Acartia tonsa
Feeding
Metabolism
Production

Acartia tonsa
Nutrition
Métabolisme
Production

Short term variations in feeding and metabolism of *Acartia tonsa* (pelagic copepod) in the Berre lagoon (France)

Raymond GAUDY [a], Marc PAGANO [b], Guillermo CERVETTO [a], Lucien SAINT-JEAN [b], Georges VERRIOPOULOS [c] and Beatriz BEKER [d]

[a] Centre d'Océanologie de Marseille, Station marine d'Endoume, rue de la Batterie des lions, 13007 Marseille, France.

[b] Centre de Recherches Océanographiques, BP V18, Abidjan, Côte d'Ivoire.

[c] Laboratoire de Zoologie, Université d'Athènes, Grèce.

[d] Centre d'Océanologie de Marseille, Faculté des Sciences de Luminy, 13288 Marseille Cedex 9, France.

Received 25/07/95, in revised form 09/05/96, accepted 14/05/96.

ABSTRACT

Feeding, respiration, and ammonia excretion of *Acartia tonsa* were studied in a brackish lagoon, near Marseilles (Southern France). The experiments were performed during the same season in two successive years, using naturally occurring particles as food. Strong variations in both quantity and quality of food particles were recorded between the two series of experiments. The ingestion of particles according to their size was studied by means of the Coulter Counter technique. Females ingested more food than males. In both sexes, there was a tendency to select median to large particles, regardless of the shape of the particles-size spectrum. In 1990, the specific production rate, deduced from the energy budget, was equivalent to or greater than the observed egg production, while in 1989 it was too small to account for the observed rate. This could be due to the poor nutritive value of particles in 1989, as evidenced by their low chlorophyll:volume ratio. The nutritive requirements would then have been completed by ingestion of nauplii and rotifers which were particularly abundant in 1989. This presumed shift to carnivorism is borne out by the lower O:N atomic ratio (oxygen consumed and NH4-N excreted) calculated for this period.

RÉSUMÉ

Variations à court terme de la nutrition et du métabolisme d'*Acartia tonsa* (copépode pélagique) dans l'Etang de Berre (France).

La nutrition, la respiration, l'excrétion d'ammoniaque et la production d'*Acartia tonsa* ont été étudiées dans une lagune saumâtre du sud de la France. Les expériences ont été réalisées à la même saison au cours de deux années successives, en utilisant les particules naturelles comme source de nourriture. De fortes variations dans la qualité et dans la quantité des particules nutritives ont été observées entre les séries d'expériences. L'ingestion en fonction de la taille des particules a été étudiée par des mesures au Coulter Counter. Le taux d'ingestion des femelles est supérieur à celui des mâles. Mâles et femelles ont tendance à sélectionner les moyennes et grandes particules quelle que soit l'allure du spectre de taille des particules disponibles. Les taux de production déduits du bilan énergétique étaient

équivalents aux taux de production d'œufs observés en 1990, et nettement inférieurs en1989. Ces plus faibles taux de 1989 pourraient résulter d'une plus faible valeur nutritive des particules (faibles rapports chlorophylle:volume). Les besoins nutritifs auraient été complétés par l'ingestion de nauplii et de rotifères, abondants en 1989. Cette tendance au carnivorisme est corroborée par l'existence de rapports O:N (oxygène consommé:N-NH4 excrété) plus faibles qu'en 1990.

Oceanologica Acta, 1996, **19**, 6, 635-644.

INTRODUCTION

The copepod *Acartia tonsa*, a widely distributed species, occurs mostly in temperate or subtropical estuaries and nearshore environments. In the Western Mediterranean Sea, it is restricted to some harbour or lagoonal environments. In the Berre lagoon, near Marseilles, *A. tonsa* constitutes, with the rotifer *Brachionus plicatilis,* the dominant species of zooplankton throughout the year (Gaudy *et al.*, 1995). Estuarine, nearshore and lagoon environments generally display high variability, in terms not only of physical or chemical factors, but also of the quantity and quality of the food available for zooplankton (Lehman, 1981). On an annual basis, in the Berre lagoon, seston biomass (expressed as nitrogen) and chlorophyll variations are synchronized only during the spring period. Thus, the food quality varies markedly during the year with a direct effect on the nitrogen incorporation by *A. tonsa* and, consequently, on its production capacity (Gaudy, 1989). The seasonal egg production of *A. tonsa* in the lagoon is also directly related to the chlorophyll variation (Gaudy, 1992). In the Berre lagoon population of *A. tonsa*, short-term variations were found during day-night cycles of feeding, respiration and spawning (Cervetto *et al.*, 1993, 1995). These were not directly related to food variation but seem to correspond to an endogeneous cycle. Between the long-time scale (annual cycle) and the short-time scale (day-night variation), the population of *A. tonsa* can be submitted to rapid changes in food conditions. The maintenance of the *A. tonsa* population in the face of such changes depends on the aptitude of individuals, particularly the reproductive stages (adults), to regulate their physiological response. In this paper, we attempt to examine this ability by comparing the feeding, respiration, excretion and eggs production rates of *A. tonsa* during successive cruises separated by intervals of a few days. In contrast with most of the published studies on the feeding strategy of *A. tonsa,* which concern only total adults or females, we examine separately the physiological responses of the two sexes.

MATERIALS AND METHODS

Five sets of field experiments were performed in 1989 (on 30 May, 2 June and 4 June) and in 1990 (on 29 May and 3 June), in the southern part of the Etang de Berre, a large (155 km^2) and shallow (6 m average depth) brackish basin located near Marseilles.

Seston analysis

For experiments, *in situ* water was collected at a depth of one metre, using a Grunfos centrifugal pump. Immediately prior to the experiments, subsamples of this water were processed for particulate carbon analysis (CHN LECO analyser), chlorophyll *a* measurement (Holm-Hansen *et al.*, 1965), phytoplankton enumeration (Utermöhl) and particle volume and size spectra determinations (analysis performed with a Coulter Counter model multisizer equipped with a 100 µm aperture tube on subsamples fixed with buffered formalin and analysed several days later in the laboratory).

