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Secondary production of the brackish copepod communities and their contribution to the carbon fluxes in the Westerschelde estuary (The Netherlands)

Vincent Escaravage[1,*] & Karline Soetaert[2,**]
[1] *Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, Vierstraat 28, NL-4401 EA Yerseke, The Netherlands*
[2] *Free University of Brussels, Pleinlaan 2, B-1050 Brussels, Belgium*
Present addresses:
**National Institute for Coastal and Marine Management/RIKZ, P.O. Box 8039, NL-4330 EA Middelburg, The Netherlands*
***Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, Vierstraat 28, NL-4401 EA Yerseke, The Netherlands*

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Abstract

The zooplankton community of the brackish part of the Westerschelde estuary (November 1989–October 1990) was dominated by two calanoid copepods, *Eurytemora affinis* and *Acartia tonsa*. *Eurytemora* was present during a longer period of the year and was much more important in terms of total abundances and biomasses than *Acartia*.

The secondary production of these species was estimated by means of the growth rate method, using weight-specific growth rates obtained from laboratory cultures (*Eurytemora*) or from the literature (*Acartia*).

Due to the substantially higher growth rates of *Acartia* compared to *Eurytemora*, total yearly productions of both communities were comparable, notwithstanding the large discrepancies in biomass. They amounted to about 5 and 6 g C m^{-2} y^{-1} by *Acartia* and *Eurytemora* respectively.

The food needed to realise this production was estimated to be about 14 and 17 g C m^{-2} y^{-1} by *Acartia* and *Eurytemora* respectively. Provided that the copepods are able to selectively ingest the phytoplankton, *in situ* net production provides sufficient carbon for zooplankton demands for a short period of the year only. As phytoplankton standing stock is very low and net phytoplankton productivity is negative from late fall to early spring, nutritional demands of the copepods have to be fulfilled by other than algal food at least during this period of the year.

Although the copepods in the brackish part can have an important impact on some food items, their contribution to total carbon fluxes in the brackish zone is negligible: each year some 6% of all consumed carbon in the brackish part of the estuary passes through the copepod food web.

Introduction

The Schelde drains large areas of Belgium, the Netherlands and France and is subjected to massive inputs of industrial and domestic sewage. This makes this river one of the most polluted in Europe (Duursma *et al.*, 1988). Due to extensive engineering works, the estuarine part of the Schelde (the Westerschelde) is the only remaining estuary in the delta area of the South-West Netherlands.

River discharge of the Schelde varies moderately on a seasonal basis (50 to 200 m^3 s^{-1}) and typically is an order of magnitude lower than tidal exchange. Thus the seawater is gradually diluted in the estuary and the salinity zones are relatively stable throughout the year. Westerschelde estuarine waters have a rather long residence time estimated as 50 to 70 days (Heip, 1988; Soetaert & Herman, 1995a).

In the upstream part of the estuary a stable turbidity maximum exists. Many of the organic and inorganic pollutants are temporarily retained in this zone and the consequently high bacterial degradation, combined with high nitrification activity there results in badly aerated conditions of the water masses (Billen *et al.*, 1988; Goosen *et al.*, 1992; Soetaert & Herman, 1995c). Chlorophyll concentrations typically are highest in the most upstream part of the estuary, due to import from the river. The unfavourable light climate in the turbid, deep water masses there and the increasing salinity results in a quick decline in phytoplankton standing stock and a sharp switch from freshwater to marine phytoplankton communities more downstream. Thus algal biomass is lowest in the brackish part of the estuary and increases towards the sea (Kromkamp *et al.*, 1995; Soetaert *et al.*, 1994). As a consequence of oxygen deficiency, copepods are absent from the turbidity maximum zone and hence they cannot profit from the high algal stocks there (Soetaert & Van Rijswijk, 1993). However, mesozooplankton biomass is peaking in the (impoverished) brackish zone immediately downstream as soon as the oxygen conditions are improving (Soetaert & Van Rijswijk, 1993; Bakker *et al.*, 1977). These high biomasses in the brackish zone can be ascribed to two species of calanoid copepods: *Eurytemora affinis* (Poppe), a perennial species and *Acartia tonsa* (Dana), only of some importance in late summer-early fall. *E. affinis* reaches maximum biomass in spring (500 mg DW m^{-3}), in summer the population declines and is then replaced by *Acartia tonsa* which gives maximum biomass of 71 mg DW m^{-3} (Soetaert & Van Rijswijk, 1993). Marine species that enter the Westerschelde in spring are declining rapidly in the estuary (Soetaert & Herman, 1994) and do not contribute significantly to the copepod biomass in the brackish part.

Due to the elevated biomasses, brackish copepod species are able to play a significant role in the estuarine trophic food web as they constitute a link to higher exploitable levels (Mauchline, 1970; Burkill & Kendall, 1982). The production of the winter species *Eurytemora affinis* was estimated by Escaravage & Soetaert (1993) but as yet we have no knowledge about the production of *Acartia tonsa*, the summer dominant species in the estuary.

Measurements of zooplankton secondary production can be made by estimating growth and mortality (yield) in cohorts over consecutive sampling intervals (Parslow & Sonntag, 1979). However, as many marine and estuarine zooplankton populations are continuously reproducing, cohorts cannot be identified. The growth-rate methods (Rigler & Downing, 1984) are a good altemative for the calculation of production in continuously reproducing populations (Kimmerer, 1987).

