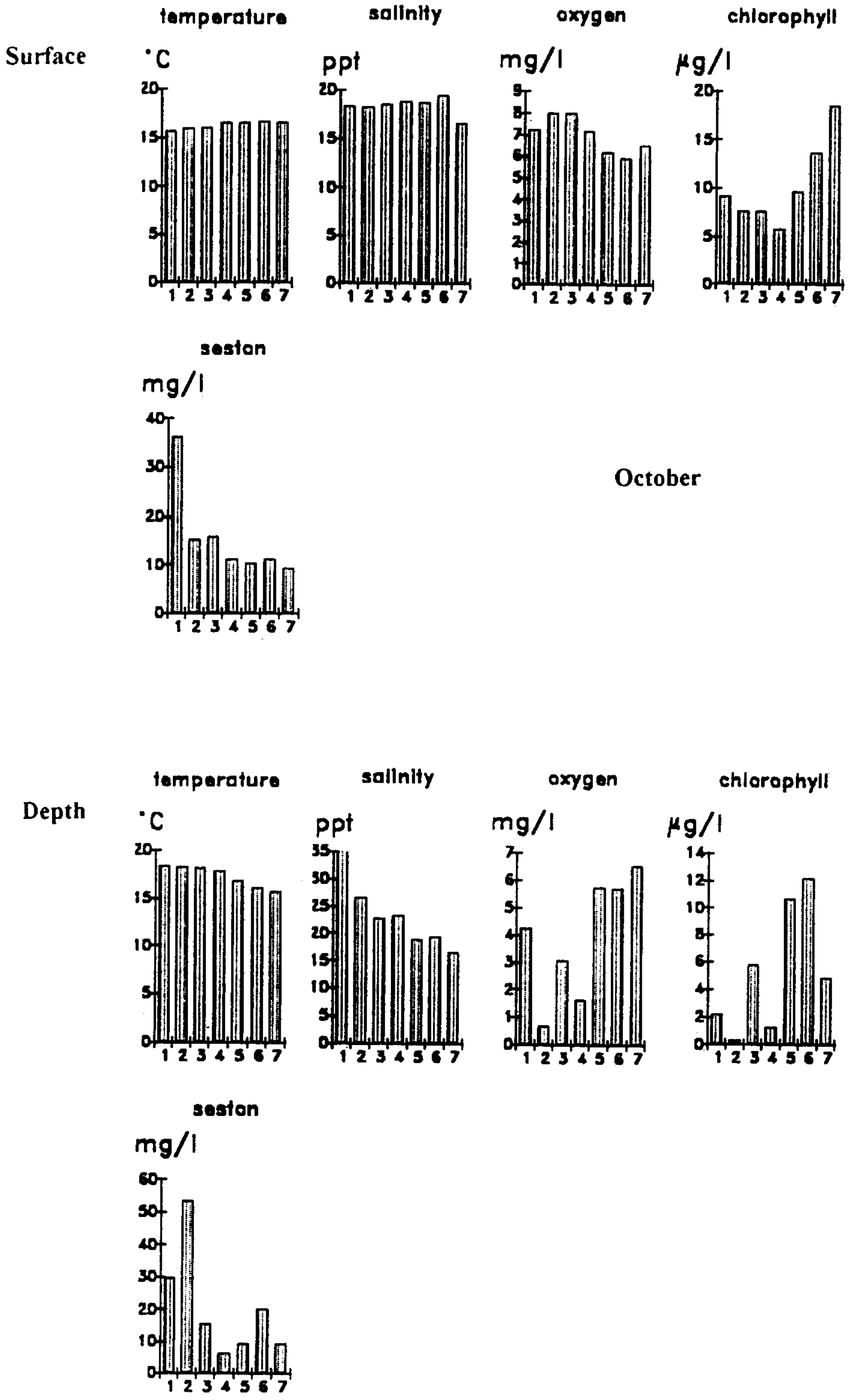
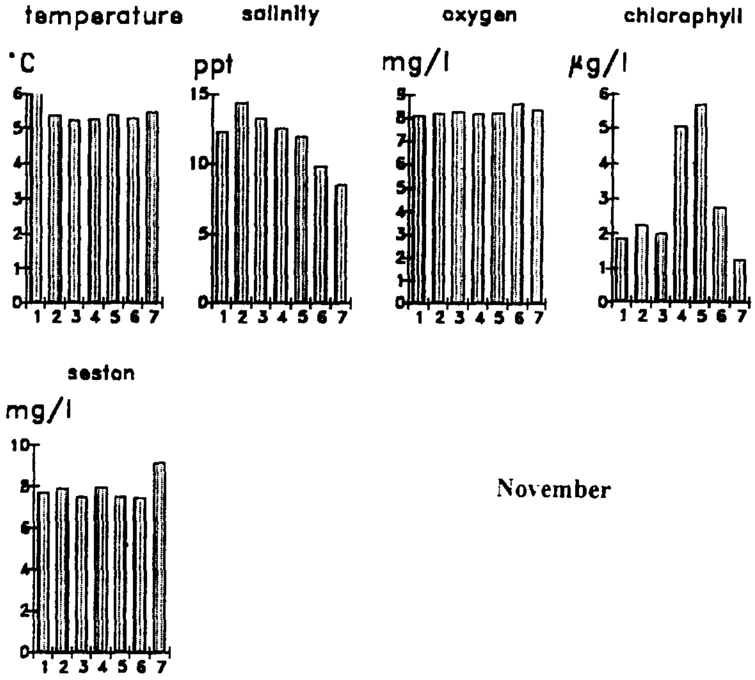