Experiments

Zooplankton was collected with vertical hauls using a 200 µm WP2 net. The cod-end content was diluted with lagoon water.

Sets of 100 to 200 adult males and females (separated for these experiments) were then constituted and incubated in 125 ml flasks for about 24 h. They corresponded to a zooplankon biomass in the jar ranging from 1.2 to 3 mgC l^{-1} which was about ten times the natural biomass, allowing accurate measurement of the size spectra modifications in such seston-rich lagoon water and, therefore, significant ingestion and filtration rate. Despite such high zooplankton densities, the seston decrease in the jars was always lower than 10 % of the initial concentration so that the clearance rates could not be modified by a food concentration effect. The low grazing impact of zooplankton was due to the high density of the Berre lagoon seston in comparison with its food needs (Cervetto *et al.*, 1995). Half of the flasks were filled with < 60 µm water for ingestion and respiration (fed animals) measurements. The remainder were filled with water filtered on Millipore HA membranes (0.45 µm) for respiration (starved animals) and ammonia excretion measurements. For each water type, three experimental bottles (with animals) and two controls (without animals) were prepared and placed on a rotating wheel (3 rpm). The experiments were run in the dark, at the temperature of collection. At the end of the experiment, subsamples were siphoned from the jars for particle volume and size spectra determinations (60 µm prefiltered water) or ammonia measurements (Koroleff, 1969) (0.45 µm filtered water). Oxygen measurements were performed immediately on siphoned aliquots of each type of water using a YSI 57 oxymeter. Zooplankton from the experimental jars was then collected on preweighed Whatman GF/F filters. Zooplankton dry weight was measured on a Mettler electrobalance, after drying at 60 °C during 24 h. Body carbon and nitrogen were determined using a LECO CHN 800 analyser.

Respiration and excretion rates were calculated from the differences in oxygen or ammonia concentrations between

control and experimental jars and related to time (h) and weight (mg C) units.

Ingestion, I (μm^3 ngC^{-1} h^{-1}) and clearance rates, F (ml water cleared of particle mgC^{-1} h^{-1}) were calculated from the difference in particle volumes between control and experimental jars, for each channel and for total size range, assuming a nil algal growth in the jar, due to darkness. They were given by

$$I = (C\,c - Ce * V/(B*t)$$
$$F = ((\ln Cc - \ln Ce)/t) * V/B$$

where Cc and Ce are the particle concentrations ($\mu m^3 ml^{-1}$) at the end of incubation in the control and experimental jars, respectively, V is the experimental jar volume (ml), B is the zooplankton carbon biomass in the jar, and t is the incubation time (h). Ingestion was also expressed in chlorophyll or carbon, using the chlorophyll:volume or carbon:volume ratios measured in the experimental water. Particle-size selectivity was evaluated using the selectivity index, Wi, from Vanderploeg and Scavia (1979):

$$Wi = Fi/\Sigma Fi$$

where Fi is the clearance rate calculated for the size-class i.

The production of organic carbon in adults was indirectly calculated from the energy budget equation, using the difference between assimilation, inferred from the ingested carbon, using an assimilation efficiency of 0.7 (average value for neritic copepods: fed natural particle, Conover, 1966) and respiration, using a maximum respiratory quotient (RQ) of 1 (carbohydrates, *i.e.* plant material used for food) and also the value of 0.7 (lipid-protein metabolic substrates utilization, Omori and Ikeda, 1984). The loss of organic carbon by excretion was neglected because copepods excrete essentially ammonia (Le Borgne, 1986).

Table 1

Experimental conditons: temperature and salinity, abundance (10^3 cells l^{-1}) and size (equivalent spherical diameter, ESD) of phytoplankton species and total algal volume (ppm) in Berre waters used for grazing experiments, particle volume (ppm), chlorophyll concentration (μg l^{-1}) and carbon:volume ratio (C/Vol) of seston <60μm.

		Date				
		30/5/89	**2/6/89**	**4/6/89**	**29/5/90**	**3/6/90**
TEMPERATURE		22.0	21.0	19.6	19.6	20.4
SALINITY		13.5	12.5	13.0	19.6	17.9
PHYTOPLANKTON	ESD (μm)					
Diatoms						
Chaetoceros curvisetus	14.7	6	100	500	–	–
Cyclotella sp.(9)	8.1	1070	1400	8000		
Melosira italica	18.1	300	–	–	–	–
Fragillaria crotonensis	13.3	9	–	–	–	–
Nitzschia closterium	5.2	200	1400	2300		
Rhizosolenia fragilissima	8.5	–	–	–	1380	100
Dinoflagellates						
Glenodinium lenticulum	31.6	2	45	11	–	–
Gymnodinium sp.	7.6	2300	3700	500	–	–
Polykrikos schwarzi	56.3	–	0.4	0.4	–	–
Prorocentrum micans	22.4	2	–	–	–	–
Prorocentrum minimum	12.3	16500	4300	7200	2800	2300
Chlorophycaea						
Chlorella sp	1.7	6500	18500	49200	–	–
Monoraphidium contortum	3.1	–	5	6	–	–
Cryptophycea	4.7	3300	100	2500	–	–
Cyanophycea						
Lyngbia limnetica	8.1	30	50	52	–	–
Spirullina subalsa	7.0	–	–	–	32100	33100
Prasinophycaea						
Pyramimonas grosi	4.7	300	–	20	–	–
Total number		30247	34960	70343	36300	35400
Algal volume (ppm)		13.0	7.8	8.2	5.2	4.7
SESTON <60μm						
Volume (Vol)		12.7	9.6	6.8	3.1	7.2
Chlorophyll (Chl)		7.7	9.3	11.4	30.0	12.1
Chla/Vol		0.6	1.0	1.7	5.1	1.8
C/Vol		184	128	114	82	231