In this paper, weight specific growth rate estimates obtained from original laboratory experiments and from the literature were combined with biomasses measured in the field for the calculation of the copepod production in the brackish part of the Westerschelde. Energy requirements inferred from these production estimates were then compared with the different food stocks available to the copepod population.

Material and methods

Zooplankton and auxiliary environmental data were collected in the Westerschelde from November 1989 to October 1990 on 37 surveys with a mean time interval of ten days between each sampling date. During each survey three stations were sampled in the brackish part of the estuary (Fig. 1). Zooplankton was sampled by means of a pump (capacity of 200 l min^{-1}), 2.5 m above the bottom, 2.5 m below the surface and from mid-depth. From each depth 100 litres of water was poured over a 55 μm mesh. These three samples were then combined and fixed in buffered 4% formaldehyde. The organisms were separated from the high amount of suspended particles by means of density gradient separation (Heip *et al.*, 1985). Developmental stages of the copepods *Eurytemora affinis* and *Acartia tonsa* were enumerated and their biomasses were calculated by length-weight regression. The cephalothorax length of 30 individuals per copepod stage was measured using a digitizing tablet. Length-weight regressions were assessed by weighing 100 pre-measured copepods on a Cahn electronic balance (precision 0.1 μg) after a 24 hours drying process at 60 °C. For the calculations we used the average biomass of the three stations. Conversion of dry weight into carbon content was made assuming that 50% of the dry weight consists of organic carbon (Lenz, 1974).

The temperature dependent weight-specific growth rate of the Westerschelde population of *E. affinis* was ascertained from small-scale culture experiments described in Escaravage & Soetaert (1993). In these experiments, the copepods were fed with natural particulate matter and kept at six temperatures in the range

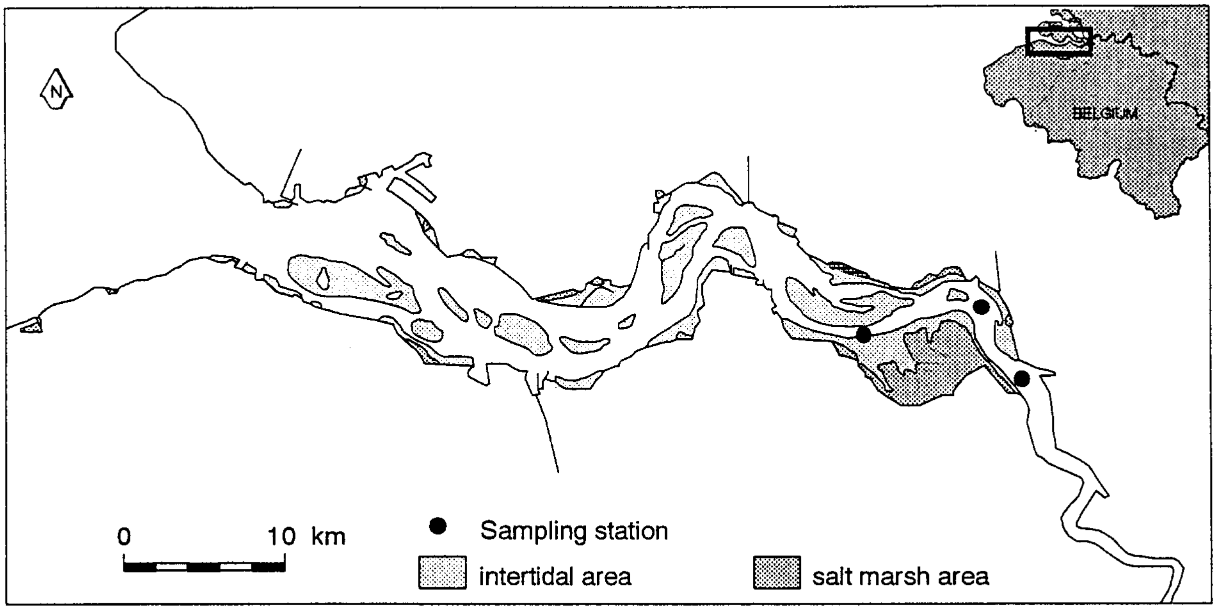

Fig. 1. Sampling positions of the three brackish stations.

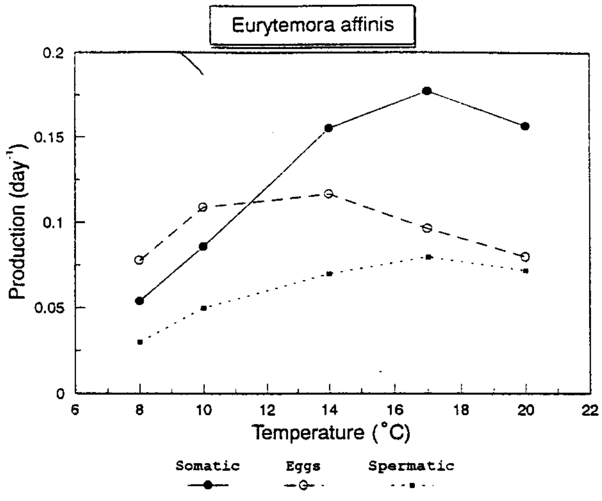

Fig. 2. Juvenile, eggs and spermatophores productions by *Eurytemora affinis* (from Escaravage & Soetaert, 1993).

of 2 to 20 °C. An attempt was made to use the same culturing procedure for *A. tonsa*. However, we only succeeded to maintain this copepod up till about the third copepodid stage, after which it died. It was then decided to resort to the existing literature on *A. tonsa* development rate, although these were mainly measured on copepods fed artificially in excess.