Surface
temperature
°C
0 5 10 15 20
salinity
ppt
0 5 10 15 20
oxygen
mg/l
0 1 2 3 4 5 6 7 8 9
chlorophyll
µg/l
0 5 10 15 20
seston
mg/l
0 10 20 30 40
1 2 3 4 5 6 7
October
Depth
temperature
°C
0 5 10 15 20
salinity
ppt
0 5 10 15 20 25 30 35
oxygen
mg/l
0 1 2 3 4 5 6 7
chlorophyll
µg/l
0 2 4 6 8 10 12 14
seston
mg/l
0 10 20 30 40 50 60
1 2 3 4 5 6 7

Fig. 2 C.

Surface



Depth

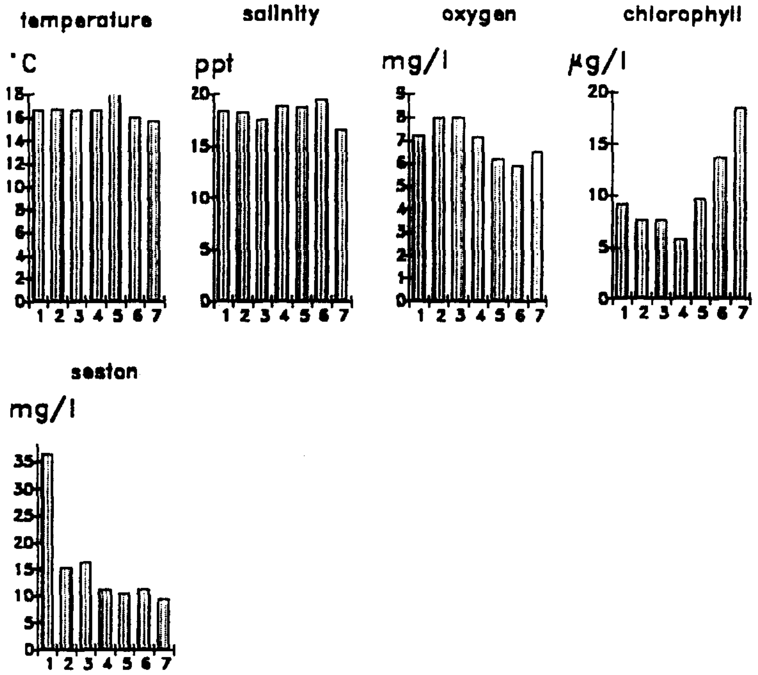


Fig. 2 D.

