

CONTRIBUTION OF PLANKTONIC AND DETRITIC FRACTIONS TO THE NATURAL DIET OF MESOZOOPLANKTON IN BAHIA BLANCA ESTUARY

DIODATO, SOLEDAD LORENA^{1,2} & HOFFMEYER, MÓNICA SUSANA^{1,3}

¹ Instituto Argentino de Oceanografía (CONICET-UNS), Camino La Carrindanga km 7.5, B8000FWB Bahía Blanca, Argentina.

² Comisión de Investigaciones Científicas de la Pcia de Buenos Aires (CIC). Calle 526 entre 10 y 11, 1900 La Plata, Argentina.

³ Universidad Tecnológica Nacional, Facultad Regional Bahía Blanca. 11 de Abril 461, B8000LMI Bahía Blanca, Argentina.

Corresponding author: sole22diodato@yahoo.com.ar

Key words: grazing, mesozooplankton, phytoplankton, microzooplankton, detritus.

Running title: Natural diet of mesozooplankton in Bahía Blanca Estuary.

"This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to *Hydrobiologia*."

Received: 04 April 2007

Abstract

The relative importance of phytoplankton and microzooplankton in the natural diet of mesozooplankton was assessed in Bahía Blanca Estuary, Argentina, in December 2005. Grazing experiments were performed using 200-to-2,000 μm grazers and natural food $<100 \mu\text{m}$. Individual and community filtration and ingestion rates were estimated for each food fraction after 24 h incubation. Abundance and carbon data of prey and grazers were qualitatively and quantitatively analyzed. Phytoplankton was mainly composed of diatoms, microzooplankton mainly of tintinnids. Both fractions were less abundant than detritus. Most of the grazers belonged to the copepod *Acartia tonsa*. Mean filtration and ingestion rates on phytoplankton + microzooplankton were $6.44 \text{ ml grazer}^{-1} \text{ d}^{-1}$ and $0.03 \mu\text{g C grazer}^{-1} \text{ d}^{-1}$, respectively. This figure increased to $6.954 \text{ ml grazer}^{-1} \text{ d}^{-1}$ and $1.648 \mu\text{g C grazer}^{-1} \text{ d}^{-1}$ when detritus was included. Mean carbon-specific ingestion rates on phytoplankton and microzooplankton were 0.006 and $0.005 \mu\text{g C } \mu\text{g C}^{-1} \text{ d}^{-1}$, respectively, whereas after the addition of detritus, the overall rate increased to $0.588 \mu\text{g C } \mu\text{g C}^{-1} \text{ d}^{-1}$. Highly significant differences were found between grazing rates on detritus and planktonic fractions. Consumers showed higher filtration rates on microzooplankton than on phytoplankton although 78% of the cells ingested (54.7% $\mu\text{g C}$) came from the latter. The results point to a higher contribution of detritus to the natural diet of mesozooplankton in late spring. The omnivory of *A. tonsa* and the high turbidity of Bahía Blanca Estuary may explain the differences observed among food fractions in terms of carbon intake.

Introduction

Some estuaries, tidal creeks and coastal lagoons are turbid environments characterized by the presence of a large quantity of suspended particulate matter (SPM) (David et al., 2006). The resuspension and transport of SPM are produced mainly by wave and wind action as well as by the turbulence generated as a result of tidal currents and mixing processes (Mann & Lazier, 1991; Federici et al., 2004). The concentrations of SPM generally found in the whole water column range between 5 and 300 mg l⁻¹ of suspended sediments according to Federici et al. (2004), reaching 1000 mg l⁻¹ in Gironde Estuary (Irigoien & Castel, 1995). Within the organic fraction of SPM, allochthonous-autochthonous detritus sometimes predominates over planktonic components (David et al., 2006).

Primary production in these estuaries is highly dependent on light penetration and water column turbidity (Irigoien & Castel, 1995; Gayoso, 1999), with the result that there is sometimes insufficient phytoplanktonic biomass to sustain secondary production. The detritic particles enriched with bacteria and ciliates provide copepods with an alternative food source (Heinle et al., 1977), although the latter is of very low nutritional value.