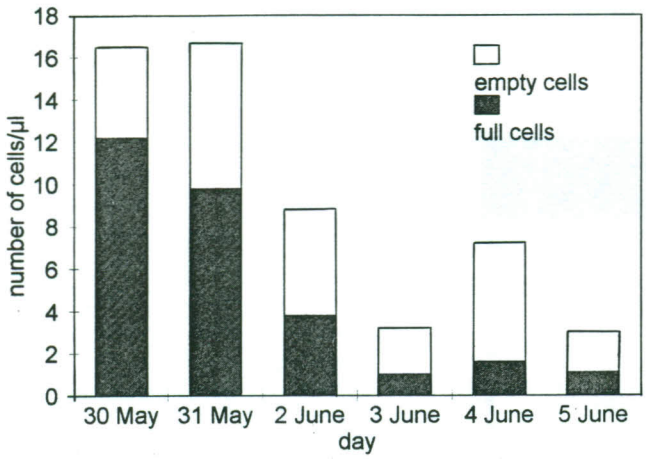


Figure 1

Changes in the number of Prorocentrum minimum *full or empty cells at different successive days between 30 May 1989 and 5 June 1989. (no data for 1 June).*

Egg production was estimated (1) at the end of the ingestion experiments by counting the eggs produced (1990 only) and (2) in specific spawning experiments performed in parallel experiments on 2 June 1989 and 3 June 1990 (see Cervetto *et al.*, 1993). In both cases, the specific production rate was derived from the number of eggs produced per female, using an average egg carbon weight of 0.031µg (Kleppel, 1992) and the average weight of females used in grazing experiments (see results).

RESULTS

Food conditions

The composition of phytoplankton is shown in Table 1. In 1989, *Prorocentrum minimum* was the most numerous alga at the beginning of the studied period, accounting for 54 % of the phytoplanktonic cells. At the end of the period, it decreased to the second rank (10 % of the cells number), behind *Chlorella* sp. In 1990, *P. minimum* contributed only 6-7 % of the cell number, but nevertheless occupied the second rank, *Spirullina subalsa* being largely dominant. When the biomass (biovolume) was taken into consideration, the relative importance of *P. minimum* further increased (64 to 93 % of the particulate volume in 1989, 29 to 34 % in 1990). In addition, observations performed in 1989 during a period which included the experimental study, showed that the proportion of living cells (as full cells) was high at the beginning and subsequently decreased, while dead cells (as empty cells) increased (Fig. 1). These variations were probably related to the evolution in time of a *P. minimum* bloom from juvenile to senescent stages.

Short-term quantitative variations in particle assemblage were also recorded. In 1989, at the end of the five-day studied period, the biomass of seston, expressed as the volume of particles between 2 and 21 µm equivalent spheric diameter (ESD), was reduced to almost 50 % of its initial value (Tab. 1). Conversely, in 1990, the seston biomass increased to more than twice its initial value. The chlorophyll biomass evolved in the opposite direction, increasing in 1989 and decreasing in 1990. Consequently, the chlorophyll:volume ratio differed greatly from one year to the other and, during each studied period, between successive analyses. For each period, when the biomass of particles was highest (30 May-2 June 1989; 3 June 1990), the particulate size spectrum was characterized by a peak located at an ESD of intermediate size (14 µm in 1989, 13 µm in 1990; Fig. 2). Taking into account the size and abundance of the algal species during these periods (Tab. 1), it is likely that this peak corresponds to the abundance of *P. minimum*. When the particulate concentration was lower (4 June 1989; 30 May 1990), this peak was much reduced or disappeared altogether.

Ingestion

In both sexes, the volume of particles ingested daily (Fig. 3) was low for ESD < 6 µm (1989) or < 4 µm (1990) and particles > 16-18 µm. It was maximum for the intermediate sizes of particles (10-16 µm), corresponding to the size of *P. minimum*. Ingestion and the electivity according to particle size were more regular in females than in males, possibly with a larger exploitation of the particle spectrum by females. Ingestion rate was significantly higher in females than in males, with systematic (and sometimes significant) differences per size class (Tab. 2). 60 to 80 % of the ingestion involved particles between 8 and 16 µm (Fig. 3). The electivity index showed a general tendency to increase with the size of particles, independent of their abundance.

The volume of particles ingested daily varied from 105 to 175 $\mu m^3\ ng^{-1}\ h^{-1}$ in females and from 29 to 98 $\mu m^3\ ng^{-1}\ h^{-1}$

Table 2

*Comparison of male and female ingestion rates (in $\mu m^3\ ngC^{-1}\ h^{-1}$) for 2 µm size-intervals of food particles. Average values (± standard deviation) of the five experiments for males and females and paired T-test for the difference female-male (t); n = 5. ns = $p > 0.05$, * $p > 0.05$, **= $p < 0.01$.*

Size class (µm)	Males	Females	t
0-2	0.00 ± 0.00	0.00 ± 0.00	–
2-4	1.00 ± 1.22	2.56 ± 1.89	3.23 *
4-6	2.90 ± 2.77	5.45 ± 2.73	1.63 ns
6-8	3.49 ± 1.36	4.64 ± 1.68	2.08 ns
8-10	10.04 ± 5.70	10.85 ± 6.07	0.98 ns
10-12	15.94 ± 5.90	21.25 ± 7.70	3.89 *
12-14	17.69 ± 10.50	25.99 ± 15.14	2.95 *
14-16	8.66 ± 4.68	14.39 ± 8.46	2.15 ns
16-18	3.71 ± 2.83	4.82 ± 2.85	3.36 *
18-20	3.10 ± 2.11	3.60 ± 3.30	0.81 ns
20-22	1.86 ± 1.43	2.01 ± 1.00	0.40 ns
Total	68.39 ± 24.75	95.5 ± 32.43	5.17 **

in males. After conversion to daily specific rates, these values correspond to 57-95 % of the body carbon weight in females and 35-77 % in males (Tab. 3). In 1989, at the end of the studied period, a decrease in the daily ration, expressed either in volume or carbon units, was observed. In 1990, on the other hand, the ingestion expressed as volume increased between 29 May and 3 June but due to the strong decrease of chlorophyll content of seston (Tab. 1), the specific ingestion in carbon unit was stable in males and even decreased in females (Tab. 3). Filtration rates ranged from 7.8 to 12.0 µl μgC^{-1} h^{-1} in males and from 9.4 to 28.5 µl μgC^{-1} h^{-1} in females. The difference was significant (ANOVA, $p < 0.05$).

