Spatial and seasonal variations in size, body volume and body proportion (prosome:urosome ratio) of the copepod *Acartia tonsa* in a semi-closed ecosystem (Berre lagoon, western Mediterranean)

R. Gaudy[1] & G. Verriopoulos[2]
[1]*Laboratoire d'Océanographie et de Biogéochimie (UMR CNRS 6535), Centre d'Océanologie de Marseille, Station marine d'Endoume, rue de la Batterie des lions, 13007 Marseille, France*
[2]*University of Athens, Faculty of Biology, Department of Zoology Marine Biology, Panepistimiopolis 157 84, Greece*
E-mail: gaudy@com.univ-mrs.fr

Abstract

Variations in size (prosome), body volume and proportion (prosome:urosome ratio) of female *Acartia tonsa* copepods were studied during three different seasons (June, October and November) in a network of 13 stations distributed throughout the Berre Lagoon, near Marseille. Strong morphological differences were found between the populations collected through the different seasonal surveys, but also between the different stations or groups of stations. They were related to the variations of environmental parameters (temperature, salinity, chlorophyll, particulate seston) according to the season and to the location of the stations (submitted to the marine influence in the south and to the intake of fresh water in the north of the lagoon). Considering all seasonal data, the size and body volume were inversely related to temperature. Body volume also showed a negative correlation with chlorophyll and carbon and a positive one with the C:N ratio of particles. The body proportion was positively correlated with temperature, chlorophyll and carbon. For each seasonal survey, the relationship between morphological features and environmental factors did not reach the significant level except in October when body proportion and volume were positively correlated to chlorophyll. Nevertheless, for each season, significant spatial changes in size or body proportion appeared in parts of the population of *Acartia tonsa*, in relation with local specific conditions of environmental factors, especially chlorophyll. These biometric differences suggest that individuals must develop in situ for at least the final period of larval growth, despite the dispersion effect caused by hydrodynamic movements. This stability in horizontal distribution may result from the diurnal vertical migrations of copepods between the surface and the bottom, two layers displaying currents of opposite directions. These results justify the use of somatic features (size and body proportion) to discriminate sets of individuals belonging to the same population.

Introduction

The size of adult copepods depends on environmental factors that act during larval development, in particular, temperature, salinity or the quantity of available food (Deevey, 1960, 1964; McLaren, 1965; Razouls & Guiness, 1973; Durbin & Durbin, 1978; Vidal, 1980a, b; Evans, 1981; Waren et al., 1986; Gaudy et al., 1988). In a given geographical area, individuals of the same species show seasonal variations in size and, in general, maximum lengths at minimum temperatures or during spring algal blooms (Deevey, 1960). Therefore, an analysis of size allows to distinguish, within the same sample, individuals belonging to different generations that have developed in different temperature or nutritional conditions (Marshall, 1949; Digby, 1950; Gaudy, 1986). Geographical variations in size can result from hydrographical conditions (Pessotti

et al., 1986), or from the effect of different latitudinal average temperatures (Sewell, 1947). Moreover, small-scale variations in size may be observed as a function of particular local conditions, for example, in the turbid zone of an estuary (Feurtet & Castel, 1988) or in a coastal area that is subject to heating due to hot water effluents originating from power stations (Gaudy & Benon, 1977).

The copepod *Acartia tonsa* is a species that is widely distributed in numerous estuarine environments or along coastal zones that are subject to desalination (Tester & Tester, 1991). In the Berre lagoon, a large brackish semi-closed area situated near Marseille (French Mediterranean coast), this species is a predominant element of mesozooplankton during most part of the year (Gaudy & Viñas, 1985). Its metabolic and nutritive physiology and its spatial and temporal distribution in the lagoon have been examined in previous papers (Gaudy & Pagano, 1987; Gaudy, 1989; Cervetto et al., 1993; Gaudy et al., 1995).

The environmental conditions of the Berre lagoon are characterised by a great degree of variability (marked vertical and horizontal gradients of temperature, salinity and oxygen concentration; rapid temporal variations of these factors, unsteadiness of the trophic conditions: Minas, 1976; Gaudy et al., 1995). Therefore it was interesting to examine the possible consequences of this variability upon the population of *Acartia*. The time and space variations of abundance were analysed in a preceding paper (Gaudy et al., 1995). During that study, we noted important somatic variations of the individuals according to the season and to the stations. As the morphology of organisms reflects the effect of environmental factors during their development, we examine in the present paper the effect of spatial and seasonal fluctuations of the Berre lagoon environment on the volume and body size and proportions (prosome:urosome) of female *Acartia tonsa,* with the purpose to establish whether morphology can be used as a tool to check the homogeneity of a population or to discriminate different groups of a same species inhabiting a common environment.

Materials and methods

The Berre lagoon is a large (155 km^2), brackish and shallow (7 m on average) lagoon that communicates in the south with the sea (Gulf of Fos) through a narrow canal of 4 km long (Canal of Caronte)(Fig. 1). In the north, the lagoon is supplied with fresh water by a branch of the river Durance, formed in order to meet hydroelectricity needs (Canal of St Chamas), which supplies 2–4 10^9 m^3 of water per year, with important seasonal variations of inflow that are related to energy demands. Maximum inflow of fresh water occurs from November to June and minimum from July to October (Arfi, 1989). Thus, important variations in salinity occur, coupled periodically with important stratification, especially in the south of the lagoon where seawater, that is heavier, accumulates near the bottom (Minas, 1976; Péchon & Samie, 1993).

