

Dynamics of the *Acartia* genus (Calanoida: Copepoda) in a temperate shallow estuary (the Mondego estuary) on the western coast of Portugal

Ulisses Miranda AZEITEIRO¹, Sónia Cotrim MARQUES^{1,2}, Luís Miguel Russo VIEIRA^{1,2}, Manuel Ramiro Dias PASTORINHO², Pedro Alfaia Barcia RÉ³, Mário Jorge PEREIRA² and Fernando Manuel Raposo MORGADO²

¹ *IMAR - Institute of Marine Research, c/o Department of Zoology, Faculty of Sciences and Technology, University of Coimbra, 3004-517 Coimbra, Portugal*
E-mail: ulisses@univ-ab.pt

² *Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal*

³ *IMAR - Institute of Marine Research, Laboratório Marítimo da Guia, Department of Animal Biology, Faculty of Sciences, University of Lisbon, 2750-374 Cascais, Portugal*

*The purpose of this work was to review the dynamics of the *Acartia* species in the Mondego estuary (a temperate North-Atlantic shallow estuary in Western Portugal) in a genus integrated perspective. The *Acartia* genus is represented in the system by the species *Acartia clausi* and *Acartia tonsa*; the samples were taken between July 1999 and June 2000, with 63 and 125 μm mesh size nets, and between January 2003 and January 2004, with a 335 μm mesh size net, in the downstream and upstream areas of the estuary. Significant differences in abundance were found between months and sampling stations for the two species (ANOVA, $P \leq 0.05$). *A. clausi* dominated in the downstream estuary, registering peaks in June (156 ind. m^{-3}) and September (73 ind. m^{-3}); in the upstream estuary this species showed a maximum of density in September (35 ind. m^{-3}). *A. tonsa* dominated in the upstream estuary with peaks of abundance occurring in December (2372 ind. m^{-3}) and October (1056 ind. m^{-3}) in the downstream estuary this species exhibited higher abundance in August (52 ind. m^{-3}). The two species of the genus coexist in time exhibiting a strong spatial segregation behavior in the estuary.*

Key words: estuaries, Mondego estuary, Copepoda, *Acartia*, ecology

INTRODUCTION

Copepoda (Crustacea) comprise the most abundant taxa of the marine and estuarine zooplankton (OMORI & IKEDA, 1984; MAUCHLINE, 1998). There they act as an efficient and direct path for energy transfer to higher trophic levels (WILLIAMS *et al.*, 1994; MAUCHLINE, 1998) and contribute substantially to the downward flux of organic material (FEINBERG & DAM, 1998). Abundance and biomass estimates for Copepoda species, in an estuarine ecosystem, provides useful information on the energy flux, and such measurements are essential in ecological studies (VIEIRA *et al.*, 2003b; PASTORINHO *et al.*, 2003).

The copepoda community of the Mondego estuary is dominated by the *Acartia* genus (Copepoda: Calanoida) (AZEITEIRO *et al.*, 1999, 2000; VIEIRA *et al.*, 2003a). The *Acartia* genus is represented in the system by the species *Acartia clausi* (Giesbrecht, 1889) (AZEITEIRO *et al.*, 1999, 2000; VIEIRA *et al.*, 2003a, b) and *Acartia tonsa* (Dana, 1848) (AZEITEIRO *et al.*, 1999, 2000; PASTORINHO *et al.*, 2003; VIEIRA *et al.*, 2003a). This selected genus is an abundant genus of temperate zooplankton communities (JEFFRIES, 1967; LEE & MCALICE, 1979; BRYLINSKI, 1981; SOBRAL, 1985; GAUDY *et al.*, 2000).

Each one of the two species *Acartia* was already studied in what concerns morphometric relations, production and turnover-rates (*A. clausi*: VIEIRA *et al.*, 2003b; *A. tonsa*: PASTORINHO *et al.*, 2003) using image analysis methods (CHRISTOU & VERRIOPOULOS, 1993; JEFFRIES *et al.*, 1998). For zooplankton, the literature reports suitable coefficients, which, starting from linear measurements of body fractions (TACKX *et al.*, 1995) reveal the weight or carbon contents of the specimens studied (SHMELEVA, 1965; PERTSOVA, 1966; KRYLOV, 1968; UYE, 1982).

PASTORINHO *et al.* (2003) also used histology, histochemistry and biometry in the species *A. tonsa* to determine whether fecundity is a limiting factor in itself or are zooplankters constrained to respond to an ever-changing environment. Analyses of maturation stage of

oocytes in adult ovigerous females demonstrated the presence of all three considered oocytical development stages: immature, vitellogenic and mature, with emphasis in the latter since it indicates a permanent capability for reproduction. Taking in account the relevance of the species, this fact demonstrated the modulating influence of ecological parameters (namely the environmental parameters) in general zooplankton reproductive traits.

The purpose of this work was to describe and interpretate the dynamics of the *Acartia* genus in the Mondego estuary with the specific published data available and new collected data.

MATERIALS AND METHODS

Study Site

The Mondego estuary, located in the Portuguese west coast (North Atlantic Ocean) (40°08'N; 8°50'W), has an area of 3.3 km² and a volume of 0.0075 km³. The hydrological basin of the Mondego, with an area of 6670 km², provides an average discharge of 8.5x10⁹ m³s⁻¹ (Fig. 1).

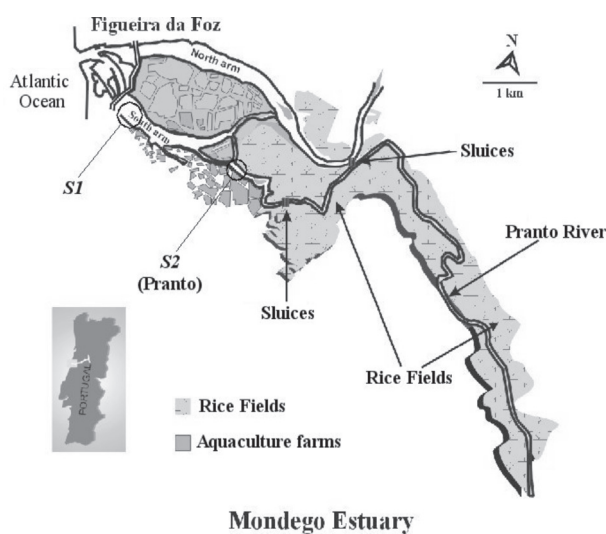


Fig. 1. Location of zooplankton sampling stations in the Mondego estuary

The circulation in the South arm of the estuary depends on the tides and, in much smaller amount on the freshwater discharge from a tributary – the Pranto River, which is controlled by a sluice located 3 km from the confluence with the Mondego River. The sampling stations were located along the southern arm of the estuary (Fig. 1): station 1 near its mouth and station 2 further inland in the inner area of the southern arm (1.7 m deep in high tide).