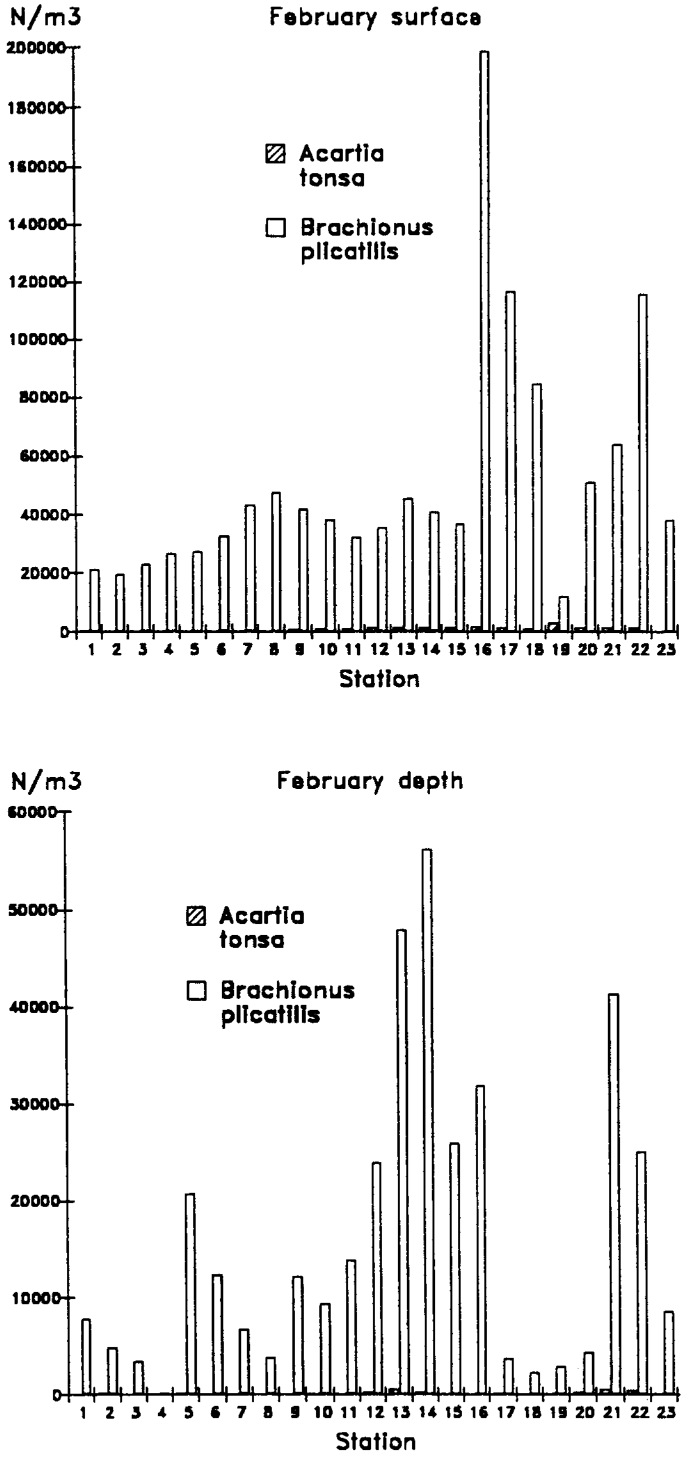


Fig. 3 A. Distribution of abundance values of *Acartia tonsa* (dark columns) and *Brachionus plicatilis* (white columns) at the different stations, at surface and at depth, for the four seasonal cruises (February, June, October, November).