Based on the weight-specific growth rates (g_i) and the copepod biomasses of stage i (B_j), the integrated production (IP) for the time interval [t_1-t_2] was calcu-

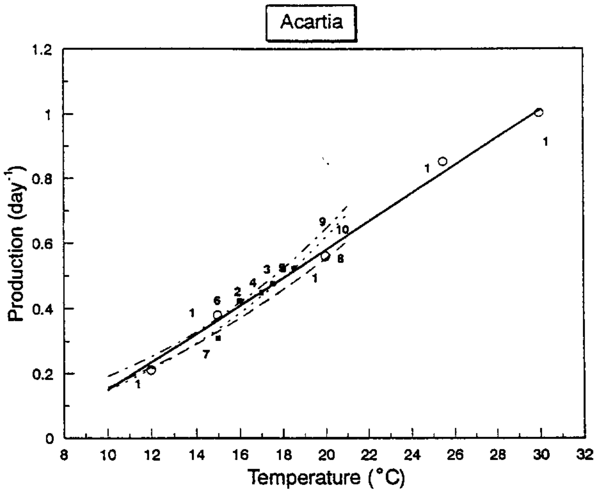

Fig. 3. Growth (G) and Fecundity (F) rates versus temperature for *A. tonsa* (or, when specified, some related species). [1] Miller *et al.* (1977)(G), [2] Bergreen *et al.* (1988) (G), [3] Kiørboe *et al.* (1985 (F), [4] Parrish & Wilson (1978) (F), [1 Stottrup & Jensen (1990) (F), [6] Raymont & Miller (1962) (F), [7] Klein Breteler *et al.* (1982) (G), [8] Uye (1981) (F-*A. steueri*), [9] Uye (1981) (F-*A. clausi*), [10] Sekigushi *et al.* (1980) (F). The solid line indicates the regression used.

lated by the formula of Polishchuk (1990):

$$IP = \sum_{i} g_i(t) \frac{B_i(t_2) - B_i(t_1)}{Ln[B_i(t_2)/B_i(t_1)]}(t_2 - t_1), \quad (1)$$

where $(t_2\text{-}t_1)$ = the period in between sampling, $B_i(t_j)$ = the biomass of stage i at time t_j and $g_i(t)$ the average growth rate during the sampling period $(g_i(t) = [g_i(t_1)+g_i(t_2)]/2)$.

Eurytemora growth characteristics

The weight-specific growth rates realised by the copepods between 8 and 20 °C (Fig. 2) were reported in Escaravage & Soetaert (1993). The juvenile production was measured from hatching to adulthood, the reproductive activity was followed from maturation to death by collecting (counting and weighing) reproductive products (eggs for females, spermatophores for males). The optimal temperature for the egg production was at 14 °C, whereas male spermatophore production and juvenile growth was maximal at 17 °C. The male production rate attained 40 to 90% of the egg production rate.

Acartia sp. growth characteristics

According to Miller *et al.* (1977), several species of the copepod genus *Acartia* (including *A. tonsa*) grow exponentially throughout their life and growth increases with increasing temperature. Thus a common weight-specific growth rate can be used for all developmental stages at a certain temperature.

In Fig. 3 we gathered several growth rate values and several equations describing the temperature dependence of the weight-specific growth rate of *Acartia* (*tonsa* and *clausi*), obtained from the literature. In all these studies the copepods were supplied with an excess of food. There is a large homogeneity in the weight-specific growth rate of *A. tonsa* but also between *tonsa* and *clausi*.

Results

Field data

Average chlorophyll concentrations were in between 1 and 18 μg l^{-1}. They were bimodal, peaking in May and in July (Fig. 4a). The average temperature in the brackish part varied from 6 °C in January to 22 °C in August. Salinity varied from 9 to 19‰ (Fig. 4b).

The populations of the calanoid copepods *Eurytemora affinis* and *Acartia tonsa* were well separated in time (Fig. 5). *Acartia* populations mainly developed between June and October. Their highest densities and biomass were observed immediately after the second chlorophyll peak, when temperature was highest. The rest of the year the copepod community was exclusively dominated by *Eurytemora affinis*. They started to decline about one month before chlorophyll was at its maximum. Highest densities were observed when the temperature was about 15 °C. Not only did *Eurytemora affinis* reach higher abundances than *Acartia tonsa*, the species was present during a significantly larger part of the year. Hence, the yearly integrated abundance of *Eurytemora* equalled three fold the integrated abundance of *Acartia* (Fig. 5a). As individuals of *Eurytemora* were significantly larger than *Acartia*, their dominance in terms of biomass is even more pronounced (Fig. 5b; Table 1).