Sampling program

Samples were taken monthly, from July 1999 to June 2000 (63 and 125 μm taxocenosis) (VIEIRA *et al.*, 2003a) and from January 2003 to January 2004 (335 μm taxocenosis).

Determination of environmental parameters, phytoplankton and zooplankton

All samples were analyzed *in situ* for salinity, temperature, dissolved oxygen and pH. Samples were also analyzed in the laboratory

(in triplicate) for their content in chlorophyll *a* concentration (BACELAR-NICOLAU *et al.*, 2002, 2003; VIEIRA *et al.*, 2002).

Sub-surface (20 cm depth) phytoplankton samples (horizontal hauls) were collected with a 25 μm mesh size net (VIEIRA *et al.*, 2002).

Sub-surface (20-40 cm depth) zooplankton samples (horizontal hauls) were collected using 63 and 125 μm (VIEIRA *et al.*, 2003A) and 335 μm mesh size nets.

Production study methodology

Each one of the two species was already studied in what concerns morphometric relations, production and turnover-rates using image analysis methods (*A. clausi*: VIEIRA *et al.*, 2003b and *A. tonsa*: PASTORINHO *et al.*, 2003).

Data analysis

ANOVA and Regression analysis were applied to find an explanatory model for the dynamics of the two species.

Table 1a. Environmental results (temperature, salinity, pH, oxygen dissolved -saturation% and chlorophyll *a* values) from monthly annual sampling cycle in the south arm of the Mondego estuary, in both sampling stations, between July 1999 and June 2000

	July		Aug		Sept		Oct		Nov		Dec	
	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂
Temp (° C)	18.9	23.6	20.0	25.0	19.1	20.7	16.9	19.6	16.8	16.6	11.8	13.2
Sal (psu)	24.5	18.1	23.0	26.0	25.0	31.0	27.0	22.0	31.1	19.5	17.9	29.3
pH	8.2	7.9	8.1	7.6	8.3	8.3	7.6	8.3	7.9	7.5	7.8	8.4
DO ₂ %	80.0	72.0	94.0	85.0	86.0	48.0	80.5	60.0	68.4	48.0	69.5	79.0
Chl <i>a</i> (mg m ⁻³)	0.605	1.445	0.415	2.275	0.250	2.270	1.080	1.620	0.670	1.390	0.260	1.160

	Jan		Feb		Mar		Apr		May		June	
	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂
Temp (° C)	11.9	11.0	14.1	14.1	-	-	14.2	14.0	15.8	18.3	18.0	22.3
Sal (psu)	23.2	23.2	29.7	29.4	-	-	31.7	9.5	21.1	12.0	26.1	10.1
pH	7.8	7.9	7.9	7.6	-	-	7.5	7.6	7.7	7.6	8.2	8.3
DO ₂ %	89.5	91.0	99.4	72.4	-	-	85.0	74.0	97.4	75.2	66.0	59.0
Chl <i>a</i> (mg m ⁻³)	0.190	0.810	0.340	2.040	-	-	0.810	1.300	0.740	2.730	0.620	2.180

Table 1b. Environmental results (temperature, salinity, pH, oxygen dissolved -saturation%, and chlorophyll a values) from monthly annual sampling cycle in the south arm of the Mondego estuary, in both sampling stations, between January 2003 and January 2004

	Jan		Feb		Mar		Apr		May		June			
	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂		
Temp (° C)	10.3	8.7	12.3	12.1	14.4	17.4	17.1	18.2	17.2	21.3	17.1	23.9		
Sal (psu)	9.8	0.8	19.5	16.9	27.5	18.0	19.9	14.0	31.1	0.6	33.8	17.7		
pH	8.0	7.8	8.2	8.1	8.1	8.0	8.2	8.0	8.2	7.0	8.2	7.9		
DO ₂ (%)	79.0	45.0	125.0	112.0	87.1	90.2	94.0	85.7	95.4	65.6	95.5	84.5		
Chl a (mg m ⁻³)	0.737	12.235	1.761	9.831	2.463	8.310	3.586	3.811	4.973	15.977	4.474	21.886		
	July		Aug		Sept		Oct		Nov		Dec		Jan	
	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂
Temp (° C)	18.7	-	17.6	23.8	17.6	19.1	16.1	16.5	16	15.7	13.2	13.2	12.9	11.3
Sal (psu)	32.1	-	33.4	15.7	31.8	22.5	33.2	26.3	20.7	18.3	13.1	5.5	29.4	19.5
pH	8.2	-	7.7	7.6	7.4	7.3	8.0	7.8	8.0	7.6	7.8	7.6	8.2	8.0
DO ₂ (%)	109.1	-	101.9	70.4	87.9	61.3	99.5	83.5	81.1	55.6	89.0	76.5	91.0	89.0
Chl a (mg m ⁻³)	4.495	5.305	4.768	14.839	1.926	5.160	4.354	4.903	1.945	2.633	1.945	2.633	1.119	4.025

RESULTS

Variation in environmental variables, phytoplankton and zooplankton

The environmental parameters, relatively to the 99/00 annual cycle (Table 1a), description and analysis were published by BACELAR-NICOLAU *et al.* (2002, 2003) and VIEIRA *et al.* (2002). Relatively to the 03/04 annual cycle the data is presented in Table 1b.

In the 99/00 annual cycle in sampling station 1 the average temperature was of 16.1 °C, varying between 20.0 °C in August 2000 and 11.8 °C in December 1999. The salinity varied along the annual cycle between a minimum of 17.9 psu in December 1999 and a maximum of 31.7 psu in April 2000. pH suffered a slight fluctuation during the year, rounding an average value between 7.5 and 8.3. The dissolved oxygen levels presented a minimum of 66.0 % in June 2000 and a maximum of 99.4 % in February 2000, with an annual average value of about 83.3 %.

The chlorophyll *a* presented an average value of 0.544 mg m⁻³, with a maximum in October 1999 (1.080 mg m⁻³) and a minimum in January 2000 (0.190 mg m⁻³) (BACELAR-NICOLAU *et al.*, 2002, 2003; VIEIRA *et al.*, 2002). In station 2, average temperature was 18.0 °C, varying between 25.0 °C, in August 1999 and 11.0 °C in January 2000. The salinity varied along the year with a minimum of 9.5 psu in April 2000, and a maximum of 31.0 psu in September 1999. pH suffered a little fluctuation during the studied period, varying between a maximum value of 8.4 in December 1999 and a minimum value of 7.5 in September 1999, with an average value of 7.9. Dissolved oxygen concentration presented a minimum value of 48.0 % in September and November 1999, a maximum value of 91.0% in January 2000 and an annual average of 69.4%. Chlorophyll *a* concentration presented higher average values than in station 1 (1.747 mg m⁻³), with a maximum of 2.730 mg m⁻³ in May 2000, and a minimum of 0.810 mg m⁻³ in January 2000 (BACELAR-NICOLAU *et al.*, 2002,

2003; VIEIRA *et al.*, 2002). In the phytoplankton, the most abundant groups were Bacillariophyceae, Cyanoprokaryota, Dinophyta, Euglenophyta and Chlorophyta. The composition of phytoplankton differed between the two sampling stations. Bacillariophyceae dominated in sampling station 1 during all the year. In station 2, Bacillariophyceae dominated September, December, February and May. Cyanophyta dominated in August and June. Chlorophyta presented important percentages in January and March (VIEIRA *et al.*, 2002).