The samples of zooplankton examined in this paper were collected from 13 stations (Fig. 1), on 15th June, 25th October and 28th November 1995. At each station, horizontal samples were taken from the surface and a deeper layer, 1 m above the bottom with a Clarke Bumpus net (80 μm mesh size). Environmental parameters were measured simultaneously at these two levels, either directly for temperature measured by a CTD, or from water samples collected with a Niskin bottle and processed in the laboratory. The salinity was measured by a YTECH salinograph; and the dissolved oxygen, using the Winkler method. Water samples (50 ml) were screened through a 5 μm mesh size gauze to eliminate eventual mesozooplankton organisms, filtered on whatman filters, for chlorophyll extraction, seston dry-weight and particular C-N analyses. For pigments, the filters were crushed and the pigments were extracted by 90% acetone. Chlorophyll *a* concentration was measured with a fluorometre Turner design, according to Yentsch & Menzel (1963). The dry weight of suspended particles (seston), was estimated by weighing the filters after 24 h drying in an oven, at 70 °C (Lovegrove, 1962). The filters used for particular carbon and nitrogen concentrations were processed using a CHN Perkin Elmer analyser.

Zooplankton samples were preserved in seawater containing formaldehyde (4%) and neutralised with borax until size was measured after several months. According to Durbin & Durbin (1978), the period of preservation has no significant effect on the length of *Acartia*. To avoid a too long time of handling before the measurement, only adults were selected. Among them, as adults males were less numerous and even absent in some occasions, only the females were used for the measurements. From each sample, 50–75 female adult *Acartia tonsa* were measured using a Nikon stereomicroscope equipped with an ocular micrometer and a screen for enlarging the image. The length and width of the prosome and the urosome were measured. These data allowed the estimation of the
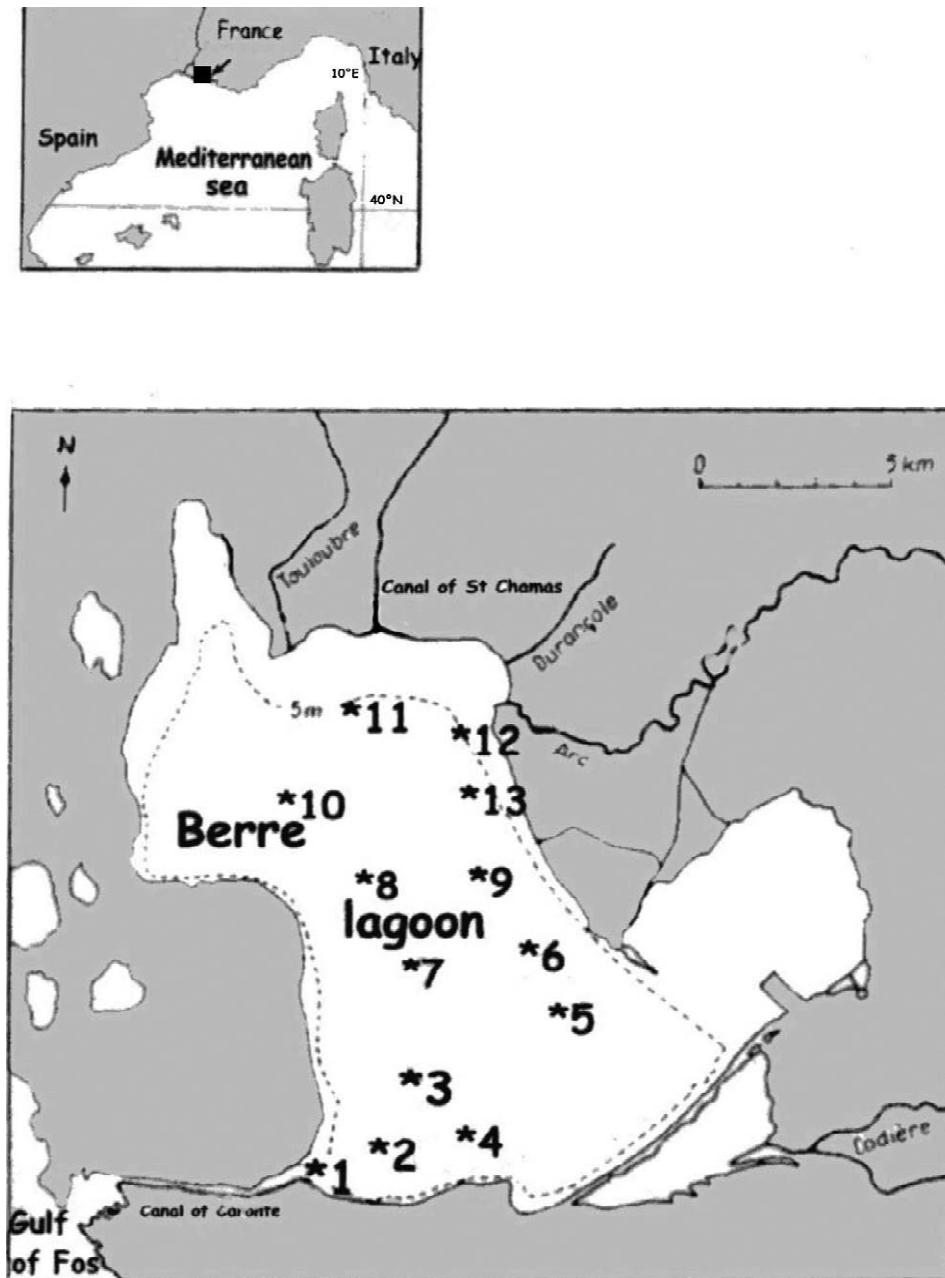
Figure 1. Map of the study area and location of the stations.

