Available online at www.sciencedirect.com
SCIENCE DIRECT®

Estuarine, Coastal and Shelf Science 56 (2003) 305–311

ESTUARINE
COASTAL
AND
SHELF SCIENCE

Selective feeding of *Eurytemora affinis* (Copepoda, Calanoida) in temperate estuaries: model and field observations

M.L.M. Tackx[a,*], P.J.M. Herman[b], S. Gasparini[c,d], X. Irigoien[c,e], R. Billiones[a,f], M.H. Daro[a]

[a] *Ecology and Systematics Laboratory, Free University of Brussels (VUB), Pleinlaan 2, B-1050, Brussels, Belgium*
[b] *Centre for Estuarine and Coastal Ecology, Netherlands Institute of Ecology, Korringaweg 7, N-4401 NT Yerseke, The Netherlands*
[c] *Biological Oceanography Laboratory, CNRS URA 197, 2, rue du Professeur Jolyet, Arcachon, France*
[d] *LOV, Station Zoologique, B.P. 28, 06234 Villefranche-sur-mer, France*
[e] *AZTI – Technological Institute for Fisheries and Food, Herrera Kaia, Portualde z/g, 20110 Pasaia, Spain*
[f] *Department of Ecology and Evolution, J.W. Goethe University Frankfurt, Frankfurt, Germany*

Received 10 July 2001; received in revised form 22 January 2002; accepted 22 January 2002

Abstract

The copepod *Eurytemora affinis* generally lives under estuarine conditions, where the suspended particulate matter (SPM) is strongly dominated by non-living particles. This article investigates as to how far *E. affinis* is capable of feeding selectively on phytoplankton under these extreme circumstances. Selectivity for phytoplankton by *E. affinis* was studied from samples taken from the Westerschelde (Belgium/The Netherlands). Copepod clearance rates exerted on natural phytoplankton quantified from the gut pigment content were significantly higher than those exerted on total particulate matter, calculated from microscopic image analysis of total gut content and total particulate matter concentration in the water. In addition, gut pigment content data on adult *E. affinis* measured during spring in three European estuaries (the Gironde (France), the Westerschelde and the Elbe (Germany)) were used to study the quantitative response of gut pigment content to varying ratios of phytoplankton to total SPM. A model, expressing maximum gut fluorescence as a function of body weight and gut fluorescence as a product of maximum gut fluorescence with the proportion of phytoplankton to total SPM in the feeding medium, satisfactory fitted the gut fluorescence observations made in the three estuaries. Over the range of phytoplankton-carbon/particulate organic carbon ratios observed in the three estuaries, gut fluorescence decreased with SPM concentration, but maximum gut fluorescence was reached when phytoplankton-carbon was >5% of particulate organic carbon. Limitation of selective feeding apparently only occurred under extremely high SPM loads, such as observed in the Gironde. Maximum gut fluorescence values corresponded exactly to those obtained previously for planktonic copepods in general, affirming the relationship with copepod size.

Keywords: *Eurytemora affinis*; Selective feeding; Phytoplankton; Detritus; Estuaries

---

1. Introduction

Calanoid copepods are known to be capable of selective feeding. Specific prey items can be collected in disproportion to their numerical abundance in the feeding medium as is often shown by the measurement of higher clearance rates on these selected preys than on the other particles (Allan, Richman, Heinle, & Huff, 1977). Selection between live prey (mainly phytoplankton) and detritus has been studied in several laboratory experiments, where they generally show a preference for live phytoplankton (DeMott, 1988, 1995; Paffenhöfer & Van Sant, 1985).

Copepod feeding on natural suspended particulate matter (SPM) has been studied in many rather turbid, detritus-rich environments, such as plumes of rivers (Chervin, Malone, & Meale, 1981; Pagano, Gaudy,

---

* Corresponding author. Centre d'Ecologie des Systèmes Aquatiques Continentaux (CESAC), 118, route de Narbonne, 31062 Toulouse Cedex 4, France.
E-mail address: tackx@cict.fr (M.L.M. Tackx).

doi:10.1016/S0272-7714(02)00182-8

Thibault, & Lochet, 1993; Turner & Tester, 1989), bays (Allan et al., 1977; Gifford & Dagg, 1988; Poulet, 1973, 1977; Richman, Heinle, & Huff, 1977) and semi-enclosed estuaries (Tackx, Bakker, Francke, & Vink, 1989). Nevertheless, (selectivity of) feeding by copepods has rarely been studied under truly estuarine conditions, where the copepods encounter, at best, one live prey item per thousand non-living particles. Studies and models considering zooplankton feeding in estuarine systems either assume unselective feeding (Hummel, Moerland, & Bakker, 1988) or a priority feeding on phytoplankton (Mallin & Paerl, 1994; Soetaert & Herman, 1995; Turner & Tester, 1989). Few experimental data exist, however, on the actual process and degree of (selective) feeding by truly estuarine species.