In the 03/04 annual cycle temperature ranged from 8.7 to 23.9 °C, reaching minimum and maximum values during winter and summer, respectively, showing a typical seasonal pattern for temperate Atlantic estuaries. Significant differences among the two stations and months were observed (ANOVA, $P < 0.05$). The spring-summer months exhibited an overall warming trend, especially, in downstream sampling station. Salinity values during the sampling period varied between 0.6 psu observed in May and 33.4 psu observed in August. Dissolved oxygen levels ranged from 45.0 % in January 2003 and 125.0 % in February. A fluctuation in these values was observed during the study period. During this study chlorophyll *a* concentration ranged from 0.74 mg m⁻³ in January to 21.89 mg m⁻³ in June. The maximum chlorophyll *a* concentrations were observed at the stations S2. Peaks of concentration occurred in June and August.

In the 99/00 annual cycle the zooplankton community, in terms of species composition and distribution, was dominated by estuarine and estuarine/marine copepods, adults and copepodites (VIEIRA *et al.*, 2003a). In the 63 µm taxocenosis *A. tonsa* occurred with low densities throughout the year, at station 1, registering a peak in April (1860 ind. m⁻³). At station 2, this species showed a peak in October (29070 ind. m⁻³) and important densities in August (3793 ind. m⁻³), November (2121 ind. m⁻³), December (2724 ind. m⁻³) and April (1966 ind. m⁻³). *A. clausi* abundances showed significant differences of abundance throughout the year (ANOVA, $0.05 > P > 0.01$), registering peaks in January (2331 ind. m⁻³) and April

(1623 ind. m⁻³), at station 1, and in October (14172 ind. m⁻³), November (1810 ind. m⁻³), December (2138 ind. m⁻³) and April (2276 ind. m⁻³), at station 2. In the 125 µm taxocenosis *A. tonsa* densities were significantly affected by the interaction between the months of the year and the sampling stations (ANOVA, $0.05 > P > 0.01$). At station 1, *A. tonsa* showed high abundances in April (1680 ind. m⁻³) and May (840 ind. m⁻³). At station 2, *A. tonsa* showed peaks in November (6520 ind. m⁻³) and February (3500 ind. m⁻³), and important densities in October (1650 ind. m⁻³), December (2960 ind. m⁻³) and April (2520 ind. m⁻³). *A. clausi* presented low abundances all year round, registering a peak in April (560 ind. m⁻³), at station 1, and in November (1160 ind. m⁻³), at station 2 (VIEIRA *et al.*, 2003a).

In the 03/04 annual cycle the copepods dominated the zooplankton community throughout the year. The species *A. clausi* and *A. tonsa* had contributed about 11% and 75%, respectively, of the total copepod abundance. Significant differences in abundance were found between months and sampling stations for the two species (ANOVA, $P \leq 0.05$). *A. clausi* (Fig. 2a) dominated in the downstream station (S₁), registering peaks in June (156 ind. m⁻³) and September (73 ind. m⁻³); at station 2 this species showed a maximum of density in September (35 ind. m⁻³). *A. tonsa* (Fig. 2b) dominated in the upstream station (S₂) with peaks of abundance occurring in December (2372 ind. m⁻³) and October (1056 ind. m⁻³). At station 1 this species exhibited higher abundance in August (52 ind. m⁻³).

Weight -length relationships

The following biomass/length relationship was estimated for specimens of *A. clausi* and *A. tonsa*, respectively: $Y = 0.11e^{3.14x}$, with a r^2 of 0.59 (VIEIRA *et al.*, 2003b) and $Y = 0.15e^{3.04x}$, with a r^2 of 0.62 (PASTORINHO *et al.*, 2003).

Production and P/\bar{B} ratio

Length-weight relationships were used to estimate production taking into account cohort growth and mortality. The annual production was calculated for specimens of *A. clausi* and *A.*