prosome-urosome ratio and body volume, in accordance with Bottrell et al's equation (1976). Statistical treatment of the data consisted in the comparison of parameters (Student's *t* test, ANOVA) and in a PCA (Principal component Analysis) of the factors and the observations, with the help of SPAD 3 software.

Results

Variations of environmental factors

Figures 2 and 3 show the existence of important seasonal variations in environmental factors that are accompanied by marked differences between surface and deep water. On the other hand, there is a north–
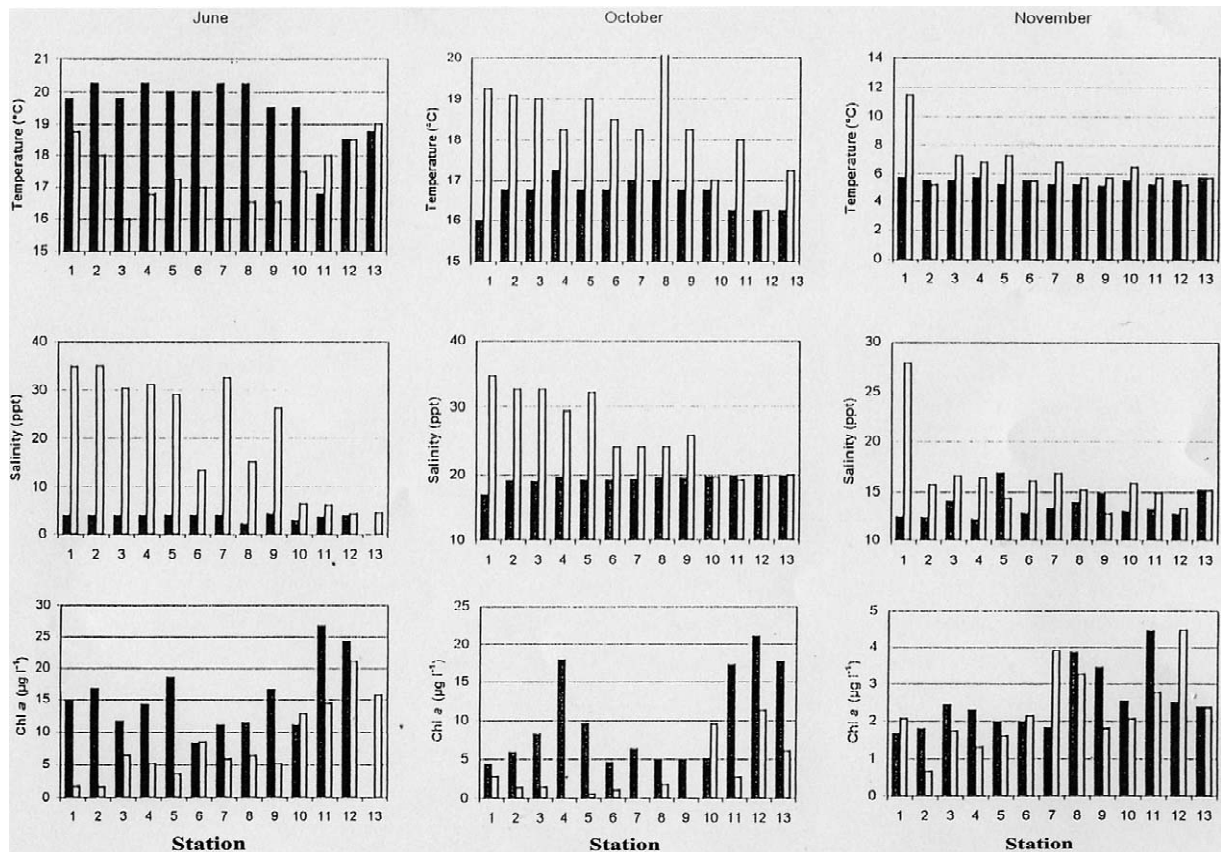
Figure 2. Temperature, salinity and chlorophyll *a* values in June, October and November at the different stations. Black columns: surface samples; white columns: depth samples.

south gradient that is linked to the inflow of fresh water (mainly the St Chamas canal) at the surface, in the north of the lagoon and the inflow of seawater, at the bottom, in the south, by the Caronte canal.