Eurytemora affinis is a typical inhabitant of temperate estuaries, usually thriving in the brackish areas, around the maximum turbidity zone (Castel & Feurtet, 1989; Castel & Veiga, 1990; Escaravage & Soetaert, 1993; Sautour & Castel, 1995; Soetaert & Van Rijswijk, 1993). Its spatial association with detritus-rich zones suggests that detritus is quantitatively important as food for the species (Heinle & Flemer, 1975; Heinle, Harris, Ustach, & Flemer, 1977).

There are indications, however, that even in estuarine conditions, copepods do feed selectively. Chervin et al. (1981) showed that in the mouth of the Hudson River, phytoplankton is assimilated by the copepod population at a higher rate than the non-phytoplankton particles, and that the copepod production was dependent on phytoplankton assimilation, although non-phytoplankton organic matter formed the bulk of the carbon food source. Sellner and Bundy (1987) measured survival, number of broods per female and nauplii development of *E. affinis* fed on phytoplankton cultures to which increasing loads of sediments from the Patuxent River were added. Using sediment concentrations between 0 and 350 mg l^{-1}, they did not detect any significant effect on the variables measured.

In a previous article, Tackx, Zhu, Coster, Billiones, and Daro (1995) compared clearance rates exerted by *E. affinis* from the Westerschelde estuary on the microplankton with clearance rates on total particulate matter. It was shown that the former are significantly ($P < 0.05$) higher than the latter.

In these experiments, clearance rates on phytoplankton (F) were quantified from incubations using microscopic counting to determine phytoplankton abundance, and those on total particulate matter (F_t) following a gut-content approach based on quantification of total gut content by microscopic image analysis (see also Section 2). Hence only F_t, and not F, was dependent on the gut clearance rate (GCR). To make a conservative test on the hypothesis that the copepods select phytoplankton from the detritus-dominated mixture of SPM, a high estimate of GCR (0.1 min^{-1}) was used in the calculation of F_t.

Another problem with the experiments of Tackx et al. (1995) was that significant concentration differences between control and grazing bottles were observed in some experiments for one or more phytoplankton species, but not in all the experiments. Because of the considerable variability occurring in the microscopic phytoplankton counts, it was not possible to discern as to how far the selection was indeed only occasional, or whether it was occurring more frequently and on more phytoplankton species, but remained undetected because of inadequate resolution of the method used.

This article further studies the occurrence of selective feeding on phytoplankton under natural estuarine conditions. The selectivity of the feeding of *E. affinis* was quantified by measuring clearance rates on Westerschelde phytoplankton and on the particulate matter, following a gut-content approach for both. The occurrence of selective feeding was explored by comparing the outcome of a gut pigment content model assuming selective feeding on phytoplankton with gut pigment content measurements on *E. affinis* feeding under a variety of phytoplankton carbon to total particulate organic carbon (POC) ratios encountered in three European estuaries: the Gironde (France), the Westerschelde (The Netherlands/Belgium) and the Elbe (Germany).

2. Materials and methods

2.1. Sampling in the Westerschelde

Animals for gut fluorescence measurements were collected in the Westerschelde brackish water region from April until July 1997. Zooplankton and water were collected at 0.5 m below the surface with a 200–300 μm mesh net and a Niskin sampler, respectively. A portion of the zooplankton catch was filtered onto a 5 × 5 cm 200 μm gauze and immediately stored in a −80 °C freezer or liquid nitrogen.

Water samples of 50–250 ml, depending on the suspended matter concentration, were filtered onto glassfibre filters (GFC) in sixfold and stored in a −80 °C freezer or liquid nitrogen for Chlorophyll *a* (Chl *a*) and determination of the dry weight of SPM. For the latter, the filters had been pre-dried and weighed. In addition, 250-ml water samples were fixed with Lugol's solution for the determination of total particulate matter concentration by microscopic image analysis.