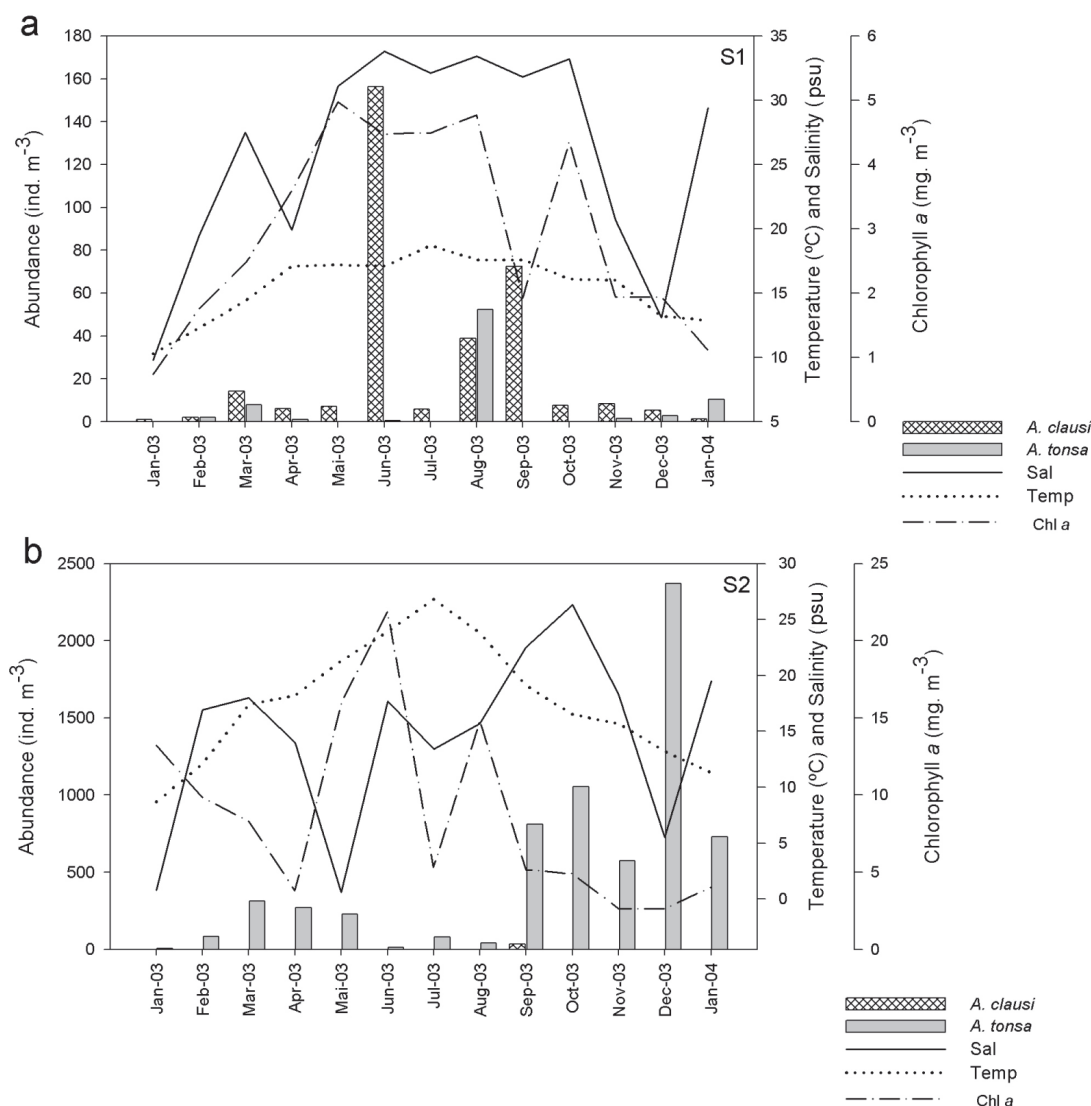


Fig. 2. Spatio-temporal distribution of salinity, temperature and chlorophyll a and *Acartia* species between January 2003 and January 2004

tonsa, respectively: $63.44 \text{ mgCm}^{-3}\text{yr}^{-1}$ (VIEIRA *et al.*, 2003b) and $43.12 \text{ mgCm}^{-3}\text{yr}^{-1}$ (PASTORINHO *et al.*, 2003). The production/biomass (P/\bar{B}) ratio was estimated, respectively, at 25.50 and 10.56 (PASTORINHO *et al.*, 2003; VIEIRA *et al.*, 2003b).

Multiple regression analysis

Multiple regression analysis between environmental parameters and zooplankton total density showed that zooplankton increases with increasing salinity, temperature and chlorophyll *a* ($r=0.859$; $r^2=0.737$) (VIEIRA *et al.*, 2003a).

In the $125 \mu\text{m}$ taxocenosis for the two species *A. clausi* and *A. tonsa*, respectively, $r=0.990$; $r^2=0.981$ ($P<0.001$) (VIEIRA *et al.*, 2003b) and $r=0.964$, $r^2=0.929$ ($P<0.001$) (PASTORINHO *et al.*, 2003), the abundance increased, respectively, with increasing salinity and temperature (VIEIRA *et al.*, 2003b) and dissolved oxygen and temperature (PASTORINHO *et al.*, 2003). The regression analysis, performed with the $335 \mu\text{m}$ taxocenosis, revealed no significant effect of the environmental factors (salinity, temperature, dissolved oxygen and chlorophyll *a*).

DISCUSSION

The distribution patterns of the environmental parameters observed are mostly in agreement with previous studies (AZEITEIRO & MARQUES 2000; AZEITEIRO *et al.*, 2002; BACELAR-NICOLAU *et al.*, 2002, 2003; VIEIRA *et al.*, 2002) defining a clear spatial unidirectional salinity gradient and secondarily a temperature-chlorophyll *a* temporal gradient (AZEITEIRO & MARQUES 2000; AZEITEIRO *et al.*, 2002; BACELAR-NICOLAU *et al.*, 2002, 2003; VIEIRA *et al.*, 2002). The estuarine and marine phytoplanktonic communities are frequently dominated by dinoflagellate and diatoms species. Both stations presented diatoms and dinoflagellates as the most abundant phytoplankton species. There were also found Chlorophyta, Euglenophyta and Cyanoprokaryota (VIEIRA *et al.*, 2002). This flora conditioned the primary consumers, not only for the form of the cells and the associations that they establish with each other, but also because of the nutritional quality of the different species. Several studies have shown the importance of food quality on fertility within the

Acartia genus (DAM *et al.*, 1994; PAGANO & SAINT-JEAN, 1994b; JONASDOTTIR, 1994; JONASDOTTIR & KIORBOE, 1996). The development of *Microcystis aeruginosa* blooms induces mortality within *A. clausi* assemblages (PAGANO & SAINT-JEAN, 1994a) and some diatoms species inhibits the fertility in *A. clausi* individuals (JONASDOTTIR, 1994; IANORA *et al.*, 1996). However the nutritional quality requirements, ecological population interactions and other ecological interactions were not studied.

The production values estimated to the two species are in accordance with values reported by other authors to the *Acartia* genus and other copepods (Table 2).

The P/\bar{B} values obtained had given expected modal turnover rates (VALIELA, 1995). Those P/\bar{B} values mean that although the biomass of small sized species (e.g. copepods) may be small, the higher specific production makes them important producers. *A. clausi* is an r-strategy-type species, characterized by a high productivity (HIRCHE, 1992). The two species differences in production values and turnover rates are due to

Table 2. Copepoda Production and Production/Biomass data

Species	Reference	Study site	Methods	P (annual)	P/B
<i>Acartia</i> spp.	(Hirst <i>et al.</i> , 1999)	Coastal station, Solent UK	weight	17.62 mg C m ⁻³ yr ⁻¹	
<i>Acartia bifilosa</i>	(Irigoien and Castel, 1995)	The Gironde (SW France)	size		28
<i>Acartia</i> spp.	(Escaravage and Soetaert, 1995)	Westerschelde estuary, Nether	growth rate methods	5 g C m ⁻² y ⁻¹	
Copepoda	(Hirst <i>et al.</i> , 1999)	Coastal station, Solent UK	weight	32.2 mg C m ⁻³ y ⁻¹	
<i>Eurytemora</i> spp.	(Escaravage and Soetaert, 1995)	Westerschelde estuary, Nether	growth rate methods	6 g C m ⁻² y ⁻¹	
<i>Paracalanus parvus</i> and <i>Pseudocalanus elongatus</i>	(Hirst <i>et al.</i> , 1999)	Coastal station, Solent UK	weight	1.67 mg C m ⁻³ y ⁻¹	
<i>Temora longi- cornis</i>	(Hirst <i>et al.</i> , 1999)	Coastal station, Solent UK	weight	4.77 mg C m ⁻³ y ⁻¹	
<i>Acartia tonsa</i>	(Pastorinho <i>et al.</i> , 2003)	Mondego estuary, Portugal	cohorts	43.12 mg C m ⁻³ y ⁻¹	11
<i>Acartia clausi</i>	(Vieira <i>et al.</i> , 2003b)	Mondego estuary, Portugal	cohorts	63.44 mg C m ⁻³ y ⁻¹	26

the ecological conditions that the two species experienced: *A. clausi* more productive in a less stable environment (a tide variable environment) and predator pressure (by medusa, shiphonophores, chaetognaths, large copepods and fishes) and *A. tonsa* less productive in a more stable environment with a direct food competitor the species *Calanipeda aquae-dulcis* (YELIZARENKO, 1992) that co-exists with *A. tonsa* (AZEITEIRO *et al.*, 1999).