Temperature dependent growth rates

For *Eurytemora affinis*, the temperature dependence of the weight-specific growth or production rates (g) was best fitted by:

$g = -0.002\ T^2 + 0.06\ T - 0.37$ for the juvenile growth ($r^2 = 0.98$)

$g = (-0.971\ T^2 + 26.629\ T - 67.768)/1000$ for the egg production ($r^2 = 0.97$)

$g = (-0.577\ T^2 + 19.701\ T - 90.346)/1000$ for the spermatophore production ($r^2 = 0.96$)

with g in d^{-1} and T (temperature) in °C.

For *Acartia* tonsa, we used a simple formula, expressing the growth rate as a linear function of temperature (solid line in Fig. 3). Our regression was based on data from Heinle (1969) as reproduced in Miller *et al.* (1977). It takes a central position among the set of estimates presented in Fig. 3.

The obtained regression was:

$$g = 0.043\ T - 0.28 \quad (r^2 = 0.99)$$

with g in d^{-1}, T in °C.

Typically, the *Acartia* females continue to produce eggs at a rate very similar to the specific growth rate of the juveniles (Landry, 1978; Sekigushi *et al.*, 1980). Hence we used the weight-specific growth rates of juveniles as estimates for the female reproductive rates. As no information exists about the male production in

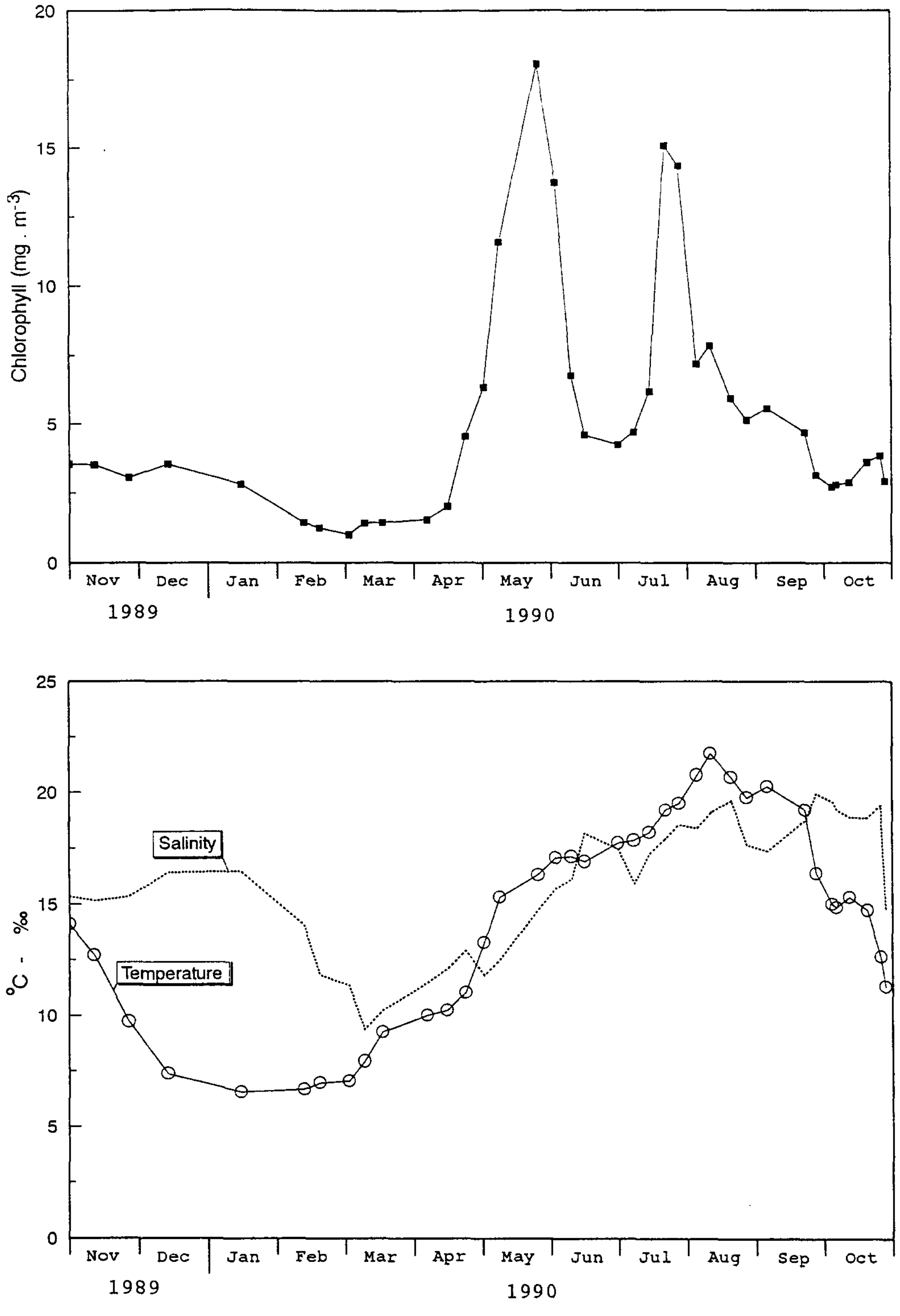

Fig. 4. Chlorophyll (above), salinity and temperature characteristics (below) of the brackish area (mean of three sampling stations).