Bahía Blanca Estuary in Argentina has been reported to be a turbid, shallow, and mesotidal environment, where tides, winds, and geomorphology are the main forcing factors (Perillo et al., 2007). This temperate estuary exhibits a high variability of radiation, temperature, and salinity conditions along the year. SPM mostly consists of silt and clay sediments alongside detritus and small planktonic fractions. The high concentration of suspended sediments results from the erosion of tidal flats and island shores (Perillo et al., 2001a) and varies from 30 to 400 mg l⁻¹ in the inner zone of the estuary during a tidal cycle. These values can increase ten- to twenty-fold as a result of dredging (Perillo et al., 2001b).

The studied estuary is a low-diversity ecosystem although it has a very complex trophic web with classical and detritic heterotrophic pathways as well as strong benthic-pelagic coupling. Phytoplankton is mainly composed of diatoms of the genus *Thalassiosira* (mainly *T. curviseriata* Takano) and *Paralia sulcata* Ehrenberg, and of phytoflagellates, dinoflagellates, and small heterotrophic flagellates. Phytoplanktonic biomass is particularly large and coincides with the highest primary productivity values registered to date during a typical winter-spring bloom dominated by *T. curviseriata*. A smaller summer diatom bloom is also registered and some phytoflagellate-dinoflagellate pulses occur during late spring and summer (Gayoso, 1999). Microzooplankton is mainly composed of tintinnids such as *Tintinnidium balechi* Barría de Cao and aloricated ciliates which peak at different times throughout the year (Pettigrosso & Barría de Cao, 2007). During certain periods

phytoplankton and microzooplankton are scarce and therefore terrestrial plant detritus mainly from *Spartina* spp. and *Sarcocornia* sp. salt marshes become the main food of plankton and benthos filter-feeding consumers. Mesozooplankton is composed mainly of small copepods such as *Acartia tonsa* Dana and *Eurytemora americana* Williams and abundant meroplankton such as *Balanus* spp. larvae, crab zoeae, and other benthic invertebrate larvae. *A. tonsa* is a key component of this estuary as a result of its dominance particularly in warm seasons (Hoffmeyer, 2004). Omnivory in this species is well documented in terms of phytoplankton, microzooplankton and detritus as food sources (Heinle et al., 1977; Roman, 1984; Gifford & Dagg, 1988). Experimental findings in natural and artificial diets as well as morphological observations of the oral field of *A. tonsa* individuals at different stages in Bahía Blanca Estuary corroborate this trophic behavior (Hoffmeyer, 1987).

One approach for the study of trophic webs focusing primarily on mesozooplankton is to measure the different feeding rates to assess herbivory, carnivory or omnivory behavior. The most reliable and direct method for quantifying feeding rates on non-pigmented taxa and on natural food in general is analysis of particle removal in bottle incubations (Båmstedt et al., 2000). This technique has been chosen for the present study, which forms part of a wider ongoing research program.

Taking into account the complexity of the trophic web in Bahía Blanca Estuary and the scarce background information currently available, our general aim was to determine the relative importance of detritic and planktonic fractions in the mesozooplankton community diet in late spring. The specific goals of our study were: i) to determine the contribution of each food fraction to the natural diet; ii) to estimate the feeding rates of the entire mesozooplankton dominated by *A. tonsa*; and iii) to assess the importance of detritus as a food source for these omnivorous grazers.

Materials and methods

The study area is located in Cuatros Port (38° 45' 05''S, 62° 22' 50'' W), in the innermost part of Bahía Blanca Estuary, close to its head (Fig. 1). Mean tidal amplitude in this area is about 4 m and its depth is approximately 5 m. The poor light penetration as a result of the large amount of suspended organic and inorganic material is reflected in the low mean depth of the Secchi disk.

Sampling of incubation seawater and mesozooplankton was carried out at high tide on December 5, 2005. In order to obtain food medium, seawater was collected from the surface layer by hand, using a bucket. The collected water was placed in a 15 l carboy.