These production results indicate that the *Acartia* genus may play a significant role in transferring energy to higher trophic levels in the estuary. Although production by nauplii is not included in the present study, this does not typically exceed 25% of copepod total production (MULLIN, 1988; LIANG & UYE, 1996; LIANG *et al.*, 1996). Most copepods reproduce throughout all the year. The cohorts represent the maximum of generations possible and the duration of the cohorts represents the longevity of the generations (BINET, 1977). Copepoda life cycle in temperate regions have an average of 25 to 45 days. In temperate regions the adult longevity exceed rarely two months (GAUDY, 1972) with variable annual growth generations (Table 3) function of the latitude of the systems analyzed. *Acartia* genus biological cycle depends on the local of study. Annual generations depend on latitude and trophic availability. Both temperature and food availability are known to play a significant role in the copepod production activity (LEE & MCALICE, 1979; KLEIN & GONZALEZ, 1988). Temperature together with food should explain

the *Acartia* genus biological cycles features in the Mondego estuary.

Histological observation of the positioning and distribution of cells and different cellular structures, qualitative evaluation of chemical contents, through histochemistry, pointing existence of differences between development stages in terms of the accumulation of reserve substances (nominately glycoproteins and, by indirect extrapolation, lipids), measurement of cellular size and determination of the C/N ratio, were applied to *A. tonsa* by PASTORINHO *et al.* (2003) in order to obtain a clear and convincing answer the environmental determination in the *Acartia* genus biological cycles. These methods and techniques allowed the identification of three very distinct stages of maturation of oocytes and hence the elaboration of a functional scales, numerically based and statistically validated, allowing comparisons between samples. It was verified that all three maturation stages were always present. The presence in the gonadic masses of the females of stage III oocytes (mature) mean that these females are fully capable of reproduction and only fecundation has to occur, since these cells possess all that is necessary for the juvenile to be viable (PASTORINHO *et al.*, 2003). The simultaneous existence of fully functional reproductive cells in registered high density epochs and in minimum density periods of the reproductive cycle of the organisms, indicate that the main modulating influence over these cycles comes out of ecological abiotic parameters which notoriously

Table 3. Number of generations

Number of Generations	Study site	Reference
2	Ocidental Atlantic	(DEEVEY, 1971)
3,4	Adriatic Sea	(VUČETIĆ, 1957)
4	Roscoff	(RAZOULS, 1965)
4	Long Island Sound	(CONOVER, 1956)
5	Plymouth	(DIGBY, 1950)
6,7	Sebastopol	(GREZE & BALDINA, 1972)
8	Black Sea	(PORUMB, 1968)
9	Karadag	(TCHAIANOVA, 1950)
Continuous	Mediterran	(BERNARD, 1958)

superimpose over the continuous reproductive capabilities of zooplanktonic organisms, namely the genus *Acartia* as referred by HEINLE (1966), creating the well described fluctuating patterns (KLEPPEL, 1992). As a corollary one could conclude that seasonal variability in zooplankton densities reflects advantageous or disadvantageous assemblages of external factors acting over a latent reproductive potential.

Temperature is an important factor controlling seasonal distribution of copepods (HALSBAND-LENK *et al.*, 2002), namely the *Acartia* species (GONZALES, 1974; SULLIVAN & MCMANUS, 1986). The thermal sensitivity of both species (CERVETTO, 1985), in the studied system, could explain their continuous distribution year around, at temperatures ranging between 11 and 25 °C. Seasonal fluctuations of both species are described by several authors (DEEVEY, 1948, 1960; CONOVER, 1956; HEINLE, 1966; JEFFRIES, 1962, 1967; SAGE & HERMAN, 1972; LEE & MCALICE, 1979; SOBRAL, 1985; SULLIVAN & MCMANUS, 1986; GAUDY *et al.*, 2000) where *A. clausi* and *A. tonsa* co-exist and reach great abundances. All these investigations have indicated a well defined relationship between seasonal changes and the temperature.

A. tonsa is a brackish water euryhaline and eurythermic species; in low concentrations of dissolved oxygen retard the development of eggs and results in death of all copepod stages of *A. tonsa* (Oxyphilic species) (SAZHINA, 1987). In the Mondego estuary adults occur in the inner and upstream estuary in a shallow, low salinity water stable area; *A. tonsa* performs both horizontal and daily vertical migrations that ensures the residence in the area; young individuals undertake migrations only within surface layers (BRODSKY, 1950) what explains the 63 and 125 µm taxocenosis distribution. The eurythermic behavior explains why *A. tonsa* copepods were found in the plankton year round. *A. clausi* occurs in the mouth of the estuary in a high

salinity/tidal area. The correlations given by the regression analysis reflected the species ecological preferences clarifying the distribution found in previous descriptive zooplankton studies in the estuary (AZEITEIRO *et al.*, 1999, 2000), and also the genus biology (KLEIN & GONZALES, 1988) and ecology (ALCARAZ, 1983; SOBRAL, 1985), namely in the Mondego estuary (AZEITEIRO *et al.*, 2000). In Atlantic temperate systems the species of the genus (namely *A. tonsa* and *A. clausi*) sometimes co-exist at the same time (LEE & MCALICE, 1979); in the Mondego estuary they co-exist (AZEITEIRO *et al.*, 1999, 2000; VIEIRA *et al.*, 2003a) but exhibiting a strong spatial segregation. This two species have different salinity (and temperature) preferences (LANCE, 1963; SAGE & HERMAN, 1972): the two species do not co-exist in the space due to the strong spatial unidirectional salinity gradient (AZEITEIRO *et al.*, 2000). The *A. tonsa* failure to develop in more saline waters (coastal marine water) is due to the sensitivity to the salinity factor (CONOVER, 1956; TESTER & TURNER, 1991; CERVETTO *et al.*, 1999; GAUDY *et al.*, 2000) and, according to PAFFENHOFER & STEARNS (1988) to the low concentrations of appropriate food in sea water comparatively to estuaries. The absence of *A. clausi* population in the estuary middle zone and upstream could result from the predation by the dense resident *A. tonsa* population (CONOVER, 1956; ANRAKU & OMORI, 1963; ANRAKU, 1964; LONSDALE *et al.*, 1979; GIFFORD & DAGG, 1988; WHITE & ROMAN, 1992) or, according to LUTZ *et al.* (1992), a failure of hatching of their eggs due to environmental disadvantageous conditions (anoxic conditions in the bottom layer); the negative impact of anoxia on the viability of subitaneous eggs of calanoid copepods as well as the impact of the benthic-pelagic coupling on their life cycle has already been evidenced in shallow coastal aquatic systems (MARCUS & LUTZ, 1994; MARCUS & BOERO, 1998).