In June, surface water is warm and quite homogeneous apart from the stations that are situated in the north of the lagoon where water is colder and the temperature is similar to that of the deep layer. There is a marked thermocline at most of the other stations. Surface salinity is below 5 ppt at all stations. In deep waters the existence of a salinity gradient indicates the entrance of seawater from the south. The northern area (starting from station 10) is particularly desalinated both at the surface and in deep waters. Chlorophyll concentration is high. It is maximum at the surface and tends to increase towards the north. Seston concentration is low at the surface but in deep waters an important decreasing gradient is observed from south to north, demonstrating the marine origin of suspended matter. The concentration of particulate carbon var-

ies slightly at the surface but tends to increase at the bottom from south to north. The variation of the C:N ratio of particles is similar to the chlorophyll one: it is higher at the surface at all stations and tends towards a maximum in the north of the lagoon.

In October, in deep water, the penetration of seawater from the south is marked by high temperatures and salinities, with a decreasing gradient towards the north. Surface waters are cooler and salinity is uniform, close to 20 ppt. Stations 11–13 are the most homogeneous, with identical values at the surface and at the bottom. At these stations, the quantity of chlorophyll is greater also, at both depths. At the surface, another maximum of chlorophyll is noted at station 4. In deep waters, chlorophyll concentrations are low, apart from the stations in the north of the lagoon. Seston abundance is maximum at the stations in the south of the lagoon. Particular carbon is higher at the surface than in deep waters apart from stations 11, 12 and 13 where its concentration is the same at both levels. The
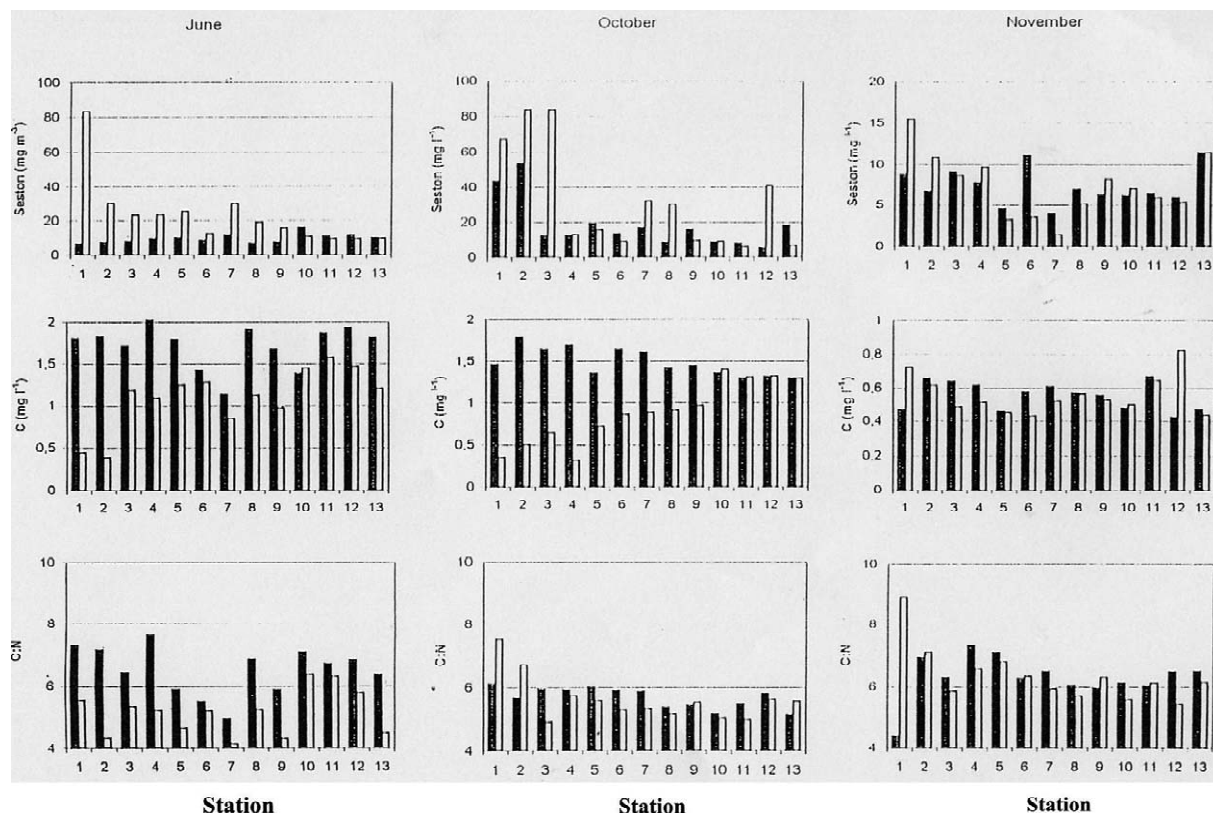
Figure 3. Seston, particulate carbon and particulate C:N ratio values in June, October and November at the different stations. Black columns: surface samples; white columns: depth samples.

C:N ratio of suspended particles is relatively homogeneous apart from at the bottom at southern stations, which are more influenced by the inflow of seawater where it is maximum. In November, temperatures are much lower and homogeneous at the two depths and at the different stations. Salinity does not indicate the presence of seawater apart from at station 1 (28 ppt). Due to the important increase in the inflow of fresh water in the north of the lagoon, water salinity is low at all other stations. Contrarily to conditions in June and October, water stratification is weak and horizontal gradients of physical or chemical environmental conditions are not very marked, given that the entire lagoon is influenced highly by fresh water. Chlorophyll is not very abundant, with maximum values in the northern half of the lagoon. The amount of seston is small too, with a minimum at the centre of the lagoon. Particular carbon is rather uniformly distributed. On the contrary, the C:N ratio tends to decrease from south to north.