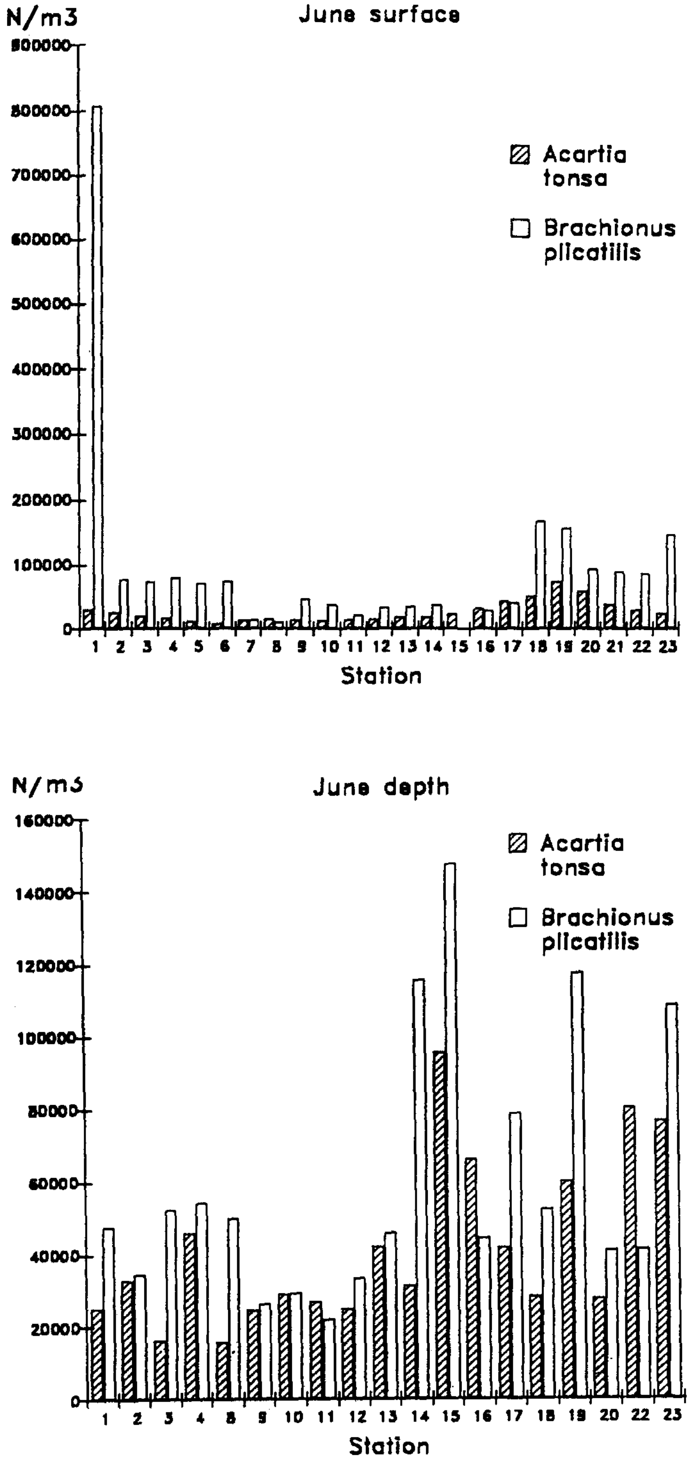

N/m3
June surface
900000
800000
700000
600000
500000
400000
300000
200000
100000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Station
N/m3
June depth
160000
140000
120000
100000
80000
60000
40000
20000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 8 9 10 11 12 13 14 15 16 17 18 19 20 22 23
Station

Fig. 3 B.

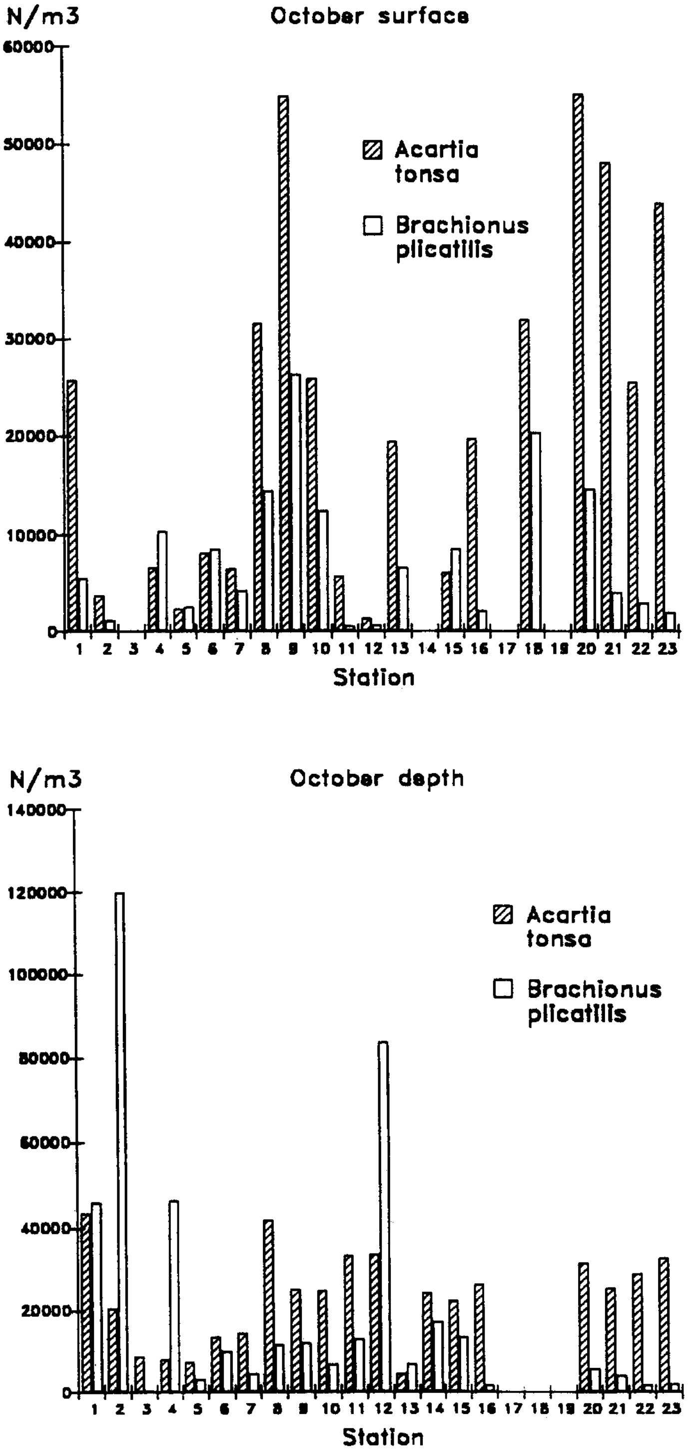

N/m3
October surface
60000
50000
40000
30000
20000
10000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Station
N/m3
October depth
140000
120000
100000
80000
60000
40000
20000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Station

Fig. 3 C.

