



# Population dynamics of *Nannopus palustris* (Copepoda, Harpacticoida) in the oligo-mesohaline area of the Gironde estuary (France)

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**Abstract:** In this study, results are presented concerning the population dynamics of the meiobenthic copepod *Nannopus palustris* in the oligo-mesohaline area of the Gironde estuary, France. Samples were taken weekly during one year (April 1992 to April 1993). Stage-specific birth and mortality rates were calculated using the Argentesi model. Clutch size, percentage of ovigerous females and sex ratio of the *Nannopus palustris* population showed clear seasonal variations strongly related to temperature. Other factors like salinity or chlorophyll-a were also significantly related to these population parameters. The development time field data obtained for *Nannopus palustris* was also significantly related to temperature. Fecundity, or egg production rate, and instantaneous birth rate showed strong variations throughout the year. In this study specific mortality rates for nauplius, copepodite and adult animals were estimated for the first time for a benthic harpacticoid. All models indicate that the nauplius stage suffers higher mortality as compared to copepodite stages or adults. Waves or peaks of mortality were detected for all stages and were probably related to the moulting process associated to the progression of different abundance pulses. All results indicate that the population increase is not food limited during the year, being mainly temperature controlled.

**Résumé:** *Etude de la dynamique de population de Nannopus palustris dans la zone oligo-mésohaline de l'estuaire de la Gironde.* Pour cette étude, l'échantillonnage a eu lieu chaque semaine pendant une année (Avril 1992-Avril 1993). Les taux de mortalité et de naissance spécifique pour chaque stade ont été calculés avec le modèle d'Argentesi. La plupart des paramètres de la population de *N. palustris* (nombre d'œufs portés par femelle ovigère, pourcentage de ces femelles, sex-ratio et temps de développement estimé in situ) ont montré une forte relation avec la température. D'autres facteurs tels que la salinité et la concentration en chlorophylle-a ont aussi été mis en relation avec les paramètres de la population de *N. palustris*. Les données sur le développement obtenues in situ pour *Nannopus palustris* ont démontré une relation significative avec la température. Les taux de production d'œufs et d'éclosion ont montré de fortes variations au cours de l'année. Pour la première fois les taux de mortalité des nauplius, copépodites et adultes ont été estimés dans une population de copépodes harpacticides. Le stade nauplius a les taux de mortalité les plus élevés comparés aux autres stades. Des valeurs maximales de taux de mortalité pour chaque stade ont été mises en évidence et paraissent associées aux processus de mue et au développement de "quasi-cohortes". Les résultats obtenus sur la dynamique de population de *N. palustris* indiquent que le facteur nourriture n'est pas limitant au cours de l'année, mais que la température contrôle le développement de la population.

**Keywords:** Population dynamics; *Nannopus palustris*; Harpacticoid copepod; Gironde estuary.

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## Introduction

Changes in population size are a function of the basic demographic processes of birth, death and growth, and a better understanding of population regulation or variability will be obtained if these demographic processes are estimated over time and related to environmental conditions.

Data on life history and population dynamics for benthic harpacticoid copepods are scant. This is mainly due to the continuous recruitment and short life cycles characteristic of most meiobenthic populations which imply that population dynamics studies require very frequent sampling and painstaking analysis of population structure coupled with size-specific growth rates estimated from laboratory cultures (eg. Ceccherelli & Mistri, 1991). Laboratory rearing of meiobenthic harpacticoids is not an easy task and many species could not be successfully cultured even using rather sophisticated techniques, apparently due to very specific food requirements (Chandler, 1986). Compared to the other free-living copepod orders, mainly composed of planktonic species, few data are thus available concerning development rates.

*Nannopus palustris* Brady, 1880 is a cosmopolitan burrowing harpacticoid copepod of estuarine muds, ranging in adult size from 0.55 to 0.65 mm for an average weight of 1.5 µg. Several studies have described its annual cycle (eg. Bodin, 1972; Phillips & Fleeger, 1985) or zonation (Coull et al., 1979) but no data are available concerning its growth or mortality rates. Santos et al. (1995) suggested that this species is a poor competitor and presented data indicating that the gut content in chlorophyll pigments of this species is similar to that of *Microarthridion littorale* (Poppe, 1881), a well-known diatom feeder. In the oligo-mesohaline area of the Gironde estuary (France) it is the dominant species representing up to 50% of total meiofauna biomass in intertidal sediments (Santos et al., 1996). Considering the importance of this species together with the necessity for more studies on harpacticoid population ecology, this study aims to describe *Nannopus palustris* population dynamics in the Gironde estuary. Several attempts were made to rear *Nannopus palustris* in the laboratory but all were unsuccessful. Due to the impossibility of obtaining size-specific growth rates in the laboratory for this species, some models designed to predict development rates (Santos et al., 1999) together with a model derived from field data were applied to study the *Nannopus palustris* population dynamics.

## Materials and methods

**Study area.** The study area is located in the middle of Gironde estuary (45°32' N, 0°47' W) 55 km seaward from

Bordeaux (France). Tidal amplitude varies between 2.5 and 5.0 m and current velocities can reach 2 m s<sup>-1</sup>. Freshwater discharge varies seasonally, reaching a maximum in January-February (mean: 1,500 m<sup>3</sup> s<sup>-1</sup>) and a minimum in August-September (mean: 250 m<sup>3</sup> s<sup>-1</sup>).