2.2. Laboratory analysis of Westerschelde samples

SPM was measured after drying at 60 °C for 24 h on three replicate filters. Three other filters were mechanically crushed in 5 ml of 90% acetone and kept in the dark at 4 °C for 24 h. Chlorophyll *a* and phaeopigment

(Phaeo) concentrations in the extracts were measured by HPLC during a 30-min run through a Waters spherisorb G column using a combination of three solvents (80 : 20 (v : v) methanol; 0.5 ammonium acetate; 90 : 10 (v : v) acetonitrile:water; ethyl acetate (Wright et al., 1991). Fluorescence was read on a Waters 470 scanning fluorescence detector (407–670 nm).

Twenty adult *E. affinis* were isolated into 5 ml of 90% acetone and were ground. The homogenate was filtered through an Acrodisc 0.45 µm filter unit, and 100 ml of filtrate was then injected into the HPLC and analysed following the same procedure as previously described.

Calibration of the HPLC was carried out using commercial Chl *a* standards (Sigma), which were acidified and subsequently neutralized for Pheao-calibration. Concentrations of Chl *a* and Phaeo together were expressed in Chl *a*-equivalents.

Gut pigment contents (G) were expressed in µg Chl *a*-eq. ind^{-1}. Ingestion rates on phytoplankton (I) were calculated by multiplying G values by GCR values which were calculated from in situ temperatures at the time of sampling using the regression $\mathrm{GCR} = 0.0117 + 0.001794T$ (°C) (Dam & Peterson, 1988) and expressed per hour. Clearance rates on phytoplankton (F, $\mathrm{ml\,ind^{-1}\,h^{-1}}$) were calculated by dividing I by the concentrations of Chl *a* and Phaeo measured in the water at the time of sampling.

For measurement of the concentration of total particulate matter (in terms of volume concentrations), the particulate matter in the Lugol-fixed water samples was concentrated into 50 ml by decantation. Sub-samples (5 ml) were poured into a cuvette and analysed under inverted microscope using 100× and 400× magnification. The microscope was connected to a Magiscan Image Analysis System (Joyce Loebl). Area concentrations (A; $\mathrm{\mu m^2\,ml^{-1}}$) of particulate matter were converted to volume concentrations (V_t; $\mathrm{\mu m^3\,ml^{-1}}$) using the equations $V = 0.3412A$ for particles between 0.5 and 60 µm equivalent spheric diameter (ESD) and $V = 32.81 \ln A - 101.53$ for particles between 60 and 1600 µm.

To determine total gut contents, animals from the frozen samples were defrosted and analysed using the same microscope–image analysis system at 25× magnification. Total gut content (G_t; $\mathrm{\mu m^3\,ind^{-1}}$) was calculated from the gut parcel area and length measurements, following the cylindrical gut model (Penry & Frost, 1990) multiplied by a factor 2 to correct for the compaction in the gut. Ingestion rates on total particulate matter (I_t; $\mathrm{\mu m^3\,ind^{-1}\,h^{-1}}$) were calculated by multiplying G_t values with the same GCR values as used for the calculation of I. Clearance rates on total particulate matter (F_t; $\mathrm{\mu m^3\,ind^{-1}\,h^{-1}}$) were calculated by dividing I_t values by V_t values. The reader is referred to Tackx et al. (1995), Billones, Tackx, and Daro (1999), and Billones, Tackx, Flacier, Zhu, and Daro (1999) for details on the image analysis procedure.

2.3. Data on the three estuaries

Sampling campaigns in the Gironde (SW France), Westerschelde (SW Netherlands) and Elbe (NW Germany) took place during three consecutive weeks between May 1993 and April 1994. Each of the estuaries was sampled over several stations within its brackish-water reach during one of these weeks. Procedures for measuring Chl *a* and Phaeo concentrations in the water and in the copepod's gut were similar to those used in the Westerschelde, except that concentrations were quantified with a Turner fluorometer before and after acidification, using 430–450 nm excitation and 650–680 nm emission wavelength. Concentrations of pigments were calculated following Lorenzen (1967). The reader is referred to Gasparini, Castel, and Irigoien (1999) for more details on the procedures.

2.4. The model

To model gut pigment content (G), the following equation was used:

$$G = a\mathrm{W}^b \, \frac{\mathrm{Chl}\ a}{k\mathrm{SPM} + \mathrm{Chl}\ a} \qquad (1)$$

The first part, $a\mathrm{W}^b$, gives the maximum gut pigment content ($G_{\max}$, $\mathrm{ng\,ind^{-1}}$) as a function of body weight (W, $\mathrm{mg\,ind^{-1}}$). The second part of the equation reflects a relative fullness index depending on external feeding circumstances, as characterized by the concentration of Chl *a* ($\mathrm{\mu g\,l^{-1}}$) and total particulate matter concentration (SPM; $\mathrm{mg\,l^{-1}}$) in the medium. This part of the equation represents the limitations met by the copepod to realize $G_{\max}$. k is a constant.