Mesozooplankton was carefully collected by means of 5 vertical tows from a depth of 4 m up to the surface using a 200 μm net. The sample was placed in a 5 l recipient and immediately transported to the laboratory with the carboy seawater, to maintain the same conditions as those of the natural environment. A grazing experiment was then carried out under laboratory conditions. The macrozooplankton present in the sample was retained on a 1.7 mm mesh filter and discarded and the mesozooplankton was kept at the same collection temperature during 1 hour for acclimation. The whole sample was divided into three replicates, each of which was placed in an Experimental bottle. Natural food was gently homogenized and drained using the reverse filtration method through a 100 μm mesh during the filling of 1.5 l plastic incubation bottles. The first series of three bottles (Control T_i) was sampled to assess chlorophyll-*a* (Chl-*a*) and particulate organic carbon (POC) and quantify phytoplankton and microzooplankton at the onset of incubation. The second series, containing no mesozooplankton grazers (Control T_f), and the third series, with grazers (Experimental), were incubated. All incubation bottles were tightly capped after filling, thus avoiding gas bubbles. They were all placed in a $20 \pm 1^\circ\text{C}$ thermostatic bath during 24 h, with constant water movement. At the end of the incubation period, all bottles were sampled in the same manner as the first series.

For chlorophyll-*a* and POC analysis, 500 ml of seawater were filtered through 0.45 μm GF/C filters with low vacuum. In the latter case, 4 ml of $\text{Na}_2(\text{SO}_4)$ were added onto the filter after sample filtration. Chlorophyll-*a* concentration was determined by spectrophotometry and POC concentration was obtained by wet oxidation and spectrophotometry according to the techniques proposed by Clesceri et al. (1998). 250 ml seawater samples were preserved in acid Lugol's solution to analyze phytoplankton and microzooplankton. Because of the high content of detritus and sediments in these samples, 10 ml subsamples with 40 ml of distilled water were placed in sedimentation chambers for 24 h using 50 ml-cylinders, following the Utermöhl method after Hasle (1978). Planktonic cells were identified, measured and counted under a Wild M20 inverted microscope for each sample. Phytoplankton cells were enumerated taking into account a defined field of the chamber (1 cm^2). Their abundance per liter was obtained by multiplying the cell number counted in this defined area by a factor depending basically on the density of phytoplankton present in samples, the sedimentation volume and the counting area. Microzooplankton individuals from the entire chamber were counted and their abundance expressed in number per liter. Cell volumes (V) of both planktonic fractions were calculated using simple geometrical configurations and converted into carbon content using standard conversion formulae. Phytoplankton biomass was estimated applying \log_{10}

$C = 0.76 \times (\log_{10} V) - 0.352$ (Eppley et al., 1970). Microzooplankton biomass was calculated using a conversion factor of $0.19 \text{ pg C} \times V (\mu\text{m}^3)$ for aloricate ciliates (Putt & Stoecker, 1989) and a linear regression equation $\text{pg C} = V (\mu\text{m}^3) \times 0.053 + 444.5$ for tintinnids (Verity & Langdon, 1984). The detritus carbon concentration was estimated on the basis of total POC minus the sum of phytoplankton and microzooplankton biomasses. Grazers were fixed with 4% formalin and identified to the lowest possible taxonomic level. Abundance values were estimated by counting the whole sample under Wild M5 stereoscopic microscope. In view of the high dominance of *A. tonsa* in the samples and the low amount of other grazers, total biomass was calculated by multiplying total mesozooplankton abundance by the individual body mass of $2.803 \mu\text{g C}$ for *A. tonsa* (Jones et al., 2002).

Feeding rates for each food type, namely phytoplankton, microzooplankton and detritus, were calculated according to Frost (1972) from the following equations:

$$F = (V \cdot g) / n$$

where F is the filtration rate ($\text{ml grazer}^{-1} \text{d}^{-1}$), V is the volume of the incubation bottle (ml), n is the number of grazers per Experimental bottle and g is the grazing coefficient;

$$g = K + ((\ln C_i - \ln C_f) / (t_2 - t_1))$$

where C_i and C_f are the initial and final concentrations of prey, respectively, per Experimental bottle and t_1 and t_2 are the initial and final times of the experiment. K is the algae growth rate

$$K = (\ln C_2 - \ln C_1) / (t_2 - t_1)$$

where C_1 and C_2 are the initial and final concentrations of prey in the Control T_f bottles. I is the ingestion rate ($\mu\text{g C grazer}^{-1} \text{d}^{-1}$)

$$I = F \times C$$

where C is the mean concentration of prey throughout the 24h incubation period: $C = (C_f + C_i) / 2$.