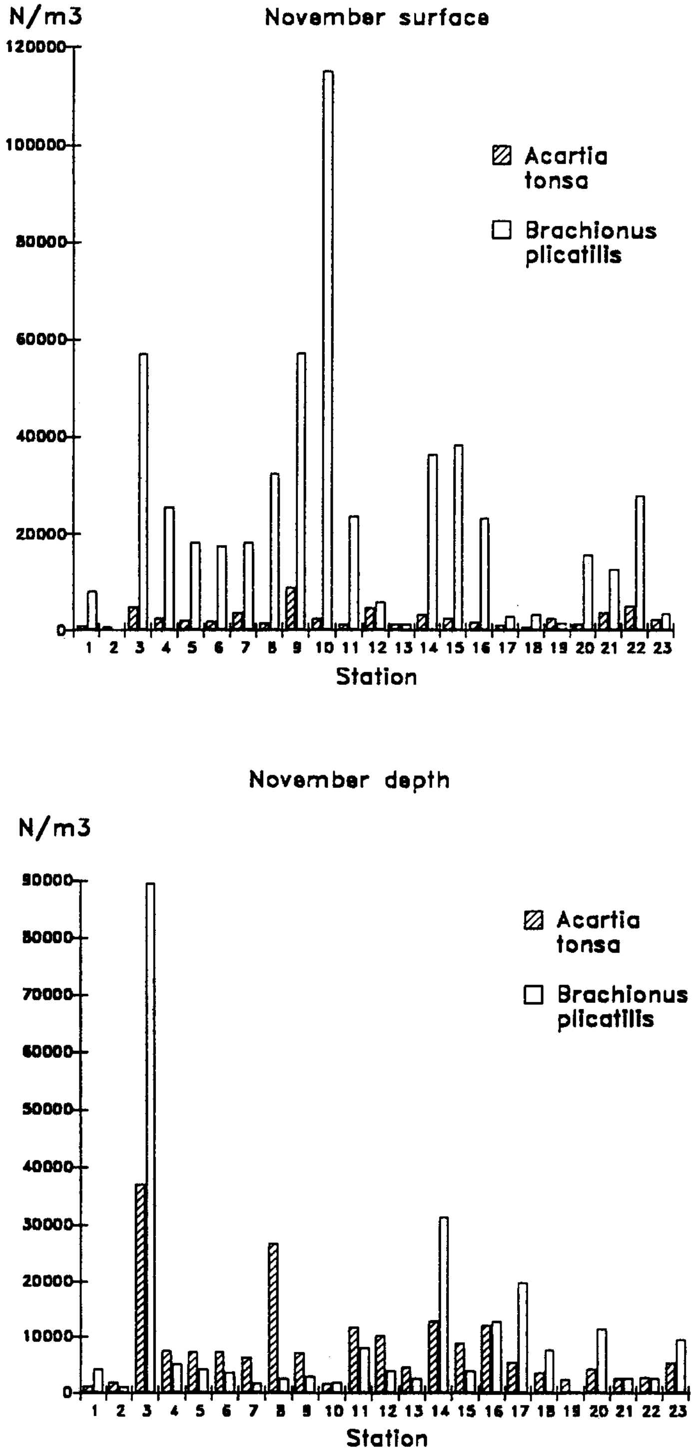

N/m3
November surface
120000
100000
80000
60000
40000
20000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Station
November depth
N/m3
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
▨ Acartia tonsa
☐ Brachionus plicatilis
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Station

Fig. 3 D.

Table 1. Abundance (ind. m^3) of *Acartia tonsa* and *Brachiomas plicatilis* in surface and at depth; mean of 23 stations +/- sd; value of *Z* (Mann & Whitney): ns = non significant. * = significant (0.05), ** = highly significant (0.01).

	Surface	Depth	*Z*	Surface	Depth	*Z*
	February			June		
Acartia tonsa						
Females	0	0		1809±1823	1973±1767	0.48ns
Males	0.38±0.65	46.68±149	0.55ns	163.8±169.6	1042±1072	4.2**
Copepodites	1.46±3.63	4.45±6.42	1.19ns	8942±7385	11270±8254	0.52ns
Nauplii	178±185	1652±859	4.08**	11621±9509	17982±12518	1.46ns
Eggs	68.2±64.5	32.5±34.8	4.6ns	8440±4148	11001±6489	1.11ns
Brachiomus plicatilis						
Individuals	12464±12274	62900±37087	3.64**	89774±72972	64098±38581	−1.5ns
Eggs	4544±4620	26880±17564	3.73**	72972±37322	60664±36925	−1.3ns
	October			November		
Acartia tonsa						
Females	22716±0075	1452±2330	−1.9ns	400.8±447.8	837.1±844	2.88**
Males	833±926	964±1319	0.09ns	198±227	855.5±945	3.9**
Copepodites	4458±3856	5838±4560	1.09ns	406.5±368.6	1022.6±896	3.18**
Nauplii	11462±7243	11029±9407	−0.5ns	607.8±711.6	2594±3626	3.92**
Eggs	4026±3637	3711±3613	−0.4ns	1166±695	2697±2930	2.4**
Brachiomus plicatilis						
Individuals	18694±30089	7521±6982	0.69ns	14999±15898	6026±11846	−2.99**
Eggs	190.7±262.6	97.6±119.4	−1.1ns	9306±10467	3528±6288	−1.65**