Eq. (1) was fitted to the G values actually measured using data on Chl *a*, SPM and *E. affinis* adult DW observed in the three estuaries during the sampling campaigns by iterative least squares fitting using quasi-Newton algorithm in STATISTICA.

To evaluate the influence of the (relative) non-phytoplankton particle concentration on the degree to which $G_{\max}$ is realized, POC concentrations were considered. In addition to the influence of total SPM demonstrated in the data of Gasparini et al. (1999) (Fig. 2), plotting G as a function of the ratio of phytoplankton and non-phytoplankton carbon provides a measure of the capacity for selection among organic particles. POC concentrations had not been determined in the samples where G was measured. POC was estimated from SPM with regressions established for the three estuaries separately on the basis of the MATURE database (Herman & Heip, 1999); database available at ftp://ftp.nioo.knaw.nl/cemo/mature).

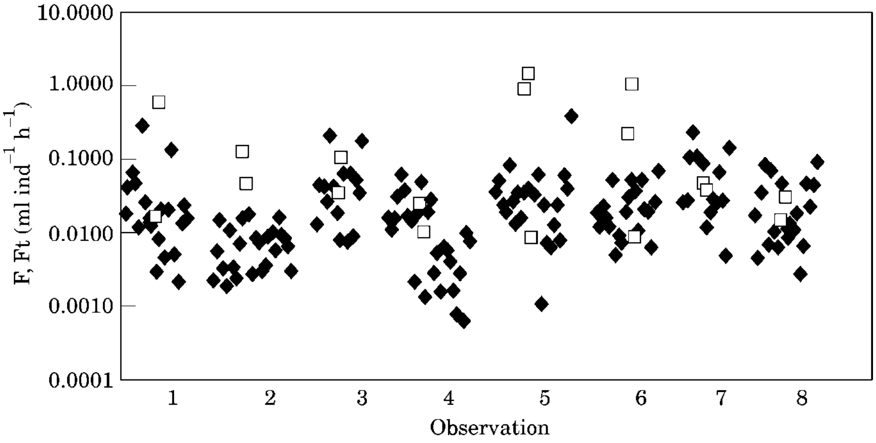

Fig. 1. *E. affinis* clearance rates on phytoplankton (F; blank squares) and on total SPM (F_t; black diamonds) in the Westerschelde estuary. Numbers on x axis refer to different samplings.

3. Results

Over the entire series of measurements performed on the 1997 Westerschelde samplings, F values measured for *E. affinis* were significantly higher than F_t values (Mann–Whitney U test, $U = 761$, $n_1 = 165$, $n_2 = 18$, $P<0.001$; Fig. 1).

As shown in a previous article by Gasparini et al. (1999), carbon-specific gut pigment contents (G_{sp}) measured in the three estuaries declines exponentially with SPM and shows no relation with Chl a concentration (Fig. 2a,b).

In the model, G rather than G_{sp} was used, in order to allow comparison with the literature (see subsequent discussion). Fig. 3 shows that G values calculated from Eq. (1) fitted satisfactory to the G values observed during the sampling campaigns in the three estuaries. With the units used, the following parameters gave the best fit ($R^2 = 0.76$):

a : 38.19 (SE, 2.42)

$k = 0.00384$ (SE, 0.00109)

b : 0.76 (no SE)

No SE was observed for b because of one singular Hessian and its value was kept constant at its optimal fit to calculate SE values for the other parameters.

Regressions between POC and SPM obtained for each of the estuaries were the following:

$$\text{Elbe}: \text{POC} = 1.638 + 0.0343\text{SPM} \ (n = 56,\ R^2 = 0.39)$$

$$\text{Gironde}: \text{POC} = 2.061 + 0.0122\text{SPM} \ (n = 63,\ R^2 = 0.63)$$

$$\text{Westerschelde}: \text{POC} = 1.892 + 0.0366\text{SPM} \ (n = 171,\ R^2 = 0.55)$$

where POC is given in mg C l^{-1} and SPM in mg l^{-1}.

Although there were indications on non-homogeneity of variance of POC with increasing SPM, we used linear regression analysis for this predictive application to avoid the bias in the estimate resulting from log-transformation. This may have been an over-cautious approach, since a comparison between linear and log–log regression showed only very minor differences in the appearance of Fig. 4.