Figure 4 shows that ingestion (I) was directly proportional to seston concentration expressed as particle volume (Vol). Within each sex, this relationship was similar in 1989 and 1990. When data were pooled for the two years, the regression equations were:

$I = 12.32 + 7.00V$ ($r = 0.90$) for males and
$I = 18.56 + 9.48V$ ($r = 0.78$) for females.

No difference was found between the slopes of the two regression lines, while their intercepts were significantly different ($p < 0.05$).

Respiration and excretion

Respiratory expenditures of fed animals expressed as carbon corresponded to 22-53 % of the body carbon (Tab. 3). They were similar in both sexes as shown by two-factor (sex-experiment) ANOVA: F sex = 0.03 for 1, 9 d.f. Respiration rates could not be related to temperature conditions, which were almost identical during the two experimental periods (Tab. 1). Considering all data, the respiration rates of fed and starved copepods were not significantly different as shown by two factor ANOVA (water-experiment) (F water = 0.59 for 1, 29 d.f.). Nevertheless, correlation analysis demonstrated a poor relationship between respiration rates and specific volume ingestion rates, only significant when considering 1989 data alone ($r = 0.60$, $n = 12$).

Ammonia excretion showed a wide range of variations, between a minimum of 0.48 and a maximum of 6.33 µgN mg^{-1} h^{-1} (Tab. 4). For each period, the O:N atomic ratio was similar in males and females, as shown by two-factor (sex-experiment) ANOVA: Fsex = 0.023 for 1, 8 d.f. When the two years were compared, the O:N was twofold higher in 1990 (23.6 ± 6.8) than in 1989 (11.6 ± 2.4).

Table 3

Individual weight (Wi in µg C), ingestion rates expressed as particle volume (IVOL, in μm^3 ngC^{-1} h^{-1}) and filtration rates (F in µl μgC^{-1} h^{-1}) of A. tonsa *males (m) and females (f) for the five feeding experiments and specific carbon daily ingestion (ING), respiration (RESP) and production (P/B) rates expressed as µg C μgC^{-1} day^{-1}. P/B are deducted from ING and RESP assuming an assimilation efficiency of 70 % and compared (in the case of females) to female egg production rates (PF, same units) estimated from spawning experiments carried out at the same date (* see Cervetto* et al. *1994, for details) or from egg counting in the jars at the end of feeding experiments (**).*

Sex	Wi	IVOL	F	ING	RESP	P/B	PF
30 May 1989							
m	1.44	97	8.0	0.53	0.53	–0.17	
m	1.55	97	8.0	0.53	0.52	–0.15	
f	2.02	105	9.4	0.57	0.39	0.01	0.62 *
f	1.97	175	15.8	0.95	0.44	0.23	
2 June 1989							
m	1.66	67	7.8	0.52	0.32	0.04	
m	1.62	98	12.0	0.77	0.36	0.17	
f	2.15	125	16.1	0.98	0.39	0.30	
f	2.20	106	13.7	0.83	0.37	0.21	
4 June 1989							
m	1.62	48	8.4	0.42	0.26	0.03	
f	2.17	54	10.8	0.47	0.26	0.07	
f	2.17	63	12.6	0.55	0.32	0.07	
f	2.16	65	13.1	0.57	0.31	0.09	
29 May 1990							
m	1.09	29	10.5	0.35	0.33	–0.08	
m	1.07	33	11.2	0.40	0.42	–0.14	
f	1.45	45	17.2	0.55	0.32	0.06	0.05**
f	1.44	68	28.5	0.84	0.43	0.15	0.06**
3 June 1990							
m	1.02	83	13.6	0.36	0.22	0.03	
f	1.29	94	16.3	0.40	0.28	0.00	0.06**
f	1.32	117	19.9	0.51	0.29	0.07	0.05**
f							0.05 *