Table 2. Results of the correlations analysis between the number of individuals of *Acartia tonsa* and *Brachionus plicatilis* in the 23 sampling stations; ns = non significant; * = significant (0.05); ** = highly significant (0.01)

		Acartia tonsa					
		Surface		Depth		Both strata	
		Copepodites + adults	Nauplii	Copepodites + adults	Nauplii	Copepodites + adults	Nauplii
Brachionus plicatilis	February	ns	+**	ns	ns	ns	+**
	June	+*	ns	ns	ns	+*	ns
	October	ns	ns	+*	ns	+*	ns
	November	+*	+**	+*	+**	ns	ns
	Total data	+**	+**	+*	+**	+**	+**

Correlation with environmental parameters

Most correlations were observed when total data was examined; out of 780 correlations tested, 111 were statistically significant. When seasonal data were considered, only 37 significant correlations were observed in October, 28 in November, 27 in June and 22 in February. This results from the decrease of the number of data and of the narrower range of several parameters, such as temperature and salinity.

Table 3. Results of correlation analysis between zooplankton parameters (abundance, eggs per female ratio) and environmental factors (temperature, salinity, oxygen, chlorophyll-*a* and seston): only significant (*, P=0.05) and highly significant (**, P=0.01) results are indicated

	Surface					Depth					Both strata				
	temp.	salin.	oxyg.	chl-*a*	sest.	temp.	salin.	oxyg.	chl-*a*	sest.	temp.	salin.	oxyg.	chl-*a*	sest.
Zooplankton total															
Feb.			+*	+*								+*		+**	
June															
Oct.		-*									-*	-*	-*		
Nov.		+*								-**					
Total data	+**		+**			+**	-*	-*	+**	-**	-**		-**	+**	+*
Brachionus plicatilis															
Feb.			+*	+**	+**							+**		+**	
June															
Oct.		-**	-**								-*	+*			
Nov.											-*				
Total data	+*	-**				-*	-*	+*	-*	-*	-**	-**		+**	+**
Brachionus eggs															
Feb.			+*	+**	+**							+*		+**	
June															
Oct.		-**	-**									-*	+*		
Nov.		+*										-*			
Total data		-**	+*		+**		-**		+**			-**		+**	
Brachionus eggs/individual															
Feb.															
June															
Oct.															
Nov.															
Total data		-**					-**		+**			-**			
Acartia tonsa females															
Feb.															
June															
Oct.															+*
Nov.	-*	+*		+**								+*		+*	
Total data	+**	+**	-**	-**	-**		-**				+**	-**	-**	-**	+**
Acartia tonsa males															
Feb.															
June											+**	-**	-**	-**	+*
Oct.															
Nov.				+*								-**	-**	+*	
Total data	+*	+**	-**	-**						+**	-**	-**	-**	+**	

Examining total data (Table 3), zooplankton was positively correlated with temperature, chlorophyll and seston (except for surface for this latter parameter). Negative correlation was found with oxygen and salinity (only in deep water).

In seasonal samples, no correlation appeared in June, or in deep water for other cruises. Seston had

Table 3 cont..

	Surface					Depth					Both strata				
	temp.	salin.	oxyg.	chl-*a*	sest.	temp.	salin.	oxyg.	chl-*a*	sest.	temp.	salin.	oxyg.	chl-*a*	sest.
Acartia tonsa copepodites															
Feb.															
June	-*						-*		+*	-*					-*
Oct.															
Nov.											-*				
Total data	+**	+*	-**		-**	+**		-**		+**	+**	-**	-**		+**
Acartia tonsa nauplii															
Feb.		+**										+*	+*	+*	
June		-**													
Oct.						-*	-*		+*		-**			+*	
Nov.															
Total data	+**	+**	-**		+**	+**		-**		+**	+**	-**	-**		+**
Acartia tonsa eggs															
Feb.												-*	+*		
June	-**				-**						-*		-*		
Oct.				+*			-*				-*			+*	
Nov.												+*			
Total data	+**	+**	-**		+**	+**		-**		+**	+**	+**	-**		+**
Acartia tonsa eggs/females															
Feb.															
June															
Oct.				+*		-*		+*						+*	
Nov.															
Total data		-*							+**	+*				+*	

Table 4. Parameters of the multiple regression equation Z = a_0 + a_1+a_2+a_3+a_4+a_5 and value of the coefficient of determination (R^2) for the four cruises, at different depth levels

Organisms	Depth	R^2	Constante (a_0)	Temperature (a_1)	Salinity (a_2)	Oxygen (a_3)	Chlorophyll (a_4)	Seston (a_5)
Brachionus plicatilis								
Individuals	Surface	0.28	16390	3010	−2305			
Individuals	Bottom	0.41	66769	ns	−2322	−4359	566	ns
Individuals	Both levels	0.27	11888	2951	−1871		ns	ns
Eggs	Surface	0.53	134812		−4016	−8659		ns
Acartia tonsa								
Eggs	Both levels	0.33	7314	329	−194	−671		ns
Nauplii	Both levels	0.36	4478	867	−231	−617		ns
Copepodites	Both levels	0.36	5411	472	−224	−587		ns
Copepodites	Surface	0.12	7572	359	−262	−727		ns
Adult males	Surface	0.29	−248	ns	31.8	ns		16

no effect. Correlations with temperature were noted only in October and November when considering both levels together. The effect of salinity was positive in February and negative in October. Positive effect of chlorophyll was noted only in February.