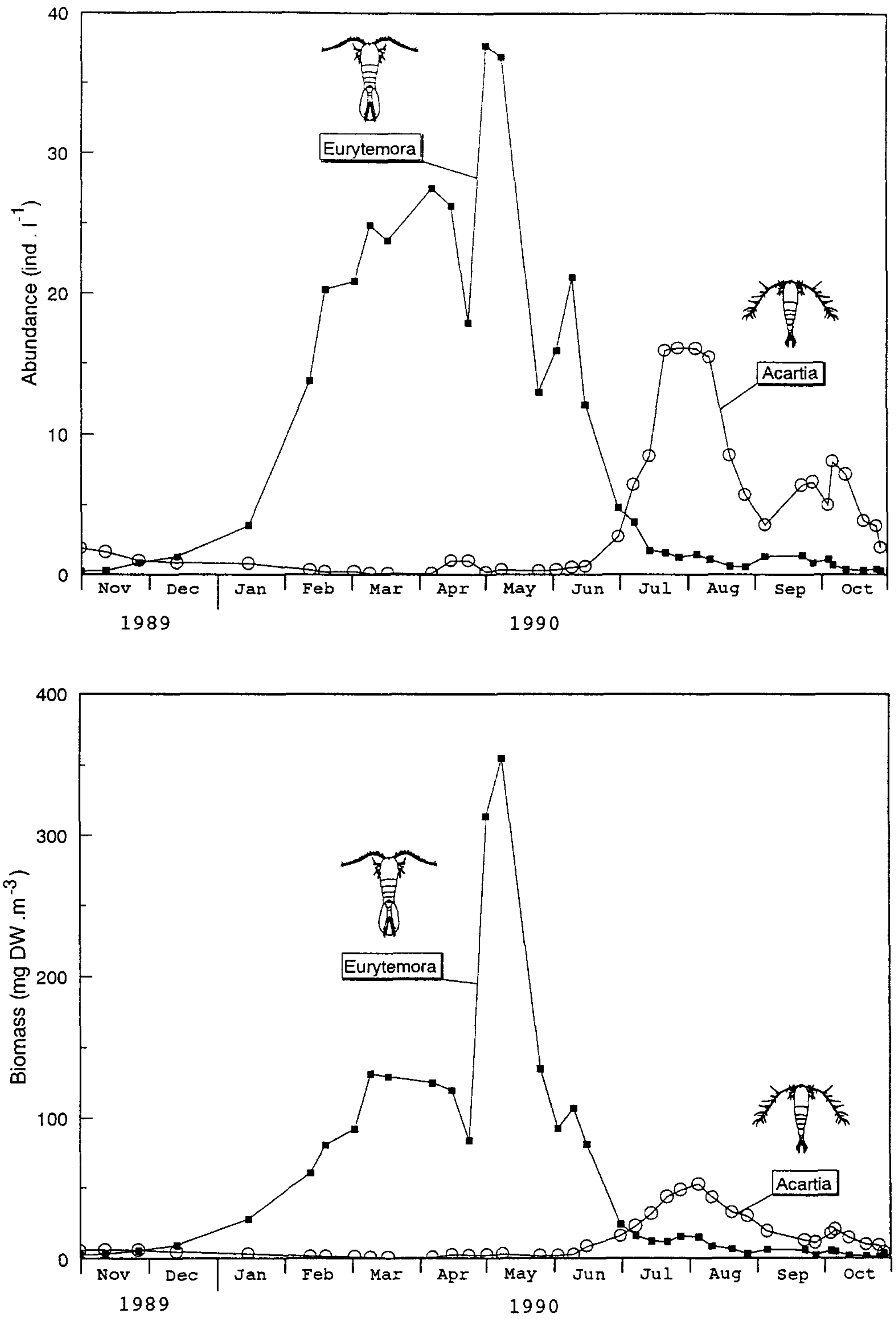

Fig. 5. a: Mean abundance (ind l^{-1}) of the copepods *Eurytemora affinis* and *Acartia tonsa* (excluding nauplii). b: Mean copepod dry weight (mg DW m^{-3}, including nauplii).