Fig. 4 shows the relative fullness index (calculated as the second part of Eq. (1)), as a function of the ratio of phytoplankton : carbon (ratio phyto:C = Chl a × 50)

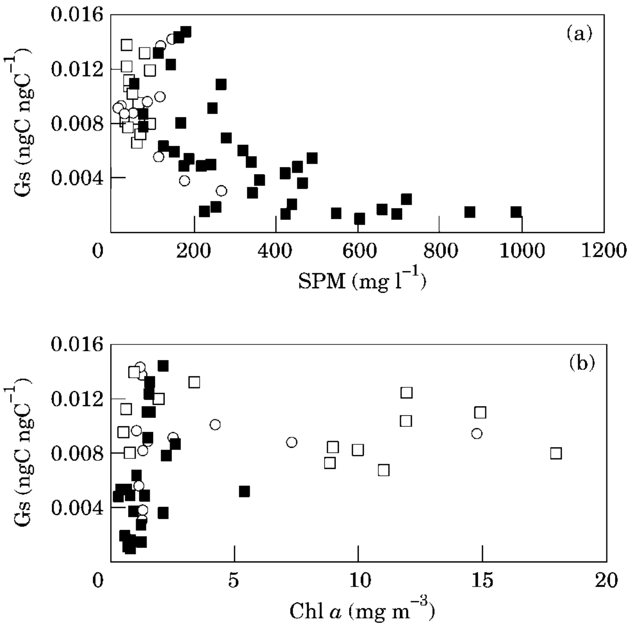

Fig. 2. *E. affinis* carbon-specific gut pigment content (G_{sp}) as a function of SPM concentration (a) and Chl a concentration (b) in the Gironde (black squares), the Elbe (open circles) and Westerschelde (open squares). From Gasparini et al., 1999.

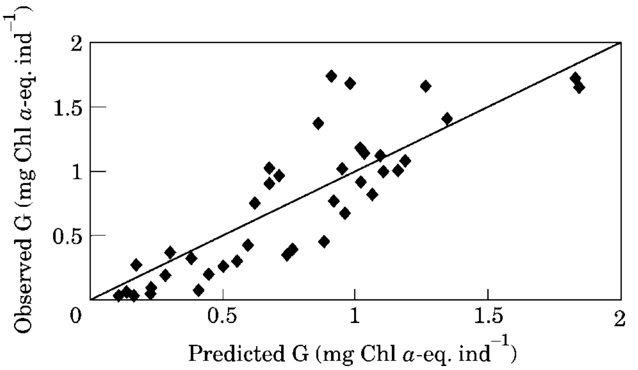

Fig. 3. Gut-pigment content is (G) predicted following Eq. (1) compared with G values observed in the three estuaries.

to POC estimated from the regressions. Over 80% of G_{max} was reached when the phyto-C : POC ratio was above 0.05.

4. Discussion

In the Westerschelde 1997 observations, clearance rates on phytoplankton (F) values were significantly higher than the clearance rates measured on total SPM (F_t) (Fig. 1). This demonstrates that *E. affinis* exerted a higher feeding pressure on phytoplankton than on the total particulate matter. Within the range of temperatures observed in the three estuaries considered in this study, GCR values calculated following Dam and Peterson (1988) varied between 0.01 and 0.05 min^{-1}. Thus, F_t values in our previous study (Tackx et al., 1995), using a GCR of 0.1 min^{-1} were overestimated, and the demonstration of selectivity for phytoplankton was indeed conservative. In this study, using a gut content approach and the same GCR values, the higher values measured for F than for F_t confirm the earlier demonstrated selective feeding of *E. affinis* on phytoplankton, and indicate its regular occurrence.

Degradation of phyto-pigment into non-fluorescent compounds could affect our estimate of phytoplankton ingestion (Conover, 1986; Head & Harris, 1992; Lopez, Huntley, & Sykes, 1988). Degradation could, however, only underestimate phytoplankton uptake, and not taking it into account makes our estimate of selection conservative. Any degradation not due to the digestion processes, such as degradation during storage, is likely to affect Chl a concentrations in SPM filters to the same degree as those in the copepods. Compaction in the gut could also be higher for phytoplankton cells, which consist of a considerable portion of liquid cytoplasm, than for non-phytoplankton particles, which are more solid. As phytoplankton in the gut was estimated from gut fluorescence, this estimate is not affected by compaction. Moreover, correcting only G_t, and not G for compaction again emphasizes the finding of selectivity.