REFERENCES

- ALCARAZ, M. 1983. Coexistence and segregation of congeneric pelagic copepods: spatial distribution of the *Acartia* complex in the Ria of Vigo (NW Spain). *Journal of Plankton Research*, 5 (6): 891-900.
- ANRAKU, M. 1964. Influence of Cape Cod canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. Respiration and feeding. *Limnol. Oceanogr.*, 9:195-206.
- ANRAKU, M. & M. OMORI. 1963. Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. *Limnol. Oceanogr.*, 8:116-126.
- AZEITEIRO, U.M., J.C. MARQUES & P. RÉ. 1999. Zooplankton annual cycle in the Mondego river estuary (Portugal). *Arquivos do Museu Bocage*, 3 (8): 239-263.
- AZEITEIRO, U.M.M. & J.C. MARQUES. 2000. Variação espaço-temporal dos parâmetros ambientais (condições físico-químicas da água e nutrientes) no estuário do Mondego (Costa Ocidental Portuguesa). In: Da Costa Duarte, A., Vale, C., & R. Prego (Editors). *Estudos de Biogeoquímica na Zona Costeira Ibérica*, Publicações da Universidade de Aveiro: 301 – 316.
- AZEITEIRO, U.M., J.C. MARQUES & P. RÉ. 2000. Zooplankton Assemblages in a shallow seasonally tidal estuary in temperate Atlantic Ocean (western Portugal: Mondego Estuary). *Arquivos do Museu Bocage*, 3 (12): 357-376.
- AZEITEIRO, U.M., P. BACELAR-NICOLAU & J.C. MARQUES. 2002. Estado Trófico Pelágico do Braço Sul do Estuário do Mondego. In: Prego, R., Da Costa Duarte, A., Panteleitchouk, A. & Santos, T.R. (Editors). *Estudos sobre Contaminação Ambiental na Península Ibérica*, ISBN 972-771-621-0 Instituto Piaget, Lisboa: 165-177.
- BACELAR-NICOLAU, P., J.C. MARQUES, F. MORGADO, R. PASTORINHO, L.B. NICOLAU & U.M. AZEITEIRO. 2002. Tidal induced variations in the bacterial community, and in physical and chemical properties of the water column of the Mondego Estuary. *Revista de Biologia (Lisboa)*, 19: 51-62.
- BACELAR-NICOLAU, P., L.B. NICOLAU, F. MORGADO, R. PASTORINHO, J.C. MARQUES & U.M. AZEITEIRO. 2003. Bacterioplankton Dynamics in the Mondego Estuary (Portugal). *Acta Oecologica*, 24: S67-S75.
- BERNARD, M. 1958. La production hivernale et printanière du plancton à Alger. Premières observations, *Rapp. Comm. Int. Expl. Sci. Mer Médit.*, 14: 3-196.
- BINET, D. 1977. Cycles biologiques et migrations ontogéniques chez quelques copépodes pélagiques des eaux ivoiriennes. *Cahiers O.R.S.T.O.M. sér. Océanographie*, Vol. XV, n° 2: 111-138.
- BRODSKY, K.A. 1950. Copepods Calanoida in the Far East seas of the USSR and Arctic basin. In: *Inventory on the USSR Fauna*. USSR AS ZIN. Moscow-Leningrad, pp. 418-420.
- BRYLINSKI, J. 1981. Report on the presence of *Acartia tonsa* Dana (Copepoda) in the Harbor of Dunkirk (France) and its geographical distribution in Europe. *J. Plankton Res.*, 3(2): 255-260.
- CERVETTO, G. 1995. Comparaison de la répartition spatio-temporelle et de l'écophysiologie de deux espèces de copépodes calanoides congénériques (*Acartia tonsa* et *Acartia clausi*) en milieu côtier et lagunaire (Golfe de Fos. Etang de Berre). Thèse Doctorale. Université Aix-Marseille II, 225 pp.
- CERVETTO, G., R. GAUDY & M. PAGANO. 1999. Influence of salinity on distribution of *Acartia tonsa* (copepoda calanoida). *J. Exp. Mar. Biol. Ecol.*, 235: 33-45.
- CHRISTOU, E. & G. VERRIOPOULOS. 1993. Length, weight and condition factor of *Acartia clausi* (Copepoda) in the eastern Mediterranean. *J. Mar. Biol. Ass. U. K.*, 73: 343-353.
- CONOVER, R.J. 1956. Oceanography of Long Island Sound 1952-1954. 6. Biology of *Acartia clausi* and *Acartia tonsa*. *Bull. Bingham, Oceanogr. Coll.*, 15: 156-233.