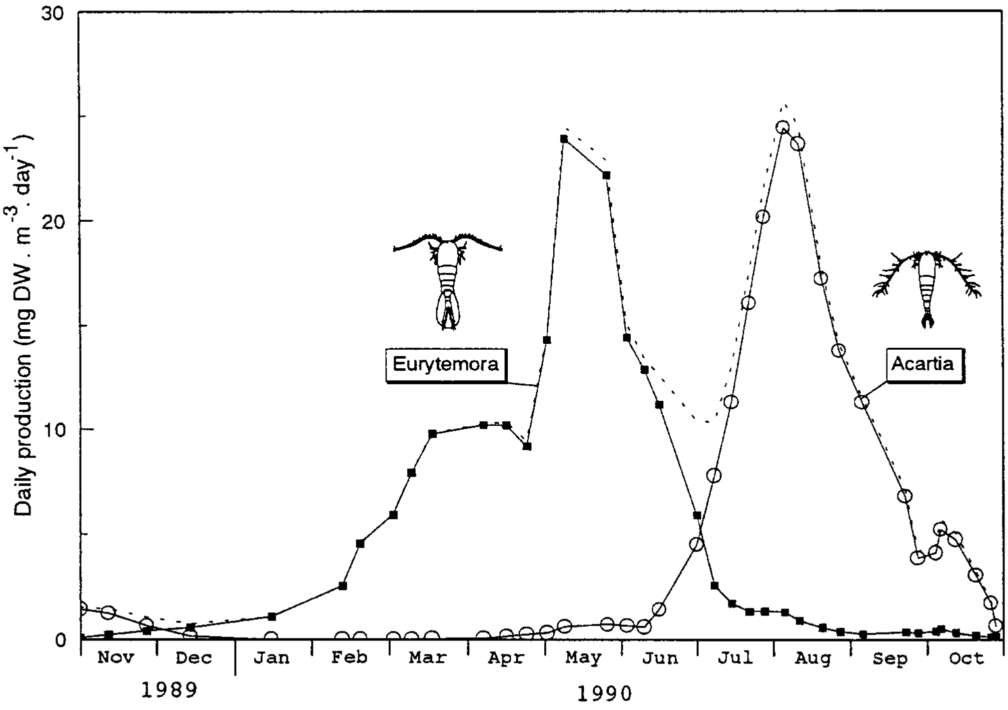

Fig. 6. a: Daily production (mg DW m^{-3} d^{-1}) of the copepods *Eurytemora affinis* and *Acartia tonsa*. The sum is indicated with a dashed line.

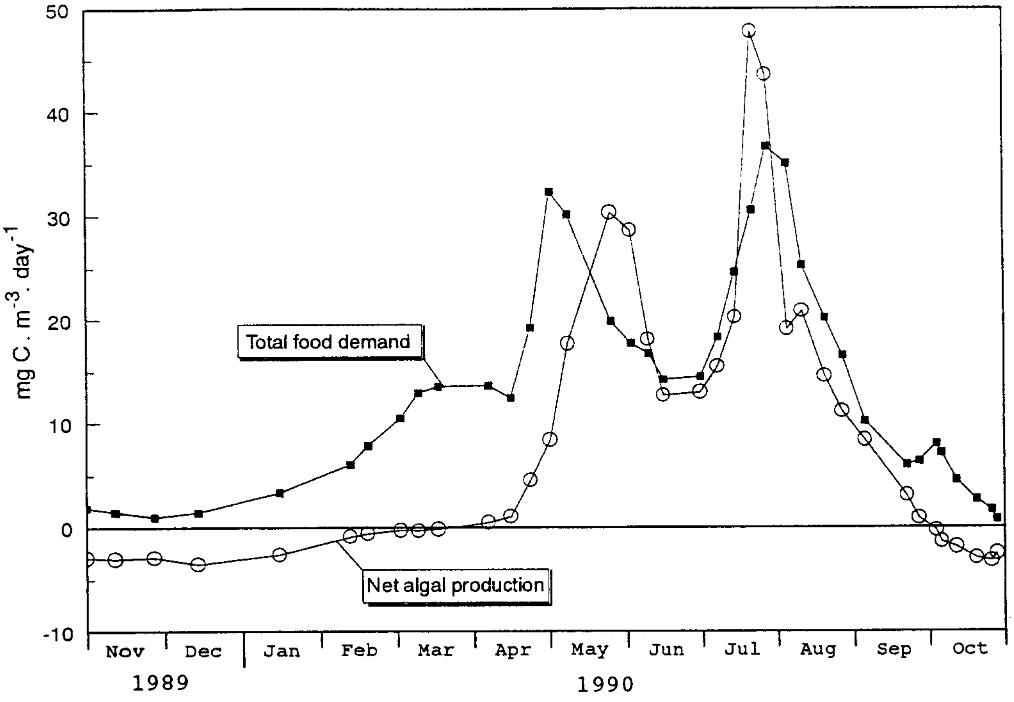

Fig. 7. Total copepod food demand and net *in situ* phytoplankton production (model result).

Table 1. Biomass, production and estimated food demand of the two most important species in the brackish part of the Westerschelde, *Eurytemora affinis* and *Acartia tonsa*. For the conversion of dry weight to carbon, a conversion factor of 0.5 g C $(gDW)^{-1}$ was used.

	Eurytemora affinis	*Acartia tonsa*
Mean biomass (mg DW m^{-3})	57	14
Mean daily production (mg DW m^{-3} d^{-1})	5.0	3.8
Annual production (mg DW m^{-3} y^{-1})	1810	1391
% Production (juveniles/females/males)	66/18/16	63/37/-
Mean daily food demand (mg C m^{-3} d^{-1})	6.5	5.4
Annual food demand (mg C m^{-3} y^{-1})	2380	1986

Acartia, males were not considered in the production estimates.