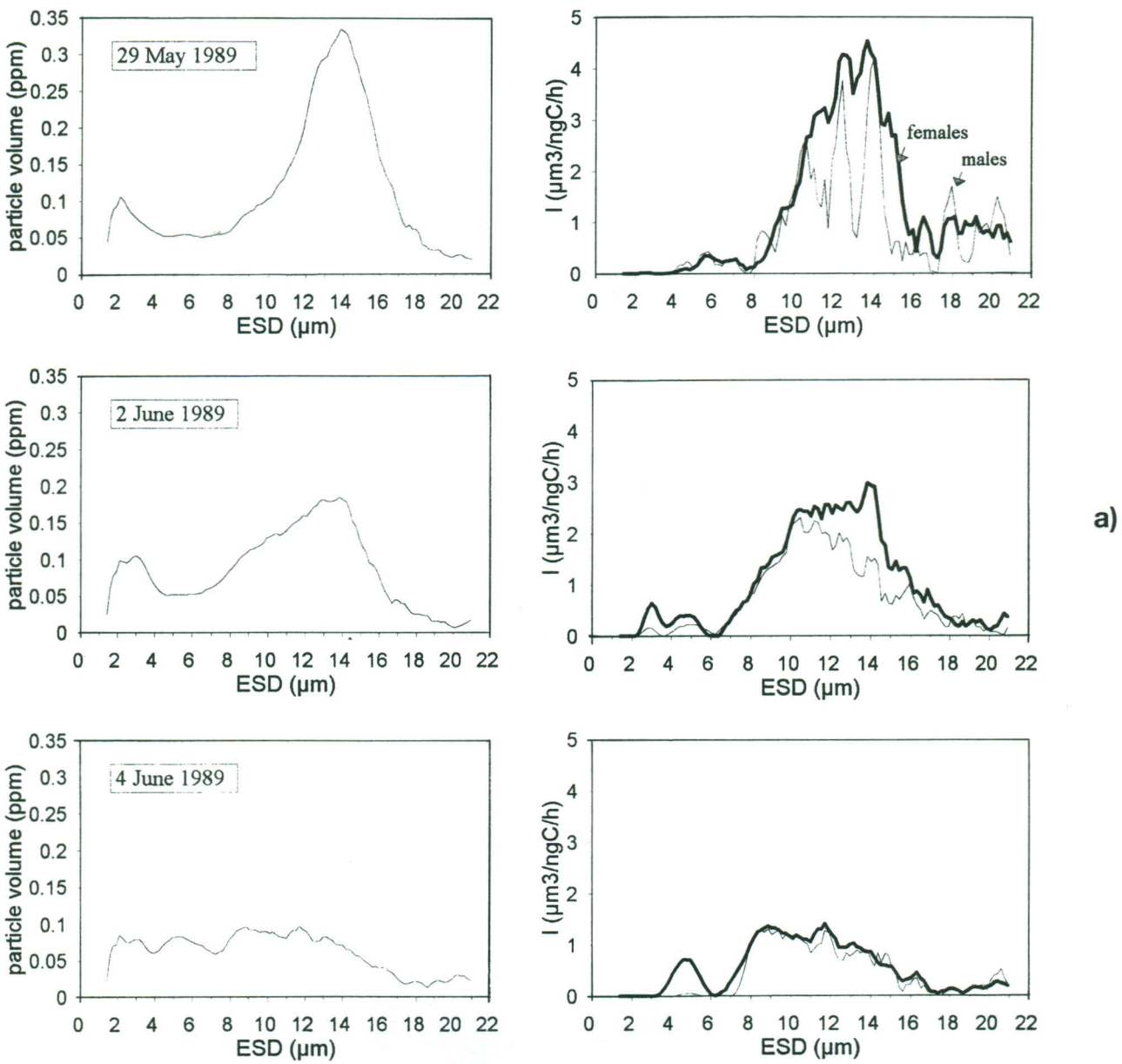
Production

In 1989, considering the protein-oriented metabolism indicated by the low O:N ratio, the most probable value of RQ was 0.7. The daily Production:Biomass ratio (P:B) calculated using this RQ value ranged from 0.13 to 0.41 µgC µgC^{-1} in females, while it could display negative or null values in males, reaching a maximum value of 0.28 µgC µgC^{-1}. In 1990, using a RQ of 1 (carbohydrate oriented metabolism, suggested by the higher O:N ratio), the daily P:B ranged between 0 to 0.15 µgC µgC^{-1} in females and negative values to 0.03 µgC µgC^{-1} in males. In females, this potential carbon production was compared with the observed daily egg production rates. In 1989, the daily egg production (0.62 µgC µgC^{-1}) was higher than the P:B calculated from the energy budget equation (maximum value: 0.36 µgC µgC^{-1}). Conversely, in 1990, the egg production calculated on the same basis from spawning experiments or from eggs produced during feeding experiments were in the same range as those deduced from the energy budget for females (Tab. 3).

DISCUSSION

In all experiments, females ingested more food than males (Tab. 3). Their daily food ration was on average 1.4 times greater. The difference in ingestion rate, which accounted for 11 to 22 % of the body carbon weight of females, corresponds to the energy needed for egg production and ranges in the corresponding values calculated by Kleppel (1992) for this species (4 to 35 %). The higher food ration of females is obtained by increasing their filtering rate and by a more complete utilization of the food spectrum.

Strong variability was observed in the quantity and quality of particulate matter in the Berre lagoon water during a period of a few days. Particle numbers and volumes and chlorophyll biomass vary more or less independently, leading to strong differences in the chlorophyll:volume ratio, as observed also by Lehman (1981) in coastal environments. This illustrates rapid changes in the quantity and quality of algae, the smallest particles being generally the richest in chlorophyll or the most productive (Eppley and