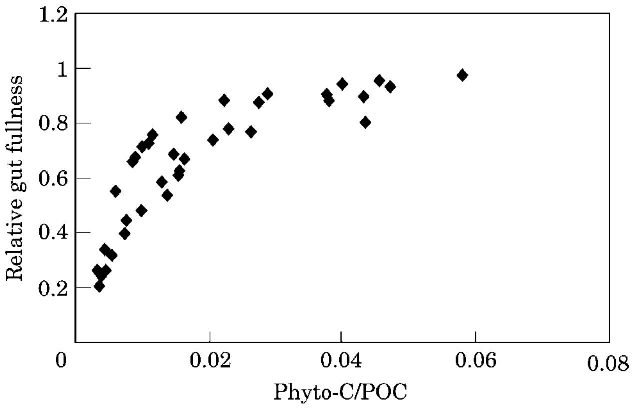

Fig. 4. Relative gut fullness as a function of phyto-C : POC ratio.

As demonstrated in Fig. 2, maximum (specific) gut pigment content was not always reached by *E. affinis* feeding in the high non-phytoplankton particle concentrations encountered in the estuaries. As shown by Gasparini et al. (1999), phytoplankton uptake by *E. affinis* seems to be hampered at SPM concentrations of the order of hundreds mg l^{-1}. Gasparini and Castel (1997) showed that, in the Gironde, *E. affinis* can also feed to a substantial degree on heterotrophic nanoplankton, especially at high SPM concentrations. Nevertheless, feeding conditions seem to deteriorate with increasing SPM, as its egg production also decreases with increasing SPM (Gasparini et al., 1999). Plotting the model outcome as a function of the ratio phyto-C:POC (Fig. 4) showed that *E. affinis* succeeded in obtaining 80% of its maximal gut pigment content when phytoplankton concentration contributed 5% of the total POC. These circumstances were met during nearly the entire growing season in both the Westerschelde and the Elbe. In the Gironde, primary production is severely limited by the high silt and clay loads (Goosen, Kromkamp, Peene, Van Rijswijk, & Van Breugel, 1999) and phytoplankton carbon rarely contributes over 5% of POC.

Each of the estuaries studied generally presented only one type of 'feeding situation' in terms of limiting (Gironde) or non-limiting (Westerschelde, Elbe) conditions for maximum phytoplankton uptake. Only combined observations obtained in the three European estuaries offered a sufficiently wide range of conditions in terms of SPM concentration and composition to reveal the complete feeding response of *E. affinis*.

Similar findings were reported by Sherk, O'Connor, Neumann, Prince, and Wood (1974), who observed a reduction in the carbon uptake by *E. affinis* and *Acartia tonsa* feeding on *Monochrysis lutheri* cultures to which various suspended solids were added. While *A. tonsa* showed a reduction in its phytoplankton carbon uptake at all concentrations of solids added between

10 and 10 000 mg l^{-1}, *E. affinis* increased the uptake of phytoplankton carbon when sediments were added at concentrations of 100 mg l^{-1} and reduced it at higher sediment concentrations. Koski (1999) showed that *E. affinis* females from the Baltic did not increase their carbon or nitrogen content when fed with natural water to which a green algae, *Brachiomonas submarina*, was added in concentrations reaching up to 300 μg C l^{-1}. However, the C : N ratio and the carbon and nitrogen content of the eggs did increase. This suggests that, while not food-limited under natural conditions, *E. affinis* can profit from increased phytoplankton concentrations to ensure lipid storage and improvement of egg organic content.

Morales, Bautista, and Harris (1990) reviewed published maximum gut content values from marine copepods in general. They reported an allometric relationship with copepod size given by: $\log G(\text{ng cop}^{-1}) = 1.61 + 0.72^{*} \log W$ (mg), or $G = 40.7^{*} W^{0.72}$. The agreement with the fitted values in our study is striking. Maximum values are attained when the relative fullness factor (right-hand part of Eq. (1) equals 1). $G_{\max}$ from our fitting is then given as $G_{\max} = 38.2 W^{0.76}$. This agreement strongly suggests that maximum gut content in *E. affinis* is in line with that of other copepod species. It also lends support to the interpretation of the other term in Eq. (1) as a relative fullness index. As suggested by Morales et al. (1990), the fact that the relationship between $G_{\max}$ and body weight can be generalized opens perspectives for straightforward evaluation of the grazing impact of copepod assemblages. Although GCR values do not show a clear relation to body size, they are sufficiently constant (within one order of magnitude) for purposes of generalization (Morales et al., 1990). As suggested by Irigoien, Castel, and Gasparini (1996), the GCR–temperature relationship (Dam & Peterson, 1988) is also applicable to copepods in general, and deviations from it could be used to detect limiting food concentrations. Our data on *E. affinis* gut pigment content show that deviations from a $G_{\max}$ could also be used as an indicative of limitations to obtain the optimum diet in terms of phytoplankton ingestion. However, as heterotrophic microplankters may in some cases be an alternative highly nutritive food source (Gasparini & Castel, 1997; Gifford & Dagg, 1988), deviations from $G_{\max}$ in terms of fluorescence could indicate both limiting food conditions or a selection of non-fluorescent food resources.