Estimated in situ copepod production and food demand

Field biomass measurements and temperature dependent growth or production rates were incorporated in Equation 1 to produce for each time interval an estimate of the copepod production. For *Eurytemora*, we distinguished three compartments: juveniles, females and males, each with their own rates of growth. *Acartia* biomass, excluding males, was considered as a whole. The two species had similar annual production values (Table I). Juveniles accounted for about 60% of total production activity in the two populations. The production realised by the males represented 16% of total *Eurytemora* production. As no male production was considered for *Acartia*, our estimate could underestimate the *in situ* production. All in all, annual productions amounted to about 1.4 and 1.8 gram Dry Weight per m^3 by *Acartia* and *Eurytemora* respectively. Assuming an average depth of 7 metres and a conversion of 0.5 gram carbon per gram dry weight, this amounts to a production of about 5 and 6 g C m^{-2} y^{-1} by *Acartia* and *Eurytemora* respectively.

The temporal evolution of daily production is given in Fig. 6. The maximum daily production of *Eurytemora affinis* was slightly lower than of *Acartia* but the species was productive during a larger part of the year. The total copepod production (ignoring the less dominant species) was bimodal and peaked in late spring and late summer.

Based on these production estimates we roughly estimated the total ingestion of the populations.

Barthel (1983) proposed an estimate of the gross growth efficiency (P/I) based on the following formula (Tranter, 1976): $[P/I = U'/100 - R/I]$. For *Eurytemora*, U', the assimilation efficiency was estimated as 89%, the mean ingestion rate (I) was estimated as 1.5 d^{-1}, the mean respiration rate (R) was 0.77 d^{-1} at 15 °C (Barthel, 1983). Thus the mean gross growth efficiency was estimated as 38% and the ingestion of *Eurytemora* was calculated as: $I = P/0.38$.

For *Acartia tonsa*, the relationship between ingestion rate (I, in d^{-1}) and production (P, same units) was estimated in the literature as:

$P = 0.23I - 0.09$	(Kleppel, 1992, where P is the egg production)
$P = 0.36I + 0.10$	(Kiørboe *et al.*, 1985)
$P = 0.44I + 0.081$	(Bergreen *et al.*, 1988)

The 'average' regression then gives $P = 0.35I + 0.03$. For comparison with the equation obtained for *Eurytemora*, we ignored the latter term and hence ingestion of *Acartia* was estimated as $I = P/0.35$.

The average estimated *in situ* food demand (Table 1) was about 2.0 and 2.4 g C m^{-3} y^{-1} or 14 and 17 g C m^{-2} y^{-1} by *Acartia* and *Eurytemora* respectively. The total food demand of the copepods was highest in the period from April to August (Fig. 7); it peaked in late spring and late summer.

Discussion

The *Eurytemora* / *Acartia* species succession is a phenomenon common to the brackish zone of many estuaries. It has for instance been observed in the Gironde (Castel, 1991), Ems-Dollart (Gaedke, 1990) and in the Patuxent River (Heinle, 1969). According to Bradley

(1975), a competition with *A. tonsa* might be an important factor influencing the distribution of *E. affinis* in summer. The feeding mode of *Acartia* on phytoplankton was assumed to give this copepod a competitive advantage in summer (Bakker & De Pauw, 1975). In the Westerschelde, the decline of the *E. affinis* population causes a decrease in total copepod grazing. At the same time the contribution of *Acartia* to total ingestion is increasing (Fig. 6). This 'gap' in total copepod grazing could indicate that apart from competitive displacement between both species, another factor should be responsible for the decline of *Eurytemora*. Several other hypotheses have been put forward to explain disappearance of the species, e.g predation of *Eurytemora nauplii* by *Acartia* (Bakker & De Pauw, 1975), selective predation of mysids or larger organisms preferentially on *Eurytemora* (Heinle & Flemer, 1975; Castel & Veiga, 1990) or seasonal changes in food quality or reproductive status (Hirche, 1992). As yet it is unclear which of these factors is responsible for the decline of *Eurytemora* populations in the Westerschelde estuary. *Acartia tonsa* has a growth efficiency which is almost four times as large as that of *Eurytemora*, and this discrepancy increases with temperature. These strong differences in growth rates could explain the fastness with which the transition between both species takes place. But in the Westerschelde, growth rates of *Acartia tonsa* are higher even at low temperatures, well before the species is seen to increase in relative abundance. Thus it appears that different responses of growth to temperature alone cannot explain the offset of *Acartia* increase and here too other, unknown factors, should be invoked.

According to Huntley & Lopez (1992), a single exponential function can describe the temperature dependence of growth for all marine copepod species. In the Westerschelde, this assumption does not hold: the (estuarine) copepod *Eurytemora affinis* has growth rates which are substantially lower than what is predicted using the general (marine) equation from Huntley & Lopez (1992), whereas those of *Acartia tonsa* are somewhat higher. Similar low growth rates for *Eurytemora affinis* were demonstrated from other studies (Poli & Castel, 1983; Burkill & Kendal, 1982; Heinle & Flemer, 1975; Vuorinen, 1982) and annual production/biomass ratios are remarkably similar between estuaries (Escaravage & Soetaert, 1993). Thus it appears that the lower growth of *Eurytemora*, when compared to marine species is a general phenomenon.