- DAM, H.G., W.T. PETERSON & D.C. BELLANTONI. 1994. Seasonal feeding and fecundity of the calanoid copepod *Acartia tonsa* in Long-Island Sound is omnivore important to egg production? *Hydrobiologia*, 293: 191-199.
- DEEVEY, G.B. 1948. The zooplankton of Tisbury Great Pond. *Bull. Bingham Oceanogr. Coll.*, 15:156-233.
- DEEVEY, G.B. 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bulletin Bingham Oceanogr. Coll., Yale University*, 17: 54-86.
- DEEVEY, G.B. 1971. The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. *Limnol. Oceanogr.*, 16 (2): 1-44.
- DIGBY, P.S.B. 1950. The biology of the small plankton copepods of Plymouth, *J. Mar. Biol. Ass. U. K.*, 29: 393-438.
- ESCARAVAGE, V. & K. SOETAERT. 1995. Secondary production of the brackish copepod communities and their contribution to the carbon fluxes in the Westerschelde estuary (The Netherlands). *Hydrobiologia*, 311: 103-114.
- FEINBERG, R.L. & H.G. DAM. 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.*, 175: 87-96.
- GAUDY, R. 1972. Contribution à la connaissance du cycle biologique des copépodes du Golfe de Marseille, 2. Étude du cycle biologique de quelques espèces caractéristiques. *Tethys*, 4: 175-242.
- GAUDY, R., G. CERVETTO & M. PAGANO. 2000. Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. *J. Exp. Mar. Biol. Ecol.*, 247: 51-65.
- GIFFORD, D.J. & M.J. DAGG. 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana, carnivores vs. herbivores in natural microplankton assemblages. *Bull. Mar. Sci.*, 43: 458-468.
- GONZALES, J.G. 1974. Critical thermal maxima and upper temperature for the calanoid copepods *Acartia tonsa* and *Acartia clausi*. *Mar. Biol.*, 27: 219-223.
- GREZE, V.N. & E.P. BALDINA. 1972. Changements de population et production annuelle d'*Acartia clausi* et *Centropages kroyeri* dans la zone néritique de la Mer Noire (in Russian). *Trudy Sevastopol. Biol. St.*, 17: 149-161.
- HALSBAND-LENK, C., H. HANS-JÜRGEN & F. CARLOTTI. 2002. Temperature impact on reproduction and development of congener copepod populations. *J. Exp. Mar. Biol. Ecol.*, 271: 121-153.
- HEINLE, D.R. 1966. Production of a Calanoid Copepod, *Acartia tonsa*, in the Patuxent River Estuary. *Chesapeake Sci.*, 7: 59-74.
- HIRCHE, H.J. 1992. Egg production of *Eurytemora affinis* – Effect of k-strategy. *Estuar. Coast. Shelf S.*, 35: 395-407.
- HIRST, A.G., M. SHEADER & J.A. WILLIAMS. 1999. Annual pattern of calanoid copepod abundance prossome length and minor role in pelagic carbon flux in the Solent. *Mar. Ecol. Prog. Ser.*, 177: 133-146.
- IANORA, A., S.A. POULET, A. MIRALTO & R. GROTTOLO. 1996. The diatom *Thalassiosira rotula* affects reproductive success in the copepod *Acartia clausi*. *Mar. Biol.*, 125: 279-286.
- IRIGOIEN, X. & J. CASTEL. 1995. Feeding rates and productivity of the copepod *Acartia bifilosa* in a highly turbid estuary; the Gironde (SW France). *Hydrobiologia*, 311: 115-125.
- JEFFRIES, H.P. 1962. Succession of two *Acartia* species in estuaries. *Limnol. Oceanogr.*, 7(3): 354-364.
- JEFFRIES, H.P. 1967. Saturation of estuarine zooplankton by congeneric associates. In: Lauff, G.M. (Editor). *Estuaries*, Am. Assoc. Adv. Sci, Washington, DC, Publ. No. 83. pp. 500-508.
- JEFFRIES, H., M. BERMAN, A. POULARIKAS, C. KATSINIS & I. MELAS. 1998. Identification of zooplankton by pattern recognition. *Mar. Biol.*, 78: 329-334.
- JONASDOTTIR, S.H. 1994. Effects of food quality on the reproduction success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar. Biol.*, 121: 67-81.

- JONASDOTTIR, S.H. & T. KIORBOE. 1996. Copepod recruitment and food composition: do diatoms affect hatching success? *Mar. Biol.*, 125: 743-750.
- KLEIN, W.C.M. & S.R. GONZALEZ. 1988. Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. *Hydrobiologia*: 167-168 (*Dev. Hydrobiologia*, 47): 201-210.
- KLEPPEL, G. S. 1992. Environmental regulation of feeding and egg production by *Acartia tonsa* off southern California. *Mar. Biol.*, 112: 57-65.
- KRYLOV, V.V. 1968. Relation between wet formalin weight of copepod and copepod body length. *Oceanology*, 8: 723-727.
- LANCE, J. 1963. The salinity tolerance of some estuarine planktonic copepods. *Limnol. Oceanogr.*, 8:440-449.
- LEE, W.Y. & B.J. MCALICE. 1979. Seasonal succession and breeding cycles of three species of *Acartia* (Copepoda: Calanoida) in a Maine estuary. *Estuaries*, 2 (4): 228-235.
- LIANG, D. & S. UYE. 1996. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan, II, *Acartia omorii*. *Mar. Biol.*, 125: 109-117.
- LIANG, D., S. UYE & T. ONBÉ. 1996. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan, I, *Centropages abdominalis*. *Mar. Biol.*, 124: 527-536.
- LONSDALE, D.J., D.R. HEINLE & C. SIEGFRIED. 1979. Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. *J. Exp. Mar. Biol. Ecol.*, 36: 235-248.
- LUTZ, R.V., N.H. MARCUS & J.P. CHANTON. 1992. Effects of the low oxygen concentrations on the hatching and viability of eggs of marine calanoid copepods. *Mar. Biol.*, 114: 241-247.
- MARCUS, N.H. & R.V. LUTZ. 1994. Effects of anoxia on the viability of subitaneous eggs of planktonic copepods. *Mar. Biol.*, 121: 83-87.
- MARCUS, N.H. & F. BOERO. 1998. Mini review: the importance of benthic-pelagic coupling and the forgotten role of life cycle in coastal aquatic systems. *Limnol. Oceanogr.*, 43: 763-768.
- MAUCLINE, J. 1998. The biology of calanoid copepods. *Adv. Mar. Biol.*, 33: 1-170.
- MULLIN, M.M. 1998. Production and distribution of nauplii and recruitment variability – putting the pieces together. In: Rothschild, B.J., (Editor). *Towards a theory on biological-physical interactions in the world ocean*. Kluwer Academic Publishers, New York, pp. 297-320.
- OMORI, M. & T. IKEDA. 1984. *Methods in Marine Zooplankton Ecology*. Wiley-Interscience, New York, 332 pp.
- PAFFENHOFER, G.A., & D.E. STEARNS. 1988. Why is *Acartia tonsa* (Copepoda, Calanoida) restricted to nearshore environments? *Mar. Ecol. Prog. Ser.*, 42:33-38.
- PAGANO, M. & L. SAINT-JEAN. 1994a. Le zooplankton. In Durand, J.R., P. Dufour, D. Guiral, G.F.Z. Zabi, (Editors). *Environment et ressources aquatiques de Côte d'Ivoire*, Paris: Orstom Editions, pp. 155-188.
- PAGANO, M. & L. SAINT-JEAN. 1994b. In situ metabolic budget for the calanoid copepod *Acartia clausi* in a tropical brackish water lagoon (Ebrie Lagoon, Ivory Coast). *Hydrobiologia*, 272: 147-161.
- PASTORINHO, M.R., L. VIEIRA, P. RÉ, F. MORGADO, M.J. PEREIRA, P. BACELAR-NICOLAU, J.C. MARQUES, & U.M. AZEITEIRO. 2003. Population dynamics, biometry, production, histology and histochemistry of *Acartia tonsa* (Crustacea: Copepoda) in a temperate estuary (Mondego estuary, Western Portugal). *Acta Oecologica*, 24: S259-S273.
- PERTSOVA, N. M. 1996. Average weights and size of abundant species of zooplankton in the White Sea. *Oceanology*, 7: 240-243.
- PORUMB, F.I. 1968. Contributions à l'étude de la reproduction, du développement et de la repartition des copépodes pélagiques dans la zone néritique du littoral roumain de la Mer Noire (*Acartia clausi* Giesbr. et *Centropages kroyeri* Giesbr.) *Travaux Museum Hist. Naturele Grigore Antipa*, 8 : 243-250.