Acknowledgements

We dedicate this article to the memory of our colleague, mentor and friend, Jacques Castel. We thank the crew of the Côte d'Aquitaine, the Luctor and the Veremans for their assistance during sampling campaigns. We very much appreciate the help of B. Verdoodt with the image analysis and of N. Fockedey with the MATURE database. This research was partially funded by the EU project MATURE and the Flemish Community project 'OMES'.

References

Allan, J. D., Richman, S., Heinle, D. R., & Huff, R. (1977). Grazing in juvenile stages of some estuarine calanoid copepods. *Marine Biology 43*, 317–331.

Billones, R. G., Tackx, M. L., & Daro, M. H. (1999). The geometric features, shape factors and fractal dimensions of suspended particulate matter in the Schelde estuary (Belgium). *Estuarine, Coastal and Shelf Science 48*, 293–305.

Billones, R. G., Tackx, M. L. M., Flacier, A. T., Zhu, L., & Daro, M. H. (1999). Image analysis as tool for measuring particulate matter concentrations and gut content, body size, and clearance rates of estuarine copepods: validation and application. *Journal of Marine Systems 22*, 179–194.

Castel, J., & Feurtet, A. (1989). Dynamics of the copepod *Eurytemora affinis hirundoides* in the Gironde estuary: origin and fate of its production. In J. D. Ross (Eds.), *Topics in marine biology* (pp. 577–584). Barcelona: Sciencia Marina.

Castel, J., & Veiga, J. (1990). Distribution and retention of the copepod *Eurytemora affinis hirundoides* (Nordquist, 1888) in a turbid estuary. *Marine Biology 107*, 119–128.

Chervin, M. B., Malone, T. C., & Meale, P. J. (1981). Interaction between suspended organic matter and copepod grazing in the plume of the Hudson River. *Estuarine, Coastal and Shelf Science 13*, 169–183.

Conover, R. J. (1986). Probable loss of chlorophyll derived pigments during passage through the gut of zooplankton and some of the consequences. *Limnology and Oceanography 31*, 878–887.

Dam, H. G., & Peterson, W. T. (1988). The effect of temperature on the gut clearance rate constant of copepods. *Journal of Experimental Marine Biology and Ecology 123*, 1–14.

DeMott, W. R. (1988). Discrimination between algae and detritus by freshwater and marine zooplankton. *Bulletin of Marine Science 43*, 486–499.

DeMott, W. R. (1995). Optimal foraging by a suspension-feeding copepod: responses to short term and seasonal variation in food resources. *Oecologia 103*, 230–240.

Escaravage, V., & Soetaert, K. (1993). Estimating secondary production for the brackish Westerschelde copepod population *Eurytemora affinis* (Poppe) combining experimental data and field observations. *Cahiers de Biologie Marine 34*, 201–214.

Gasparini, S., & Castel, J. (1997). Autotrophic and heterotrophic nanoplankton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*. *Journal of Plankton Research 19*, 877–890.

Gasparini, S., Castel, J., & Irigoien, X. (1999). Impact of suspended particulate matter on egg production of the estuarine copepod, *Eurytemaora affinis*. *Journal of Marine Systems 22*, 195–205.

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

Goosen, N. K., Kromkamp, J., Peene, J., Van Rijswijk, P., & Van Breugel, P. (1999). Bacterial and phytoplankton production in the maximum turbidity zone of three European estuaries: the Elbe, Westerschelde and Gironde. *Journal of Marine Systems 22*, 151–172.

Head, E. J., & Harris, L. R. (1992). Chlorophyll and carotenoid transformation and destruction by Calanus sp. grazing on diatoms. *Marine Ecology Progress Series 86*, 229–238.

Heinle, D. R., & Flemer, D. A. (1975). Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Marine Biology 31*, 235–247.

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

Herman, P. M. J., & Heip, C. H. R. (1999). Biochemistry of the maximum turbidity zone of estuaries: some conclusions. *Journal of Marine Systems 22*, 89–104.

Hummel, H., Moerland, G., & Bakker, C. (1988). The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde estuary. *Hydrobiological Bulletin 22*, 35–41.