A possible source of error in our estimates lies in the use of laboratory-defined growth rates for the calculation of field production estimates. Both temperature and food availability are known to play a significant role in the copepod production activity (Burkill & Kendall, 1982; Durbin *et al.*, 1983; Klein Breteler & Gonzalez, 1988). According to Miller *et al.* (1977), isochronal and thus exponential growth does not occur by *Acartia* species when excess food is not present. Thus we could have overestimated growth rates of this species. However, for the Westerschelde, it has been shown that individuals of *E. affinis* were growing at very similar rates whether cultured in excess algal food or by using natural food as culture medium (Escaravage & Soetaert, 1993). Like *E. affinis*, *A. tonsa* is an opportunistic grazer, combining microzooplankton, phytoplankton and detritus diets (Roman, 1984; Kleppel, 1992). Moreover, growth rates obtained in cultures of this species were very comparable, even when fed other algae (Fig. 3). Thus it seems reasonable to assume that laboratory-defined growth rates of *A. tonsa* can be used for the estimation of secondary production in the field, as suggested by Huntley & Lopez (1992). The fact that we were unable to culture *Acartia* in our small-scale experiments whereas *Eurytemora* grew well, was merely due to the absence of stirring in the culture vessels. Individuals of *Eurytemora* were able to feed from particles on the bottom whereas individuals of *Acartia* were not.

The diet of calanoid copepods most often consists of phytoplankton, but they can obtain food from any known stock of organic matter (Poulet, 1983; review in Kleppel, 1993). Thus in some attempts to define a food budget of a filter-feeding zooplankton community, it has been necessary to assume that part of the zooplankton diet is obtained from detrital material in the water column. This is particularly so during the winter months when there is very little primary productivity and a low algal standing stock. Based on production measurements of the dominant estuarine copepod *Eurytemora affinis* and primary production measured from light and chlorophyll data, Heinle & Flemer (1975) estimated that algal production in the Patuxent river estuary (USA) was too small to satisfy the carbon requirements of this copepod. They postulated that the population of *Eurytemora affinis* thrives on the abundant detritus in the area. This hypothesis was adopted by Hummel *et al.* (1988) for the Westerschelde estuary. They suggested the existence of two food chains, one based on detritus in the brackish part of the estuary, the other one based on primary production in the marine part of the estuary. Since that paper much scientific effort has been directed towards the Westerschelde estuary and the magnitude of the different food stocks and primary production is now better known.

The total amount of particulate organic carbon in the brackish part of the Westerschelde was highest from October till April (about 4 g C m^{-3} in 1989–1990), it was lowest from May to September (about 1 g C m^{-3} in 1990). If we exclude coprophagy, then in the worst possible case (combining the highest food demand of 0.04 g C m^{-3} d^{-1} with the lowest POC values) copepods would need 25 days to ingest all available POC. This is longer than the residence time of the water mass (and of POC) in this part of the estuary (Soetaert & Herman, 1995a). Hence, although not all particulate organic carbon may be available as food for the copepods, it seems likely that the high stocks of POC could meet at least part of the copepods nutritional demand.

By means of a dynamic simulation model, Soetaert *et al.* (1994) and Soetaert & Herman (1995b) were able to estimate net phytoplankton growth in the Westerschelde estuary. The brackish part of the estuary was characterised by low standing stocks of phytoplankton; it was the site of a rapid transition of freshwater-based towards marine-based phytoplankton communities (Soetaert *et al.*, 1994; Kromkamp *et al.*, 1995). Moreover, net primary production was low here and amounted only to about 15 to 30 g C m^{-2} y^{-1}. This is about the food demand of the two copepod species together (estimated as 31 g C m^{-2} y^{-1}). To see in how far the *Eurytemora* and *Acartia* communities can depend on an algal diet, we compared net phytoplankton production values with total copepod food demand during the year. Algal net production was estimated by multiplying net production/chlorophyll ratios derived from the model (Soetaert *et al.*, 1994), with observed chlorophyll values. The results are given in Fig. 7. Provided that copepods can graze all primary production, *in situ* produced phytoplankton would be sufficient for growth during a limited period of the year only, when algal biomass is at its highest (May–July). In fall, winter and spring, *in situ* algal production cannot meet nutritional demands of the copepods. In reality, only part of the phytoplankton is consumable by the copepods, implying that even less is available.

Finally we can calculate the impact of the brackish water community on the carbon budget of the Westerschelde estuary, using the simulation model of the Westerschelde (Soetaert & Herman, 1995 a, b, c). Each year some 100.10^3 ton of carbon is net imported in the entire estuary by means of the river or through waste discharges (Wollast, 1976; Soetaert & Herman, 1995b), while some 20.10^3 ton of carbon are primary produced. The estuary is only a small net exporter of carbon (some 6.10^3 ton of carbon per year, Soetaert & Herman, 1995b) but much of the refractory carbon leaves the estuary at the seaside, while more reactive organics (e.g. marine copepods, Soetaert & Herman, 1994) are imported from the sea (Soetaert & Herman, 1995c). In the brackish part of the estuary, some 65.10^3 ton of carbon is imported, mainly from the upstream part; some 4.10^3 ton of carbon is primary produced (mainly benthic algae). Total carbon consumption in this part is estimated as 30.10^3 ton of carbon per year, mainly by pelagic and benthic mineralisation processes. Considering a total volume of the brackish zone of 394.10^6 m^3 (model compartments 5–8), the amount of carbon passing through the brackish mesozooplankton can be estimated as $1.7.10^3$ ton C per year, or some 6% of all consumed carbon, some 2% of all imported or *in situ* produced carbon.

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