The carbon specific ingestion rate (CSI, in $\mu\text{g C} \mu\text{g body C}^{-1} \text{d}^{-1}$) was calculated taking into account the total mesozooplankton biomass. The grazing rate (G , in $\mu\text{g C m}^{-3} \text{d}^{-1}$) is the ingestion rate per m^3 . Grazing pressure (GP, in %) was calculated by dividing the grazing rate by the initial food concentration ($\mu\text{g C m}^{-3}$).

One-way ANOVA was used to analyze the differences in feeding rates among the food components of the natural diet. The Scheffé test was used to compare food types. When necessary, log transformed data was used.

Results

The initial measurements of chlorophyll-*a* and POC were $9.25 \mu\text{g l}^{-1} \pm 4.13$ and $3293.71 \mu\text{g l}^{-1} \pm 186.5$, respectively. The values obtained from the incubation bottles were variable. The mean POC:Chl-*a* ratio obtained from initial replicates was 566.35 ± 253.47 . The temperature recorded at the initial time was $17.8 \text{ }^{\circ}\text{C}$ and salinity was 32.98.

The phytoplankton in the natural particulate matter used as food consisted of 13 species of diatoms with no evidence of phytoflagellates or dinoflagellates (Table 1). *Paralia sulcata* was the dominant species in all the Experimental bottles, whereas *Melosira* sp. and *Thalassiosira* sp 1 were the least consumed. In general the Control T_f bottles showed no phytoplankton growth and a decrease in biomass ($16.35 \mu\text{g C l}^{-1} \pm 0.59$). A decrease in phytoplankton biomass was also observed in the Experimental bottles ($9.92 \mu\text{g C l}^{-1} \pm 0.91$) with respect to that in Control T_i bottles ($20.27 \mu\text{g C l}^{-1} \pm 5.37$). Only 51% of the available cells were consumed.

Microzooplankton in all bottles consisted of nine species of tintinnids and one of aloricate ciliates (Table 1). Within tintinnids, *Tintinnidium balechi* was the dominant species in terms of both abundance and carbon, followed by *Tintinnopsis brasiliensis* Kofoid & Campbell and *T. parva* Merkle. Tintinnid growth was observed in the Control T_f bottles ($14.71 \mu\text{g C l}^{-1} \pm 1.87$) whereas a decrease in their biomass was registered in the Experimental bottles ($0.89 \mu\text{g C l}^{-1} \pm 0.17$) with respect to the Control T_i ($4.05 \mu\text{g C l}^{-1} \pm 0.61$). This drastic decrease in biomass implies that 88% of the available microzooplankton was consumed as against 51% of phytoplankton.

Of available POC, detritus showed the highest values (99.2%) of carbon concentration (Table 1). Planktonic fractions therefore constituted a very low portion of available food compared to detritus. A decrease in detritus concentration was observed in the Experimental bottles ($2604.39 \mu\text{g C l}^{-1} \pm 299.48$). Though only 20.3% of the available detritus was consumed, in carbon terms this represents the highest consumption value ($665 \mu\text{g C l}^{-1}$).

Grazer assemblage was mainly composed of approximately 98.5 % of *A. tonsa* (adults and copepodids) and a low abundance of *Paracalanus parvus* Claus, decapod zoeae, and other meroplankton. The average experimental grazer density was 803.33 ± 96.58 per bottle.

Filtration rates were higher on microzooplankton than on phytoplankton and detritus (Table 2). In contrast, the highest ingestion, carbon-specific ingestion and grazing rate values were observed on detritus (about 98.1 %). These feeding rates were two orders of magnitude lower on phytoplankton and microzooplankton than on detritus. The grazing

pressure was very low in all cases, the highest being in microzooplankton, as with the filtration rate.