Irigoien, X., Castel, J., & Gasparini, S. (1996). Gut clearance rate as predictor of food limitation situations. Application to two estuarine copepods: *Acartia bifilosa* and *Eurytemora affinis*. *Marine Ecology Progress Series 131*, 159–163.

Koski, M. (1999). Carbon: nitrogen ratios of Baltic copepods—indication of mineral limitation? *Journal of Plankton Research 21*, 1565–1573.

Lopez, M. D. G., Huntley, M. E., & Sykes, P. F. (1988). Pigment destruction by *Calanus finmarchicus*: impact on the estimation of water column fluxes. *Journal of Plankton Research 10*, 715–734.

Lorenzen, C. J. (1967). A method for the continuous measurement of in vivo chlorophyll concentration. *Deep Sea Research 13*, 223–227.

Mallin, M. A., & Paerl, H. W. (1994). Planktonic trophic transfer in an estuary: seasonal, diel and community structure effects. *Ecology 75*, 2168–2184.

Morales, C. E., Bautista, B., & Harris, R. P. (1990). Estimates of ingestion in copepod assemblages: gut fluorescence in relation to body size. In M. Barnes, & R. N. Gibson (Eds.), *Trophic relationships in the marine environment. 24th European biological symposium* (pp. 565–577). Barcelona: Aberdeen University Press.

Paffenhöfer, G. A., & Van Sant, K. B. V. (1985). The feeding response of a marine planktonic copepod to quantity and quality of particles. *Marine Ecology Progress Series 27*, 55–65.

Pagano, M., Gaudy, R., Thibault, D., & Lochet, F. (1993). Vertical migrations and feeding rhythms of mesozooplanktonic organisms in the Rhône River plume area (North-west Mediterranean sea). *Estuarine, Coastal and Shelf Science 37*, 251–269.

Penry, D. L., & Frost, B. W. (1990). Re-evaluation of the gut fullness (gut fluorescence) method for inferring ingestion rates of suspension-feeding copepods. *Limnology and Oceanography 35*, 1207–1214.

Poulet, S. A. (1973). Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. *Limnology and Oceanography 18*, 564–573.

Poulet, S. A. (1977). Grazing of marine copepod developmental stages on naturally occurring particles. *Journal of the Fisheries Research Board of Canada 34*, 2381–2387.

Richman, S., Heinle, D. R., & Huff, R. (1977). Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. *Marine Biology 42*, 69–84.

Sautour, B., & Castel, J. (1995). Comparative spring distribution of zooplankton in three macrotidal European estuaries. *Hydrobiologia 311*, 139–151.

Sellner, K. G., & Bundy, M. H. (1987). Preliminary results of experiments to determine effects of suspended sediments on the estuarine copepod *Eurytemora affinis*. *Continental Shelf Research 7*, 1435–1438.

Sherk, J. A., O'Connor, J. M., Neumann, D. A., Prince, R. D., & Wood, K. V. (1974). Effects of suspended sediments on feeding activity of the copepods *Eurytemora affinis* and *Acartia tonsa*. In N. R. Institute (Ed.), *Effects of suspended and deposited sediments on estuarine organisms phase II* (pp. 164–202). Barcelona: University of Maryland.

Soetaert, C., & Van Rijswijk, P. (1993). Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. *Marine Ecology Progress Series 97*, 47–59.

Soetaert, K., & Herman, P. M. J. (1995). Carbon flows in the Westerschelde estuary (The Netherlands) evaluated by means of an ecosystem model (MOSES). *Hydrobiologia 311*, 247–266.

Tackx, M. L. M., Bakker, C., Francke, J. W., & Vink, M. (1989). Size and phytoplankton selection by Oosterschelde zooplankton. *Netherlands Journal of Sea Research 23*, 35–43.

Tackx, M. L. M., Zhu, L., Coster, W. D., Billiones, R., & Daro, M. H. (1995). Measuring selectivity of feeding by estuarine copepods using image analysis combined with microscopic and Coulter counting. *ICES Journal of Marine Science 52*, 419–425.

Turner, J. T., & Tester, P. A. (1989). Zooplankton feeding ecology: non-selective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* Giesbreacht in the plume of the Mississippi River. *Journal of Experimental Marine Biology and Ecology 126*, 21–34.

Wright, S. W., Jeffrey, S. W., Mantoura, R. F. C., Bjornland, T., Repeta, D., & Welschmeyer, N. (1991). Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. *Marine Ecology Progress Series 77*, 183–196.