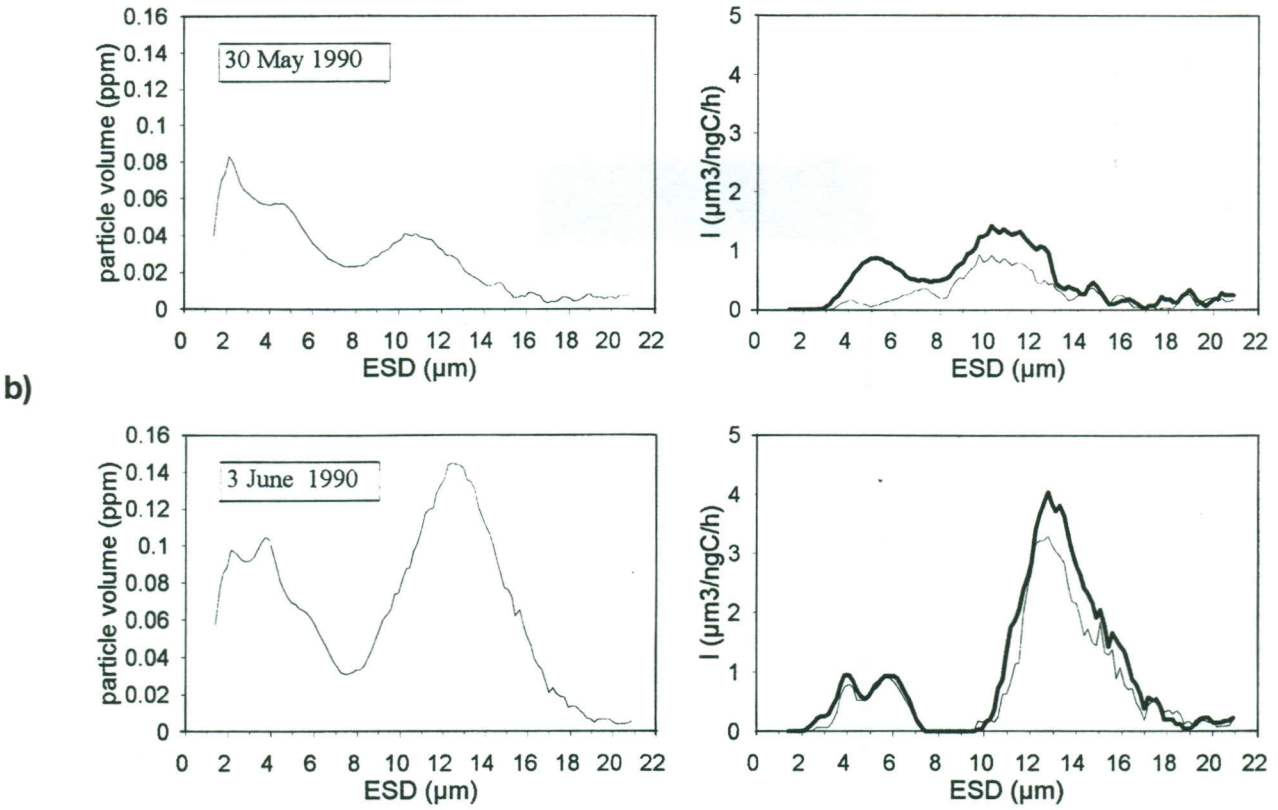


Figure 2

Concentration of natural particles and ingestion rates by Acartia tonsa *males and females in relation to the size (ESD: equivalent spheric diameter) of particles in the five experiments: a) (left) in 1989; b) (above) in 1990.*

Sloan, 1966; Taguchi, 1976). In 1989, the joint effect of the increase of small *Chlorella* in the phytoplankton assemblage and the decrease of number et proportion of living *P. minimum* cells (Fig. 1) would then explain the increase of the chlorophyll:volume ratio noted at the end of the investigated period. In 1990, the strong chlorophyll:volume values decreased with time as the proportion of *Prorocentrum minimum* increased. Despite these strong changes, specific carbon ingestion rates remained in the same range, showing the ability of *Acartia tonsa* to optimize its energy intake. As a matter of fact, *A. tonsa* was able to use the major part of the available size spectrum for its food. Females, which require more energy than males to fulfill their reproduction needs, ingested most of the particles present, except the smallest ones, probably inadequately retained by their filtering appendices (Nival and Nival, 1976). The electivity tended to increase for the sizes of particles corresponding to the frequency peaks, and also for the biggest particles. This result agrees with most of the previous studies (Poulet, 1973, 1974; Cowles, 1979; Gamble, 1978) and is in conformity with the theory of optimal foraging (Pyke *et al.*, 1977). The aptitude to select large particles does not necessarily lead *Acartia* to complete its food ration with this material, which was scarce during the investigated period, but indicates the ability to change its nutrition strategy in the direction of raptorial feeding upon large-sized prey (microzooplankton), as indicated by several previous studies (*i.e.* Anraku and Omori 1963; Lonsdale *et al.*, 1979; Tackx and Polk, 1982).

Table 4

Specific metabolic rates measured in 0.2 µm filtered water: respiration (RESP) and ammonia excretion (ENH4) rates expressed as µg O2 or µg N per µg body C and per hour, and atomic O/N-NH4 ratio for male (m) and females (f) of A. tonsa, *nd = non determined.*

Date	Sex	RESP	ENH4	O/N-NH4
30 May 1989	m	73.0	6.33	10.1
	m	61.0	3.49	15.3
	f	51.3	3.81	11.8
	f	40.3	2.88	12.2
2 June 1989	m	50.1	3.86	11.3
	m	56.9	3.67	13.6
	m	53.5	2.74	17.1
	f	39.6	2.83	12.2
	f	54.6	5.22	9.2
	f	33.4	3.07	9.5
4 June 1989	m	36.7	3.11	10.3
	f	38.5	nd	nd
	f	39.3	nd	nd
	f	38.7	nd	nd
29 May 1990	m	50.7	0.73	30.4
	m	42.0	1.10	16.8
	f	36.9	0.69	23.3
	f	41.3	1.29	14.1
3 June 1990	f	35.0	0.48	31.7
	f	32.1	0.54	26.2