In all cases, the ANOVA results on the feeding rate demonstrate highly significant differences among the three foods (Table 3). The filtration rate data yielded by the Scheffé test showed significant differences between phytoplankton-microzooplankton and between microzooplankton-detritus. The data regarding ingestion, carbon-specific ingestion and grazing rate revealed significant differences between phytoplankton–detritus and microzooplankton–detritus.

Discussion

The incubation protocol followed in this study gave rise to a 500-fold higher grazer count in the Experimental bottles than the *in situ* density on the collection date (1697 ind m⁻³). This may therefore mean that the calculated rates are underestimated because of the “bottle effect” (Båmstedt et al., 2000).

Owing to the high POC:Chl-*a* ratio found in seawater as a result of the typically high detritus concentration in Bahía Blanca Estuary in late spring, POC was not considered a sufficiently reliable tool for calculating phytoplanktonic carbon. Carbon values derived from phytoplankton biovolumes were therefore used to estimate feeding rates on the natural algae assemblages. The chlorophyll-*a* and POC values found in this study are similar to those reported at the same site and season over recent years.

Though evidence was found of phytoplankton consumption by mesozooplankton, not all the phytoplankton species present at the beginning of the experiment (*Melosira* sp., *Thalassiosira* sp 1, *Thalassiosira* sp 3 and *Thalassiosira* sp 4) were consumed. This may be due to their small size, thus excluding them from *A. tonsa*'s food preference. Copepods have uniform retention efficiencies of particles above a certain size; for example, female *A. clausi*, a morphologically similar congener of *A. tonsa*, retains particles > ca. 10 µm with 100% efficiency (Nival & Nival, 1976). Even though no algae growth was registered in the controls at the end of the experimental period, the observed decrease in abundance and biomass is indicative of microzooplankton grazing. Grazing pressure on phytoplankton could not be quantified since it was not possible to separate microzooplankton from phytoplankton and detritus in the mixed natural food. This drawback in the protocol possibly led to an overestimation of the resulting mesozooplankton feeding rates.

Gifford & Dagg (1991) reported that calanoid copepods such as *Neocalanus plumchrus* Murukawa and *A. tonsa* cleared protozoans from seawater at higher rates than those at

which they cleared phytoplankton cells. These observations are in agreement, with the values registered in the present study where the filtration rate on microzooplankton is approximately 5.5-fold higher than on phytoplankton. On the other hand, *A. tonsa*'s daily phytoplanktonic carbon ingestion as observed in the present study is much lower (16 ng C grazer⁻¹ d⁻¹ in Bahía Blanca Estuary as compared with 181 ng C grazer⁻¹ d⁻¹ in Gironde Estuary) than that reported by Irigoien & Castel (1995), who used the gut content fluorescence method. This high variation is probably due to the ability of *Acartia* to ingest large quantities of detritic particles, satisfying its energetic requirements from alternative food sources such as microzooplankton and detritus, both widely available in this turbid environment.

Microzooplankton growth was evident during the experimental period. Although some species did not appear at the beginning of the experiment because of their very low number, they were present in the final controls. Although microzooplankton biomass was lower than that of phytoplankton, mesozooplankton consumption on tintinnids was higher (88%). Microzooplankton (ciliates and heterotrophic dinoflagellates) generally has a lower C:N ratio than phytoplankton and it may contain other chemical constituents such as fatty acids which are essential for copepod egg production (Stoecker & Capuzzo, 1990). This is corroborated by the high preference of grazers for loricate ciliates. The microzooplankton carbon: phytoplankton carbon ratio observed in this study was 0.875, higher than the maximal value observed for *A. tonsa* feeding on natural assemblages in Terrebonne Bay, Louisiana, USA (Gifford & Dagg, 1988) during late summer. This ratio highlights the importance of the role of microzooplankton in the natural diet of *A. tonsa* in Bahía Blanca Estuary.