For *Acartia* females, considering total data, positive correlation with temperature, salinity and seston and negative ones with oxygen and chlorophyll were noted. The same relationships were observed in copepodites nauplii and eggs, except that a non-significant correlation was found with chlorophyll. The eggs/female ratio was correlated with seston and/or chlorophyll depending on the water layer. When considering separately the different seasons, in females no correlation was found in deep water and only a few correlations appeared in other cases. In larval stages and eggs most relations were not significant.

In *Brachionus*, considering all data, the main difference with *Acartia* was the positive correlation with chlorophyll. The negative one with salinity and the absence of a correlation with oxygen, but a positive correlation with temperature and seston were found as in *Acartia*. The same relationships were observed for *Brachionus* eggs. Seasonal data did not show any significant correlations with depth. In the surface positive correlations with oxygen in February, and negative ones in October were noted. For the eggs/individual ratio correlations appeared only when all data were considered. The egg ratio was negatively correlated with salinity and positively with chlorophyll, but for this latter only in deep water. Seston had no effect.

Multiple regression between abundance and environmental factors

Table 4 shows the results obtained using the stepwise method. When considering the total data the number of eggs, nauplii and copepodites of *Acartia tonsa* were directly related to temperature and inversely to salinity and oxygen, with these factors explaning 33 to 42% of the variance. For *Brachionus plicatilis*, considering total data or surface data, the model was directly related to temperature and inversely to salinity (as for *Acartia*), the joint effect of environmental factors explaining only 27 to 28% of the variance. When only deep water values were selected, the model was inversely related to salinity and oxygen and directly to chlorophyll instead of temperature, a large part of the variance (41%) being explained by these factors. Significant multiple regression with *Brachionus* eggs were found only in the surface, where negative relationships with salinity and oxygen explained 53% of the total variance found.

Discussion

Acartia tonsa and *Brachionus plicatilis*, which constitute almost the total zooplankton assemblage are known for their high degree of tolerance to the fluctuating physical and chemical conditions of their habitat. Both are positively correlated to temperature, in accordance to many observations on their thermophilic character. In temperate areas *A. tonsa* is absent or scarce during the cold season and reaches its maximum abundance when temperature is high (Conover, 1956; Lee & McAlice, 1979; Jeffries 1962) while, in tropical areas, it generally occurs all year (Woodmansee, 1958). Laboratory experiments show that its upper thermal tolerance exceed the value found in the congeneric species *A. clausi* (Gonzalez, 1974). *B. plicatilis* is also generally considered as thermophilic (Pascual & Yufera, 1983), with significant reproduction in nature only when temperature is above 10–15 °C (Arndt, 1988). This is demonstrated also in laboratory cultures (Blanchot & Pourriot, 1982). Pascal & Yufera (1983) showed that a spanish strain of this species attained maximum densities and yields at 30 and 35 °C demonstrating the adaptability of this organisms to tropical environments. In the case of the Berre lagoon, both species occur all the year, even when temperatures are low.

Although both species cohabit and react similarly of temperature variations, their relative abundance can depend on their different reactions to variations of salinity and oxygen. *Acartia* is possitively correlated to salinity, contrary to *Brachionus*. The preference of *B. plicatilis* for low salinities is observed in nature (Arndt, 1988) and under experimental conditions (Pascual & Yufera, 1983). The abundance of *Brachionus* in Berre lagoon increased steadly in June towards the north, according to south–north decreasing salinity gradient, but no special trend of distribution was noted in October despite the existence of a similar gradient. The horizontal distribution of *Acartia* seemed not affected by the existence of salinity gradients. As for *Brachionus*, the individuals can be very abundant at some stations independently of salinity conditions. This type of patchy distribution could result more from behavi- oural response than from external factors (Omori & Hamner, 1982). High salinity water from the southern part of the lagoon at depth, corresponded to low concentrations of oxygen. The negative correlation of *Acartia* with oxygen shows the good adaptation of this species to low oxygen concentrations which often characterize its habitat (Vargo & Sastry, 1977). These authors have demonstrated the high degree of tolerance of *A. tonsa* to para-anoxic conditions.