Morphological variations according to the season

The average value of the prosome length was the lowest in June (0.89 ± 0.3 mm) and the highest in November (1.01 ± 0.2 mm). An intermediate value characterised October data (0.98 ± 0.05 mm). Corresponding body volumes were respectively 43.6 ± 3.9; 59.65 ± 5.4 and $73.8 \pm 5.5 \ 10^2$ mm^3. The ratio between the prosome and the urosome was 5.31 ± 0.09 in June, 5.29 ± 0.17 in October and 4.86 ± 0.15 in November. The t test of Student showed that the difference between prosome lengths were highly significant between June and October ($P = 7.3 \ 10^{-10}$), but not between October and November. The prosome–urosome ratio was significantly different ($P = 2.83 \ 10^{-12}$) between October and November, but not between June and October. The body volume was highly significantly different between the three surveys.
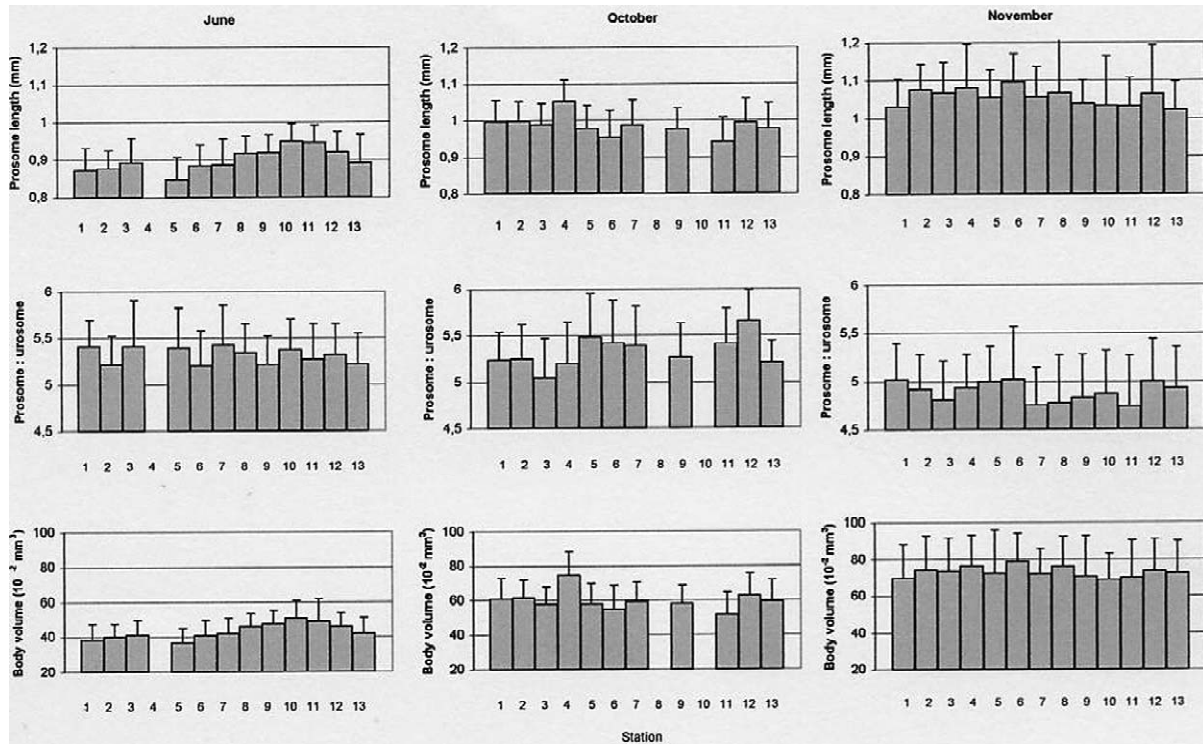
Figure 4. Prosome length, prosome–urosome ratio and body volume (means ± standard deviation) of *Acartia tonsa* females sampled at the different stations (surface and depth data of each station are pooled), in June, October and November.

Morphological variations according to horizontal distribution

Considering the population of *Acartia tonsa*, for a given station, as no significant differences were observed between the measurements of individuals collected at the surface and those collected in deep water (Student's test; $P > 0.05$), the data at the two levels were pooled for the presentation of the figures.

In June, the length of the prosome of female *Acartia tonsa* shows a significant difference (ANOVA, $F = 18.5$; $P < 0.0015$) between southern stations (1–6; an average of 0.88 mm) and those in the north (7–13) where it reaches a maximum of about 0.95 mm, i.e. a 7.4% increase in size. Body volume follows the same tendency. Maximum values were found at stations 10 and 11 where they were 20% higher than the volumes of individuals from the south of the lagoon. The prosome:urosome ratio varies as well according to the stations but no marked tendency appeared according to the geographical position of the stations.

In October, the length of the prosome and body volume of *Acartia tonsa* are rather stable at all stations, except for the individuals collected at sta-

tion 4 which were significantly larger than at the other stations (Student's test; $P < 0.05$). The prosome:urosome ratio gives lower significant figures ($F = 7.06$; $P < 0.004$) at the stations further to the south (1–4).