After the experimental period, the detritus concentration decreased in both Control T_f and Experimental bottles probably as a result of microzooplankton grazing in the former and micro-mesozooplankton grazing in the latter. Detritus has been reported to be a good food source for copepods (Heinle et al., 1977; Roman, 1984; Irigoien & Castel, 1995). Roman (1984) demonstrated that the ingestion rate of *A. tonsa* on detritus (alone and mixed with algae) increased over the range of the concentrations tested. This may explain the considerable incorporation of detritus by *A. tonsa* seen in the results. Thus, the high concentration of POC in Bahía Blanca Estuary all along the year becomes an alternative food source for mesozooplankton in terms of quantity rather than quality. It has also been observed that detritus constitutes a supplementary diet to algae because it increases the *A. tonsa* production rate, although copepods cannot grow from eggs to adults on a detritic diet alone (Roman, 1984). In Long Island Sound, *A. tonsa*'s herbivorous behavior

accounted for roughly half (56%) of egg production. In the event that carnivory and detritivory account for the other half, it may be concluded that omnivory is quantitatively important for egg production in copepods (Dam et al., 1994).

The fact that the maximal abundances of *A. tonsa* populations in Bahía Blanca Estuary occur during warm seasons could be related to the consumption of a natural mixed food diet with sufficient nutritional value to produce high egg production rates. Further studies will be necessary to prove this hypothesis and to assess the quality-quantity of detritus and its relationship with the other natural components of the mesozooplankton diet throughout the year.

Acknowledgements

Thanks are due to the staff of IADO for their assistance with the sampling. Thanks are also due to CIC for the fellowship awarded to S.L.D. during the study period. This work was funded by ANPCYT-FONCYT grant PICTR N° 090/2002.

References

Båmstedt, U., D. J. Gifford, X. Irigoien, A. Atkinson & M. Roman, 2000. Feeding. In Harris, R. P., P. H. Wiebe, J. Lenz, H. R. Skjoldal & M. Huntley (eds.), *Zooplankton Methodology Manual*, Academic Press, San Diego: 297–399.

Clesceri, L. S., A. E. Greenberg & A. D. Eaton, 1998. *Standard methods for the examination of water and wastewater*. 20th edition. APHA, Washington.

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 omnivory important to egg production? *Hydrobiologia* 292 / 293: 191–199.

David, V., B. Sautour, R. Galois & P. Chardy, 2006. The paradox high zooplankton biomass – low vegetal particulate organic matter in high turbidity zones: What way for energy transfer?. *Journal of Experimental Marine Biology and Ecology* 333: 202–218.

Eppley, R. W., F. M. H Reid & J. D. H. Strickland, 1970. The ecology of the plankton off La Jolla, California, in the period April through September, 1967. In Strickland, J. D. H. (ed.),

pt III. Estimates of phytoplankton crop size, growth rate and primary production. *Bulletin of the Scripps Institution of Oceanography* 17: 33–42.

Federici, G. A., D. G. Cuadrado & E. A. Gómez, 2004. Procesos hidrosedimentológicos y meteorológicos relacionados con la sedimentación de un puerto. *Geoacta* 29: 71–81.

Frost, B. W., 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17: 805–815.

Gayoso, A. M., 1999. Seasonal succession patterns of phytoplankton in the Bahía Blanca estuary (Argentina). *Botánica Marina* 42: 367–375.

Gifford, D. J. & M. J. Dagg, 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. *Bulletin of Marine Science* 43: 458–468.

Gifford, D. J. & M. J. Dagg, 1991. The microzooplankton – mesozooplankton link: consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murukawa. *Marine Microbial Food Webs* 5: 161–177.

Hasle, G., 1978. The inverted microscope method. In Sournia, A. (ed.), *Phytoplankton Manual*. Monographs on Oceanographic Methodology, vol 6. UNESCO, Paris: 88–96.

Heinle, D. R., R. P. Harris, J. F. Ustach & D. A. Flemer, 1977. Detritus as food for estuarine copepods. *Marine Biology* 40: 341–353.