The strong positive correlation with seston found with *Acartia tonsa* could be due to its ability to use seston as a food source independently of its chlorophyll content. Gaudy (1989) demonstrated that in Berre Lagoon the metabolic budget of *A. tonsa* allowed an efficient production of organic matter (growth and reproduction) only when high concentration of particulate matter was present. The omnivorous regime of *A. tonsa* is well documented. This species is able to use efficiently, beside phytoplankton, many other food source such as detritus or protozoans (Roman, 1972; Robertson, 1983; White & Roman, 1992). The absence or a negative correlation with phytoplankton can be explained if it is considered that algae constitutes only a part of the usual food of *A. tonsa*. *Brachionus* was also correlated but less significantly to seston concentration. Konnur et Azaziah (1987) also observed a positive correlation between *Brachionus* and seston in an Indian estuarine region, but found that very high concentration of suspended particulate matter brought about a reduction of the biomass of the rotifer. Contrary to *Acartia*, *Brachionus*, which is strongly positively correlated to chlorophyll, must depend more narrowly on phytoplankton for its food, as demonstrated in many aquaculture production experiments (Hirayama & Funamoto, 1983).

The abundance of both zooplankters also depends on the success of their reproduction process. The specific eggs abundance appears to be chlorophyll dependant in *Brachionus* and also for *Acartia*, despite the absent or negative correlation found with chlorophyll in the swimming stages. Thus, in last species general nutritional needs can be supported by a large variety of food, but egg production seems favoured by a plant diet, in accordance with the experimental studies of Cahoon (1981) and Durbin *et al.* (1983). The absence of a clear spatial separation of the habitat of the two species observed in their horizontal distribution was also found in the water column, both species did not show special preference for a given depth in October and June, but in February while *Acartia* was equally distributed in the water column *Brachionus* was more abundant at the bottom. This could be the result of the avoidance of the colder surface water by rotifers during the period of the temperature minimum. A clearer difference in the vertical distribution of the two species was noted in November when *Acartia* dominated at depth while *Brachionus* was more abundant in the surface. The distribution of *Brachionus* could reflect the less saline and slightly richer chlorophyll conditions prevailing in surface water during this oligotrophic period. The greatest abundance of *Acartia* found with depth in November could be the consequence of vertical migration, with a deeper distribution during the day (Stearns & Forward, 1984), but it remains unclear why no significant difference was found for other months. Moreover, in June adult males were more abundant in depth while females, copepodites and nauplii were evenly distributed. These results illustrate the complexity of the mechanisms acting on diurnal migration of *Acartia tonsa*, including the effect of physical and chemical factors, but also the different behaviour of males and females as experimentally noted by Patriti (1992) for *A. tonsa* from the same area. Because of the multiplicity of external and intrinsic factors acting together on the distribution of the lagoonal zooplankton, the multiple regression equations, which are based on a limited number of identified factors, are unable to explain a large part of the observed variations.

Due to their simultaneous presence in the same environment, *Acartia* and *Brachionus* are potentially in competition for food, mainly when the food resource is poor or low. Horizontal and vertical differences in their abundance are generally slight, and the separation of the two species is never complete. A different timing in feeding activity could be a possible way to use more efficiently the food resource. *A. tonsa* is a nocturnal grazer according to our own results of gut fluorescence analysis during a day-night period. This is also in agreement with the previous studies of Durbin *et al.* (1990) who showed that the chlorophyll gut content of *A. tonsa* was about three times higher during the night. On the contrary, *Brachionus* appears as a diurnal feeder. Arndt & Heerkloss (1989), have noted that *Brachionus plicatilis* has about double feeding rate during the day than during night. Another process allowing a better utilization of the food resource could be the different size selection of food particles. In Berre lagoon, we carried out parallel experiments with *A. tonsa* and *B. plicatilis* using the Coulter Counter technique to measure the ingestion of particles during an annual cycle (unpublish results). On several occasions, we observed that rotifers grazed in a larger size range of particles than *Acartia*, and they were able to use small sized particles (1.6 to 3 μm) while *Acartia* did not feed on or ingested very few particles of this size. The ability of *Brachionus* to use small sized material (2 to 5 μm) has also been demonstrated by Pourriot (1977), Chotiyaputta & Hirayama (1978), and Rothhaupt (1990). The poor utilization of small particles by *A. tonsa* was also noted by Stottrup & Jensen (1990), who showed that this species retains inefficiently *Isochysis galbana* (size 4.8 μm) comparated to four larger algae. Probably in nature some other mechanisms also play a role on food utilization. e.g., *A. tonsa* and *B. plicatilis* do not behave as passive filter feeders, but are able to select their food and to reject the undesirable particles, not only in function of their size, but also according to their quality (Cahoon, 1981; Arndt & Heerkloss, 1989; White & Roman, 1992). This behavioural aspect of feeding, which is probably of great importance in nature, needs more attention in the future to contribute to a better understanding of food web mechanisms.

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