In November, the length of the prosome and body volume of copepods are much more important than in October and especially in June. They show a small decrease starting from station 6 towards the stations in the north of the lagoon. The prosome:urosome ratio is significantly lower at the intermediate stations 7–11 ($F = 12.35$; $P < 0.048$).

Relationships between somatic variations and environmental factors

Considering all the data, the length of the prosome is inversely correlated to temperature ($r = -0.25$; $P < 0.05$) but not significantly to chlorophyll and particular carbon (Table 1). Body volume shows a much more significant negative correlation with temperature, and also with Chlorophyll and particular carbon. The prosome–urosome ratio also displays a highly significant positive correlation with temperat-

Table 1. Correlations between morphological variations of *Acartia tonsa* and environmental factors in the Berre lagoon (*$P < 0.05$; **$P < 0.01$)

	Temperature	Salinity	Chl *a*	Seston	C	C:N
Total data ($N = 72$)						
Prosome length	–0.25*	0.07	–0.17	–0.05	–0.20	0.08
Prosome:urosome	0.80**	0.06	0.49**	0.27*	0.61**	–0.28*
Body volume	–0.82 **	0.1	–0.49**	–0.22	–0.6**	0.26*
June ($N = 24$)						
Prosome length	–0.26	–0.18	0.27	–0.14	0.11	0.2
Prosome:urosome	0.01	0.10	–0.17	0.27	–0.05	–0.01
Body volume	–0.24	–0.07	0.22	0.00	0.01	0.18
October ($N = 22$)						
Prosome length	0.02	–0.05	0.21	–0.06	0.11	–0.06
Prosome:urosome	–0.31	–0.28	0.39	–0.08	0.18	–0.01
Body volume	–0.14	–0.13	0.47*	–0.17	0.22	–0.01
November ($N = 26$)						
Prosome length	0.00	–0.03	–0.09	0.1	–0.17	0.04
Prosome:urosome	0.12	0.27	–0.12	0.04	0.06	–0.06
Body volume	–0.02	–0.04	–0.17	–0.05	–0.08	0.2

ure, chlorophyll and carbon. It is correlated positively with seston also and negatively with the C:N ratio of particles.

Considering separately each cruise, significant correlations were found only in October, between body volume and chlorophyll.

The PCA performed on all the data shows that the three first factorial axes explain 69% of the variance (Table 2). The positive part of Axis 1 (Fig. 5) corresponds to a decreasing temperature, chlorophyll and particular carbon gradient. Prosome and volume are related to this part while the prosome–urosome ratio is in the opposite part of the axis. Axis 2 explains the influence of seawater entering the lagoon from the south, which is identified by high salinity, sestonic charge and low C:N ratio values. The prosome–urosome ratio is the only morphologic variable which is partially associated with this axis. Axis 3 is linked positively to the sestonic charge and its C:N ratio. The prosome length is correlated to this axis. Observations (Fig. 6) are divided into three seasonal groups, the most individualised being the November one, in the positive part of axis 1 (large sized individuals). The concentration of the points is due to the homogeneity of the environmental factors in this season. In June, the sta-

Table 2. Percentages of variance explained by the three first axes of the ACP and correlations between factors and axes

Axis and % of variance	Axis 1: 42.4%	Axis 2: 24.5%	Axis 3: 10.3%
Temperature	–0.89	0.28	0.17
Salinity	0.23	0.69	0.07
Chl *a*	0.74	0.49	0.12
Seston	0.14	0.77	0.36
C	–0.86	–0.35	0.14
C:N	0.2	–0.52	0.46
Prosome	0.41	–0.06	0.71
Prosome:urosome	–0.85	0.26	0.08
Body volume	0.87	–0.17	0.09