Hoffmeyer, M. S., 1987. Estudios relativos a la alimentación del copépodo planctónico *Acartia tonsa* Dana en el estuario de Bahía Blanca. Tesis Doctoral. Universidad Nacional de La Plata. La Plata, Argentina. 259 pp.

Hoffmeyer, M. S., 2004. Decadal change in zooplankton seasonal succession in the Bahía Blanca Estuary, Argentina, following introduction of two zooplankton species. *Journal of Plankton Research* 26: 1–9.

- 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.
- Jones, R. H., K. J. Flynn & T. R. Anderson, 2002. Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 235: 147–156.
- Mann, K. H. & R. N. Lazier, 1991. *Dynamics of Marine Ecosystems. Biological-Physical Interactions in the Oceans*. Blackwell Scientific Publications, Boston.
- Nival, P. & S. Nival, 1976. Particle retention efficiencies of an herbivorous copepod, *Acartia clausi* (adult and copepodite stages): effects on grazing. *Limnology and Oceanography* 21: 24–38.
- Pettigrosso, R. E. & M. S. Barría de Cao, 2007. Ciliados planctónicos. In Piccolo, M. C. & M. S. Hoffmeyer (eds.), *Ecosistema del estuario de Bahía Blanca*, Editorial de la Universidad Nacional del Sur, Bahía Blanca: 121–131.
- Perillo, G. M. E., M. C. Piccolo, E. R. Parodi & R. H. Freije, 2001a The Bahía Blanca estuary, Argentina. In Seeliger, U. & B. Kjerfve (eds.) *Coastal Marine Ecosystems of Latin America*, *Ecological Studies* 144, Springer: 205–217.
- Perillo, G. M. E., J. O. Pierini, D. E. Pérez & E. A. Gómez, 2001b. Suspended sediment circulation in semi-enclosed docks, Puerto Galván, Argentina. *Terra et Aqua* 83: 13–20.
- Perillo, G. M. E., M. C. Piccolo, E. D. Palma, D. E. Pérez & J. O. Pierini, 2007. Oceanografía física. In Piccolo, M. C. & M. S. Hoffmeyer (eds.), *Ecosistema del estuario de Bahía Blanca*, Editorial de la Universidad Nacional del Sur, Bahía Blanca: 61–67.
- Putt, M. & D. K. Stoecker, 1989. An experimentally determined carbon: volume ratio for marine “oligotrichous” ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34: 1097–1103.
- Roman, M. R., 1984. Feeding of detritus by the copepod *Acartia tonsa*. *Limnology and Oceanography* 29: 949–959.

Stoecker, D. K. & J. M. Capuzzo, 1990. Predation on Protozoa: its importance to zooplankton. *Journal of Plankton Research* 12: 891–908.

Verity, P. G. & C. Langdon, 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *Journal of Plankton Research* 6: 859–868.

Tables

Table 1. Individual biovolume, individual biomass, abundance and biomass of the natural food available to the mesozooplankton community in Bahía Blanca Estuary in December 2005.