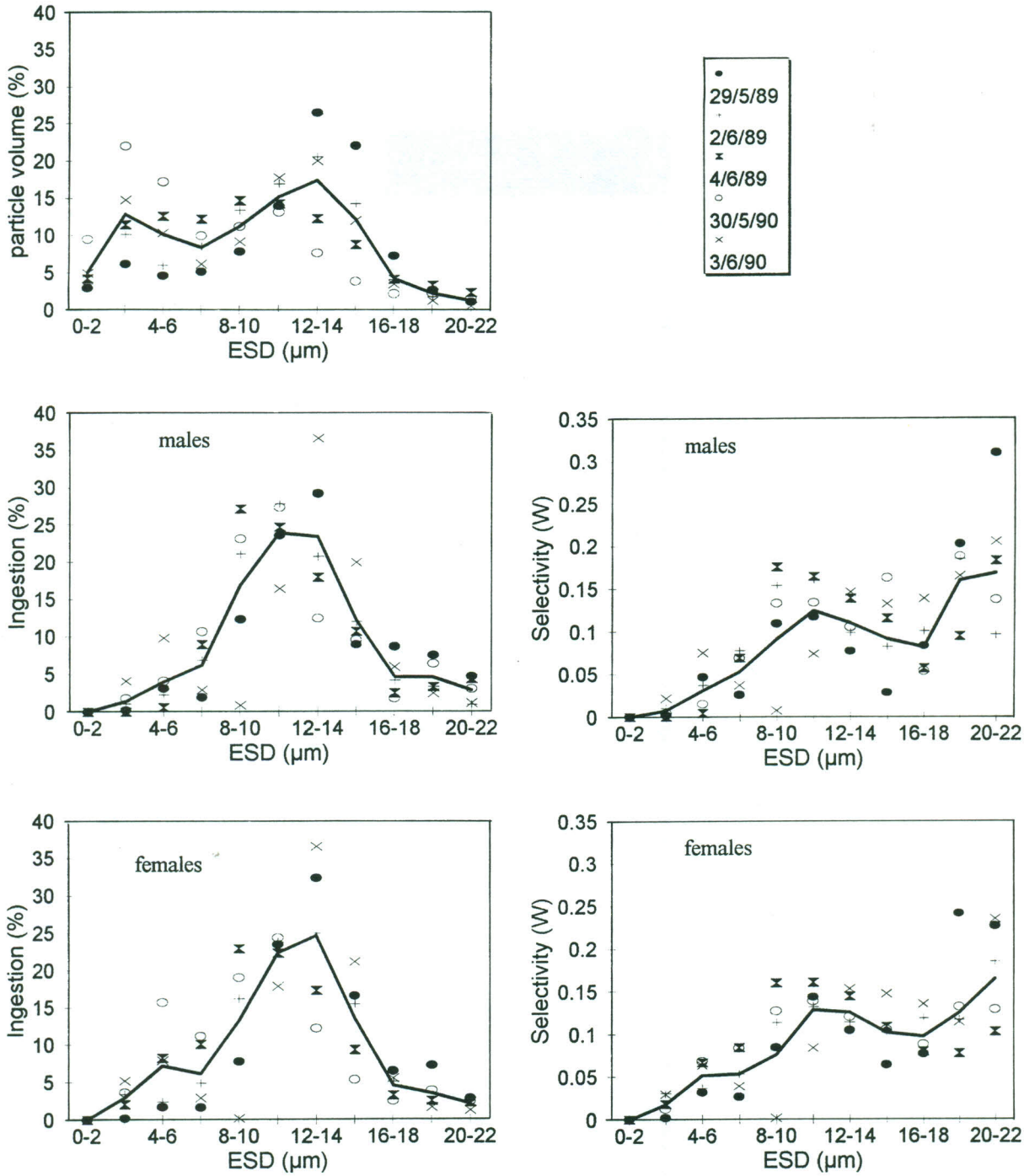


Figure 3

Average data for the available food (natural particles), ingestion rates by Acartia tonsa *males and females (expressed as percentage of total ingestion) and corresponding selectivity index in relation to the size (ESD: equivalent spheric diameter) of particles.*

The low O:N ratios of the 1989 experiments indicate a tendency to carnivorism, well known in *Acartia tonsa* (Anraku and Omori, 1963; Tackx and Polk, 1982). Indeed, potential preys such as rotifers or nauplii were abundant (40 *Brachionus plicatilis* and 15 nauplii per litre, unpubl. data) in 1989 and very scarce in 1990 (0.2 *B. plicatilis* l^{-1} and 2 nauplii l^{-1}). The possibility to complete their food ration by animal prey could explain the discrepancy between the low production rate of females calculated from the energy balance equation (based on seston utilization) and the rich egg production measured in 1989 (*cf.* Tab. 3). When the phytoplankton is relatively scarce, *A. tonsa,* which is adapted to high food concentrations (Paffenhöfer and Stearns, 1988), must partly shift from a suspension-feeding to a predatory behaviour in order to complete its food ration, as shown as well for this species (Anraku and Omori, 1963; Richman *et al.*, 1977; Robertson, 1983; Stoecker and Sanders, 1985) as for other marine copepods submitted to oligotrophic conditions (Landry, 1981). This was possible in 1989 when potential preys were abundant, and explains the high egg production measured during this period.

The higher O:N ratios observed in 1990 corresponded to the utilization of a food containing more plant material than in

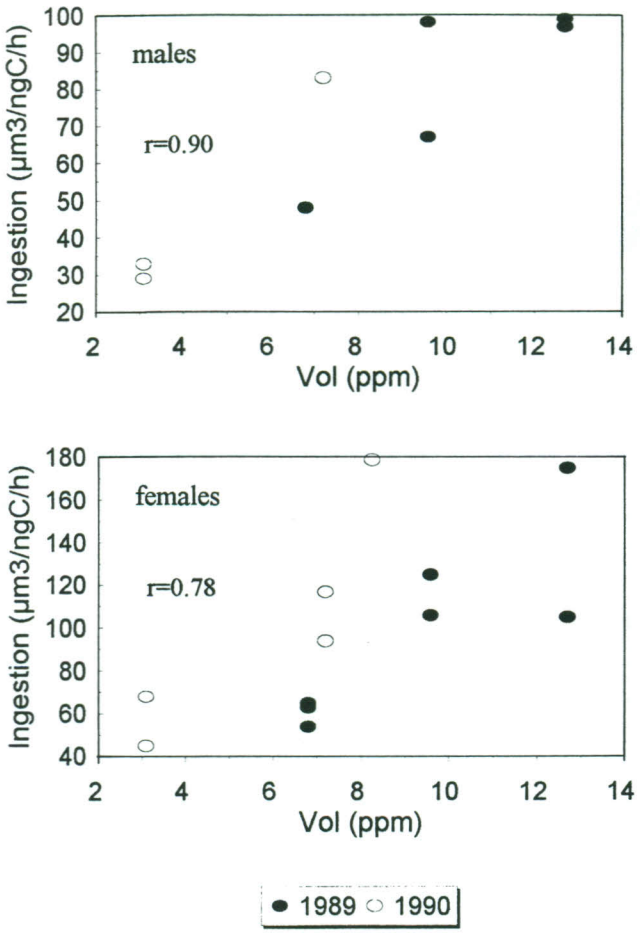


Figure 4

Relation between volume ingestion rates by Acartia tonsa *males and females and total particle concentration.*

1989. This is in agreement with the quality of seston composed of more small sized and chlorophyll-rich particles in 1990. This type of relationship beween trophic conditions, food regime and excretion is classical where omnivorous copepods are concerned (Le Borgne 1986; Thibault *et al.*, 1994).

When *Prorocentrum minimum* prevailed in the algal biomass, the particle size spectrum displayed a clear medium peak, while a more flattened spectrum appeared when *Prorocentrum* was scarce. The ingestion of particles was oriented towards those of the peak in the first case, and towards the smallest particles, more abundant, in the second case, despite the preference for largest ones shown by the electivity index. Similar observations (for example, Tackx *et al.*, 1989) were done in nearshore areas where blooms can occur.

Considering the energy budget, the greater ability of females to produce matter is directly related to their higher capability to enhance their food acquisition without increasing their metabolic expenditure, which remains stable and comparable for both sexes. More realistic P:B values were found using a RQ value of 0.7 in 1989 instead of 1: all values were then positive for the males and closer to the egg production values for the females. This supports the hypothesis of a food regime different in 1989 (more animal prey eaten) and 1990 (mainly plant food).