tions are mainly located in the area delimited by the negative parts of axis 1 and 2 (zone mainly influenced by carbon and chlorophyll) while in October, they are grouped close to the positive part of axis 2 (seston and salinity values expressing the marine influence). The scattering of the points is the consequence of the existence of marked vertical and horizontal gradients of environmental factors during these two periods.
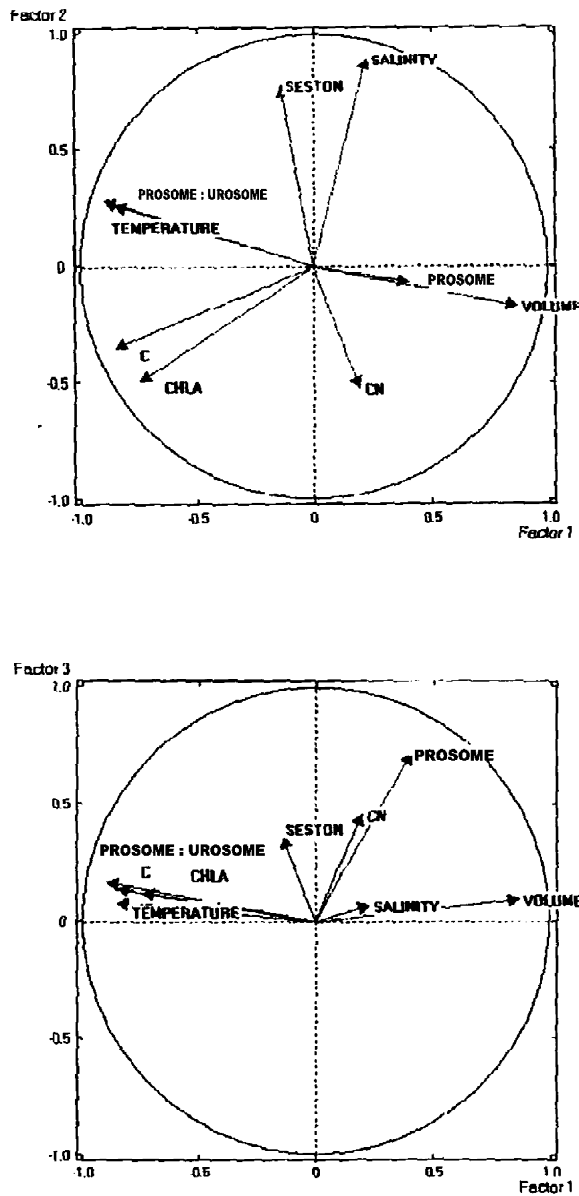
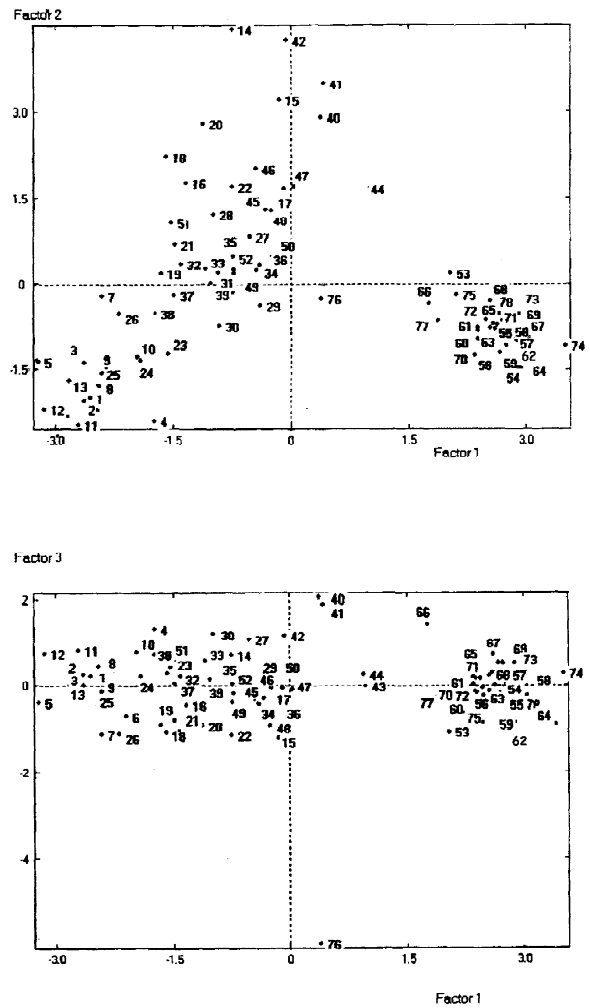Figure 5. Principal Component: Analysis: Analysis of the Factors.

Figure 6. Principal Component Analysis: Mapping of the observations. (Numbers 1 to 26 = stations 1 (surface, depth) to 13 surface, 13 depth) of June; Numbers 27 to 52 = stations 1 (surface, depth) to 13 (surface, depth) of October; Numbers 53 to 78: stations 1 (surface, depth) to 13 (surface, depth) of November.

Discussion

As the annual range of temperature is particularly extended in the shallow environment of the Berre lagoon (6–26 °C), strong variations in size and body volume among the population of *Acartia* are observed, in inverse relationship with seasonal temperatures. The individuals collected in November are, on average, 1.33 larger than June individuals. Such seasonal differences in size, with a winter maximum, are frequently ob-

served in copepods during an annual cycle, especially when there is a wide range of seasonal temperatures (Deevey, 1960; Mauchline, 1998). In our data, the body proportion also changes with the season: the prosome–urosome ratio is lower in big than in small individuals, for example in November, compared to June or October. As shown by the PCA processing, the prosome–urosome ratio is correlated with chlorophyll and sestonic particulate carbon, two potential food parameters. These body variations seem mainly due to proportionally more rapid changes in the prosome length, the part of the body containing the gut and the ovarian, according to variations in food abundance

or quality. Similarly, Christou & Verriopoulos (1993) have demonstrated that for *A. clausi*, body weight for a given length of cephalothorax (conditioning factor), varies according to the quantity of available chlorophyll. In the literature, very few data are available concerning somatic variations other than the size of copepods. Gaudy (1971) has shown that, for *Centropages typicus*, the size ratio between the antennula and the prosome varied seasonally, this being interpreted as an adaptation process to resist sinking into water of different density. As far as the variations in the relative length of the prosome are concerned, Deevey (1960) has demonstrated, during an annual cycle in the western Mediterranean, the seasonal appearance of female *Centropages typicus* with a totally different prosome/total length proportion from that observed during the rest of the year, these individuals being considered as of exogenous origin. For the same species, Vianello (1968) showed that the populations in the north and the south of the Adriatic presented a different value for the prosome/total length ratio, which according to the author characterises genetically separate populations. For *Acartia tonsa*, a species recently introduced into the Black Sea, similar differences in the prosome:urosome proportion (3.8) have been observed in relation to the Adriatic population (4.1). They are accompanied by small modifications of the spinal ornamentation. These differences are of a genetic nature according to Belmonte et al. (1994). Moreover, for the same species, Garmew et al. (1994) show similar morphological differences between separated populations along the American coastline. In a coastal area, in the region of Trieste, Furlan et al. (1983) observed a positive correlation between the relative length of the prosome of *A. clausi* and seasonal temperatures. Furlan et al.'s data together with our own results, show that, in these cases, variations in proportion are probably phenotypic because they are observed within the same population in a restricted area, without the influence of exogenous populations.