	Individual		Control T _i	
	Biovolume ($\mu\text{m}^3 \text{ ind}^{-1}$)	Biomass (pg C ind^{-1})	Abundance (cells l^{-1} or ind l^{-1})	Biomass ($\mu\text{g C l}^{-1}$)
Phytoplankton				
<i>Actinoptychus senarius</i>	6283.1	342.46	530.00 \pm 0.00	0.18 \pm 0.00
<i>Cyclotella</i> sp.	7128.31	376.94	-	-
<i>Dytilum brithwelli</i>	318126.27	6760.45	-	-
<i>Melosira</i> sp.	1884.58	137.14	4240.00 \pm 3475.44	0.58 \pm 0.48
<i>Paralia sulcata</i>	6784.11	363.02	40810.00 \pm 12395.66	14.81 \pm 4.5
Pennate diatom	20029.27	826.54	176.67 \pm 176.67	0.15 \pm 0.15
<i>Podosira stelliger</i>	3619.14	225.19	1060.00 \pm 306.00	0.24 \pm 0.07
<i>Thalassiosira minima</i>	6788.4	363.2	706.67 \pm 353.33	0.26 \pm 0.13
<i>Thalassiosira</i> sp. 1	3710	229.47	3886.67 \pm 2037.42	0.89 \pm 0.47
<i>Thalassiosira</i> sp. 2	5986	330.08	1060.00 \pm 611.99	0.35 \pm 0.20
<i>Thalassiosira</i> sp. 3	14138.49	634.32	883.33 \pm 467.42	0.56 \pm 0.30
<i>Thalassiosira</i> sp. 4	84017.31	2457.65	530.00 \pm 306.00	1.30 \pm 0.75
<i>Thalassiosira</i> sp. 5	94028.1	2677.17	353.33 \pm 176.67	0.95 \pm 0.41
Total			54236.67 \pm 17021.54	20.27 \pm 5.37
Microzooplankton				
<i>Codonellopsis lusitanica</i>	42345.53	2688.81	-	-
<i>Tintinnidium balechi</i>	17918.86	1394.2	2166.67 \pm 375.65	3.02 \pm 0.52
<i>Tintinnidium</i> aff. <i>semiciliatum</i>	28670.17	1964.02	-	-
<i>Tintinnopsis baltica</i>	12370.02	1100.11	66.67 \pm 33.33	0.07 \pm 0.04
<i>Tintinnopsis beroidea</i>	34353.32	2265.23	-	-
<i>Tintinnopsis brasiliensis</i>	51317.92	3164.35	200 \pm 57.74	0.63 \pm 0.18
<i>Tintinnopsis glans</i>	5972.95	761.07	33.33 \pm 33.33	0.03 \pm 0.03
<i>Tintinnopsis parva</i>	12468.98	1105.36	200 \pm 0.00	0.22 \pm 0.00
<i>Tintinnopsis parvula</i>	34339.7	2264.5	33.33 \pm 33.33	0.08 \pm 0.08
<i>Strombidium</i> sp. 1	47712.94	9065.46	-	-
Total			2700.00 \pm 416.33	4.05 \pm 0.61
Detritus			3269.39 \pm 184.63	

Table 2. Mesozooplankton feeding rates on different natural food assemblages.

	Filtration rate		Ingestion rate		Carbon-specific ingestion rate		Grazing rate	Grazing pressure	
	(ml grazer ⁻¹ d ⁻¹)		(µg C grazer ⁻¹ d ⁻¹)		(µg C µg body C ⁻¹ d ⁻¹)		(µg C m ⁻³ d ⁻¹)	(%)	
Phytoplankton	1.006 ± 0.268	14,46	0.016 ± 0.007	1,00	0.006 ± 0.002	1,02	28.057 ± 11.137	1,00	0,14
Microzooplankton	5.434 ± 0.603	78,14	0.014 ± 0.003	0,83	0.005 ± 0.001	0,85	23.235 ± 4.322	0,83	0,58
Detritus	0.514 ± 0.307	7,40	1.618 ± 1.046	98,17	0.577 ± 0.373	98,13	2758.806 ± 1783.397	98,17	0,08
Total	6.954 ± 1.564	100	1.648 ± 0.655	100	0.588 ± 0.191	100	2810.097 ± 911.054	100	0,80

Table 3. One-way ANOVA of mesozooplankton feeding rates on natural food assemblages. Scheffé test results of mean rate comparisons. p- level **: < 0.01, *: 0.01-0.05, ns: > 0.05. N= 9. P: phytoplankton, M: microzooplankton, D: detritus.

Source of Variation	One-way ANOVA	Scheffé test		
	P - M - D	P - M	P - D	M - D
Filtration rate (ml grazer ⁻¹ d ⁻¹) ^	F = 41.540 **	**	ns	**
Ingestion rate (µg C grazer ⁻¹ d ⁻¹)	F = 14.174 **	ns	*	*
Carbon-specific ingestion rate (µg C µg body C ⁻¹ d ⁻¹)	F = 14.187 **	ns	*	*
Grazing rate (µg C m ⁻³ d ⁻¹)	F= 14.174 **	ns	*	*

^ Not transformed data

Figure legends

Figure 1. Map of Bahía Blanca Estuary.