As a conclusion, our results show that sexual differences occur in the feeding strategy of *A. tonsa*, females needing more energy than males for reproduction. They also indicate the adaptability of *A. tonsa* to short- or medium-term variations in the quantity and quality of food and their capability to feed upon animal prey. This flexibility perhaps contributes to explain the abundance of *A. tonsa* in nutritionally fluctuating biotopes such as nearshore, estuarine or lagoonal environments.

REFERENCES

Anraku M., M. Omori (1963). Preliminary survey of the relationship between the feeding habit and structure of the mouth-parts of marine copepods. *Limnol. Oceanogr.* **8**, 116-126.

Cervetto G., R. Gaudy, M. Pagano, L. Saint-Jean, G. Verriopoulos, R. Arfi, M. Leveau (1993). Diel variations in *Acartia tonsa* feeding, respiration and egg production in a Mediterranean lagoon. *J. Plankt. Res.* **15**, 11, 1207-1228.

Cervetto G., M. Pagano, R. Gaudy (1995). Feeding behaviour and migrations in a natural population of the copepod *Acartia tonsa*. *Hydrobiologia* **300/301**, 237-248.

Conover R.J. (1966). Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* **11**, 338-345.

Cowles T.J. (1979). The feeding response of copepods from the Peru upwelling system: food size selection. *J. Mar. Res.* **37**, 601-622.

Eppley R.W., P.R. Sloan (1966). Growth rates of marine phytoplankton: correlation with light absorption by cell chlorophyll *a*. *Physiol. Plant.* **19**, 47-59.

Gamble J.C. (1978). Copepod grazing during a declining spring phytoplankton bloom in the Northern North Sea. *Mar. Biol.* **49**, 303-315.

Gaudy R. (1989). The role of zooplankton in a Mediterranean brackish lagoon. *Sci. Mar.* **53**, 609-616.

Gaudy R. (1992). Biologie de la population du copépode *Acartia tonsa* Dana dans un milieu semi-clos: l'étang de Berre. *Ann. Inst. océanogr. Paris* **68**, 1-2, 159-168.

Gaudy R., G. Verriopoulos, G. Cervetto (1995). Space and time distribution of zooplankton in a Mediterreanean lagoon. *Hydrobiologia* **300/301**, 219-236.

Holm-Hansen O, C.J. Lorenzen, P.W. Holmes, J.D.H. Strickland (1965). Fluorimetric determination of chlorophyll. *J. Cons. Int. Explor. Mer* **30**, 3-15.

Kleppel G.S. (1992). Environmental regulation of feeding and egg production by *Acartia tonsa* off southern California. *Mar. Biol.* **112**, 57-65.

Koroleff F. (1969). Direct determination of ammonia in natural waters as indophenol blue. *International Council for the Exploration of the Sea,* Comm. Meeting **C9**, 1-6.

Landry M.R. (1981). Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Mar. Biol.* **65**, 77-82.

Le Borgne R. (1986). The release of soluble end products of metabolism. *In*: The biological chemistry of marine copepods (EDS Corner and SZCM O'Hara, eds): Oxford Univ. Press, Oxford, 109-164.

Lehman P.V. (1981). Comparison of chlorophyll *a* and carotenoid pigments as predictors of phytoplankton biomass. *Mar. Biol.* **65**, 237-244.

Lonsdale D.J., D.R. Heinle, C. Siegfried (1979). Carnivorous feeding behaviour of the adult calanoid copepod *Acartia tonsa* Dana. *J. exp. mar. biol. ecol.* **36**, 235-248.

Nival P., S. Nival (1976). Particle retention efficiencies of the herbivorous copepod *Acartia clausi* (adult and copepodites stages): effects on grazing. *Limnol. Oceanogr.* **21**, 24-38.

Omori M., T. Ikeda (1984). Methods in marine zooplankton ecology, John Wiley and Sons, New York, 332 p.

Paffenhöfer G.A., D.E. Stearns (1988). Why is *Acartia tonsa* (Copepoda: Calanoida) restricted to nearshore environments ? *Mar. Ecol. Progr. ser.* **42**, 33-38.

Poulet S.A. (1973). Grazing on *Pseudocalanus minutus* on naturally occurring particulate matter. *Limnol. Oceanogr.* **18**, 564-573.

Poulet S.A. (1974). Seasonal grazing of *Pseudocalanus minutus* on particles. *Mar. Biol.* **25**, 109-123.

Pyke G.H., H.R. Piulliam, E.L. Charnov (1977). Optimal foraging: a selective review of theory and test. *Q. Rev. Biol.* **52**, 137-154.

Richman S., D.R. Heinle, R. Huff (1977). Grazing by adult estuarine copepods of the Chesapeake Bay. *Mar. Biol.* **42**, 69-84.

Robertson J.R. (1983). Predation by estuarine calanoid zooplankton on tintinnid ciliates. *Estuar. Coast. Shelf Sci.* **16**, 27-36.

Stoecker D.K., N.K. Sanders (1985). Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid. *J. plankt. Res.* **7**, 85-100.

Tackx M.L.M., P. Polk (1982). Feeding of *Acartia tonsa* Dana (Copepoda, Calanoida): predation on nauplii of *Canuella perplexa* T. and A. Scott (Copepoda, Harpacticoida) in the sluice-dock at Ostend. *Hydrobiologia* **94**, 131-133.

Tackx M.L.M., C. Bakker, J.W. Francke, M. Vink (1989). Size and phytoplankton selection by Oosterschelde zooplankton. *Neth. J. Sea Res.* **23**, 35-43.

Taguchi S. (1976). Relationship between photosynthesis and cell size of marine diatoms. *J. Phycol.* **12**, 185-189.

Thibault D., R. Gaudy, J. Le Fèvre (1994). Zooplankton biomass. feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front, western Mediterranean. Significance to pelagic food web. *J. mar Syst.* **5**, 297-311.

Vanderploeg H.A., D. Scavia (1979). Two indices for feeding with special reference to zooplankton grazing. *J. Fish. res. Bd. Canada* **36**, 4, 362-365.