When considering separately the results obtained from each of the three seasonal cruises, it is evident that the narrower range of environmental variations in the lagoon and the more limited number of data used in the processing, signify in most cases that it is impossible to obtain significant correlations with the morphological variations. Nevertheless, the comparison of groups of station inhabiting some parts of the lagoon differing by their environmental characteristics allow to discuss the effect of the environment upon the morphology of the species, on a small geographic scale. Strong horizontal and vertical gradients of environmental factors were noted in June and October whereas in November the important inflow of fresh water results in the homogenisation of physical parameters throughout the lagoon. In June, maximum values of prosome length and body volume were found at the coldest and richest stations. Such relations are classical in copepods (Deevey, 1960), but the effect of chlorophyll on the increase in size varies according to the tendency of a species to be more or less vegetarian (Moraitou Apostolopoulou, 1975). In the Berre lagoon, this positive effect of chlorophyll is observed in October as well, with larger individuals at southern stations 1–4. The effect of temperature however, is not apparent even though the range of temperatures in the lagoon is only slightly lower than in June. In November, the homogeneity of environmental conditions and the general lack of chlorophyll result in the absence of significant relations between somatic features and environmental factors.

As far as body proportion is concerned, environmental factors that can affect the prosome:urosome ratio differ according to the season. In June, the prosome:urosome ratio was more or less constant, despite the variation of environmental factors. Contrarily, in October this ratio varied in relation with chlorophyll concentration. For example, at station 4, the richest in chlorophyll, the individuals were the largest and presented one of the higher prosome:urosome ratio, a result which corresponds to the result obtained when using all the seasonal data (existence of a positive correlation with chlorophyll). In November on the other hand, due to the homogeneity of physical conditions, no significant correlation was obtained between the environmental factors and the body proportion of copepods.

This study shows that the size of copepods inhabiting a given ecosystem varies according to the time of the year in relation with the seasonal changes of the main environmental factors (temperature and chlorophyll). This result is not new but it appears that size variation is mainly due to the prosome, while the urosome is less dependent on ecological variations during growth. This results in marked seasonal morphological differences. Considering space distribution, the prosome–urosome ratio allows to discriminate easily individuals developed at different temperature or food conditions. Thus, in June, larger individuals occupy the stations in the north of the lagoon, the richest in chlorophyll. In October, certain individuals are significantly larger in isolated stations; for example,

station 4 where there is a clear chlorophyll peak. In November, the size and volume of individuals is homogeneous but organisms inhabiting stations 7–11 in the north of the lagoon present prosome:urosome ratios that are lower than at other stations. As morphological characteristics of adults are the result of the effect of factors on larval growth, this suggests that individuals remain in the area where they were sampled for at least part of their period of development. According to Berggreen et al. (1988), the duration of interesdysis of the copepodic stages of *Acartia tonsa* is from 25 to 36 h for individuals with no food limitations, at temperatures of 17–18 °C. These authors also demonstrate that the increase in offspring growth as a function of the increase in the quantity of food in cultures is proportionally more marked during the last copepodic stages, and especially C5. In the Berre lagoon, at June and October temperatures, it suffices therefore that copepodites C5 remain for one or two days in richer trophic conditions for a positive difference to be observed in the sizes of newly formed adults. The inflow of fresh water in the north of the lagoon creates a surface current, part of which supplies an anticyclone gyre in the north west of the lagoon, whereas the rest flows towards the south of the lagoon. Part of this water is then flushed into the sea via the Caronte canal. The rest forms a small gyre, near the coast, in the south and turns towards the north near the bottom (Péchon & Samie, 1993). This situation is favourable for the maintenance of the population of *Acartia tonsa* in a specific geographical area. As this species displays daily vertical migrations in the lagoon (Cervetto et al., 1993), it meets, alternatively, currents moving towards the south at the surface and towards the north in deep waters, helping it to remain in the same location. The hydrodynamical gyre structures described in the lagoon are equally favourable to the maintenance of the local populations at stations 10, 11 in the north and 4 in the south.

Our results show that the morphological characteristics of a species vary not only according to the season, with temperature as a determining factor, but also within a limited geographical zone, according to local differences in food abundance mainly. Body proportion (prosome:urosome) seems to depend on a combination of various factors, either of physical-chemical nature (temperature, salinity) or of trophic nature (chlorophyll, particulate carbon,). This criteria, rarely considered in studies of the somatic variations of copepods, might prove useful for the morphological characterisation of populations.

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