- RAZOULS, C. 1965. Etude dynamique et variations saisonnières du plancton dans la région de Roscoff (première partie, les Copépodes). Cahiers Biol. Mar., 6 (2) : 219-254.
- SAGE, L.E. & S.S. HERMANN. 1972. Zooplankton of the Sandy Hook Bay area. Chesapeake Sci., 13:29-39.
- SAZHINA, L.I. 1987. Reproduction, growth, production of marine copepods. Kiev, 156 pp.
- SHMELEVA, A.A. 1965. Weight characteristics of the zooplankton of the Adriatic Sea. Bulletin Inst. Océanographique Monaco, 65 (135): 24 pp.
- SOBRAL, P. 1985. Distribuição de *Acartia tonsa* Dana no estuário do Tejo e sua relação com *Acartia clausi* Giesbrecht. Bol. Inst. Nac. Invest. Pescas, 13: 61-75.
- SULLIVAN, B.K. & L.T. MCMANUS. 1986. Factors controlling seasonal succession of the copepods *Acartia hudsonica* and *A. tonsa* in Narragansett Bay, Rhode Island: temperature and resting egg production. Mar. Ecol. Prog. Ser., 28: 121-128.
- TACKX, M., L. ZHU, W. DE COSTER, R. BILLONES & M. DARO. 1995. Measuring selectivity of feeding by estuarine copepods using image analysis combined with microscopic and Coulter counting. ICES J. Mar. Sci., 52: 419-425.
- TCHAIANOVA, L.A. 1950. Production et croissance des copépodes pélagiques de la Mer Noire (in Russian). Trudy Karadag Biology St., 10: 78-105.
- TESTER, P., & T. TURNER. 1991. Why is *Acartia tonsa* restricted to estuarine habitats. Proc. 4th Int. Conf. on Copepoda, Vol I (special issue), Bull. Plankton Soc. Jpn, pp. 603-611.
- YELIZARENKO, M.M. 1992. Feeding of kilka in the Middle Caspian during the summer season In: Biological resources of the Caspian Sea. Abstracts of the 1st International Conference, September, 1992. BIVTS Kaspyrba, Astrakhan, pp. 111-113.
- UYE, S.I. 1982. Length-Weight Relationships of Important Zooplankton from the Inland Sea of Japan. Journal of Oceanographic Society, 38: 149-158.
- VALIELA, I. 1995. Marine Ecological Processes. Springer, 686 pp.
- VIEIRA, L., U.M. AZEITEIRO, J. FONSECA, R. PASTORINHO, F. MORGADO, P. BACELAR-NICOLAU, J.C. MARQUES & M.J. PEREIRA. 2002. Condições físico-químicas, nutrientes, clorofila a e fitoplâncton no estuário do Mondego. In R. Prego, A. Da Costa Duarte, A. Panteleitchouk & T.R. Santos (Editors). Estudos sobre Contaminação Ambiental na Península Ibérica, ISBN 972-771-621-0 Instituto Piaget, Lisboa, pp. 113-132.
- VIEIRA, L., U. AZEITEIRO, P. RÉ, R. PASTORINHO, J. C. MARQUES & F. MORGADO. 2003a. Zooplankton distribution in a temperate estuary (Mondego estuary southern arm: Western Portugal). Acta Oecologica, 24: S163-S173.
- VIEIRA, L., F. MORGADO, P. RÉ, A. NOGUEIRA, R. PASTORINHO, M.J. PEREIRA, J.C. MARQUES & U.M. AZEITEIRO. 2003b. Population dynamics, biometry and production of *Acartia clausi* (Crustacea: Copepoda) in a temperate estuary (Mondego estuary, Western Portugal). Invertebrate Reproduction and Development, 44(1): 9-15.
- VUČETIĆ, T. 1957. Zooplankton investigations in the Sea Water Lakes "Malo Jezero" and "Veliko jezero" on the Island of Mljet. Acta Adriat., 6(4): 51 pp.
- WHITE, J.R., & M.R. ROMAN. 1992. Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay, the importance of food resource and temperature. Mar. Ecol. Prog. Ser., 86: 239-249
- WILLIAMS, R., D. CONWAY & H. HUNT. 1994. The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. Hydrobiologia, 292/293: 521-530.

Received: 8 September 2003

Accepted: 4 May 2004

Dinamika roda *Acartia* (Calanoida: Copepoda) u temperiranom plitkom estuariju (ušće rijeke Mondego) na zapadnoj obali Portugala

Ulisses Miranda AZEITEIRO¹, Sónia Cotrim MARQUES^{1,2}, Luís Miguel Russo VIEIRA^{1,2}, Manuel Ramiro Dias PASTORINHO², Pedro Alfaia Barcia RÉ³, Mário Jorge PEREIRA² i Fernando Manuel Raposo MORGADO²

¹ IMAR, Institut za istraživanje mora, Odjel zoologije, Fakultet znanosti i tehnologije, Sveučilište Coimbra, 3004-517 Coimbra, Portugal
E-mail: ulisses@univ-ab.pt

² Odjel biologije, Sveučilište u Aveiru, 3810-193 Aveiro, Portugal

³ IMAR, Institut za istraživanje mora, Morski laboratorij u Guia, Odjel animalne biologije, Fakultet znanosti, Sveučilište Lisabon, 2750-374 Cascais, Portugal

SAŽETAK

Cilj ovog rada je dati pregled dinamike vrsta *Acartia* u estuariju Mondego (temperirani sjevernoatlantski plitki estuarij u zapadnom Portugalu) za sve nađene vrste toga roda. Rod *Acartia* je prisutan s tri vrste: *Acartia clausi*, *Acartia bifilosa* var. *inermis* i *Acartia tonsa*; uzorci uzeti od srpnja 1999 do lipnja 2000 su dobiveni pomoću mreže veličine oka 63 i 125 μm , a od siječnja 2003 do siječnja 2004 pomoću mreže veličine oka 335 μm , u nizvodnom i uzvodnom dijelu estuarija. Nađene su znatne razlike u abundanciji dviju vrsta (ANOVA, $P \leq 0.05$). *A. clausi* je bila dominantna u nizvodnom estuariju s maksimumom u lipnju (156 ind. m^{-3}) i rujnu (73 ind. m^{-3}); u uzvodnom estuariju ova vrsta je imala maksimum gustoće u rujnu (35 ind. m^{-3}). *A. tonsa* je bila dominantna u uzvodnom estuariju s maksimumom gustoće u prosincu (2372 ind. m^{-3}) i listopadu (1056 ind. m^{-3}). U nizvodnom estuariju ova je vrsta bila obilatije zastupljena u rujnu (52 ind. m^{-3}). Dvije vrste se u estuariju javljaju istovremeno, ali su prostorno izrazito odijeljene.

Ključne riječi: estuarij, kopepodi, *Acartia*, ekologija