**Sampling.** Between April 1992 and April 1993 one intertidal station, located on the mudflat at the mid-tide water level, was surveyed weekly during low water, resulting in 47 sampling data points. During this period data were recorded on water salinity using a hand refractometer and sediment temperature measured with an electronic thermometer at 3 cm depth. Published data were used for insolation (Bulletin Climatologique de la Gironde) and for tidal amplitude expressed as tide coefficient, a specifically French unit (approximate scale: tide coefficient 30-50 = neap tide; 80-100 = spring tide) (Annuaire des marées. Port Autonome de Bordeaux).

Replicate cores (inner diameter 2.8 cm) were taken for meiofauna (4 replicates to a depth of 5 cm), microphytobenthic pigments, particulate organic carbon (3 replicates to a depth of 1 cm) and sand content of sediment (2 replicates to a depth of 1 cm). Meiofauna samples were preserved in 10% formalin and, after extraction from the sediment using the Ludox technique (Jonge & Bouwman, 1977), animals retained on a 63 µm sieve were stained with Rose Bengal (more than 95% of total individuals, including nauplii, were extracted and retained with this method). Nauplii, copepodites and adults of *Nannopus palustris* were counted in each replicate. The coefficient of variation for nauplii and copepod numbers among replicates was rarely above 50%. For copepodite stage and adult sex ratio determinations, up to 300 animals were generally examined for each sample (this number was available in replicates for 29 out of 49 sampling dates and only in six samplings the number of examined animals was lower than 150 individuals). The number of eggs per egg sac was also counted for at least 25 egg sacs when these were available in sufficient numbers in each sampling date.

Methods used to determine the environmental factors (microphytobenthic pigments, particulate organic carbon and sediment sand content) are described elsewhere (Santos et al., 1996).

**Demographic analysis.** Several attempts were made to rear *Nannopus palustris* but these were not successful (see also Chandler, 1986). In spite of using different foods (artificial food and cultured diatoms or bacteria) with or without natural sediment, females always drop their egg sacs after some days in the laboratory and born nauplii never developed into copepodites. Clear cohort structure was absent in the field data but pulses of nauplii production could be found sometimes and development times were thus estimated from the field data using Bhattacharya's method as available in the routine MPA of Compleat ELEFAN 1.10

program (Gayaniilo et al., 1989) to determine peaks on the stage abundance data for each sampling date. Models designed to predict development rates for harpacticoid copepods (Santos et al., 1999; Table 1) were also applied to study the population dynamics of this species.

Fecundity (number of eggs produced per female per day) was calculated as:  $F = Ne/Nf.De$  where **Ne** and **De** are numbers and development time of eggs respectively and **Nf** is adult female numbers. Egg development time for *N. palustris* was obtained from a general model developed for harpacticoids by Santos et al. (1999).

As recommended by Taylor & Slatkin (1981) several methods were used to estimate the demographic parameters of birth and death. Thus, for the birth rate estimates, the methods of Edmondson (1960), Paloheimo (1974) and Argentesi et al. (1974) were used and compared. Stage specific mortalities were expressed as instantaneous rates and estimated by the single basic model of Argentesi et al. (1974) but with different inputs of estimated development rates. An important parameter used in the specific mortality estimation is the proportion of time spent as nauplii (**Dn**) compared to the total development time (**Dt**). Thus, for the estimation of mortality rates of *N. palustris* stages an average value of **Dn/Dt**, estimated from Santos et al. (1999) model for this proportion, as well as its confidence limits were used. Since the field data contain some sampling error or noise, data were regularized by smoothing (running mean of three terms) before analysis.

**Models' statistics.** Stepwise multiple regression analysis (MRA) (a combination of forward and backward selection procedures) and simple regression analysis (RA) were used to identify the most important predictors of demographic parameters. The significance level for including variables in the MRA and for accepting the RA was 0.05. Adjusted values for the coefficient of determination ( $R_a^2$ ) were calculated and standardized partial regression (beta) coefficients were used to indicate the relative importance of the various  $X_i$ 's in determining the value of Y. Normal probability plots of studentized residuals were used to check for normality (Zar, 1996). Cross-correlation analysis was used to investigate the existence of lag phases between variables.

**Table 1.** Equations for models developed by Santos et al. (1999) for harpacticoid copepods used in this work (*ln* is natural logarithm; **T** is temperature; **mT** is maximum monthly temperature at the collection site; **L** is animal's length). **Dn**, time spent as nauplius; **Dt**, total development time.

**Tableau 1.** Equations des modèles, développés par Santos et al. (1999) pour les copépodes harpacticoides, utilisées dans ce travail (*ln* - logarithme naturel ; **T** - température ; **mT** - température mensuelle maximum dans l'aire d'échantillonnage ; **L** - taille de l'animal) ; **Dn**, durée de la période nauplius ; **Dt**, durée totale du développement.

## Results

### *Environmental and Nannopus palustris field data*

The sediment temperature varied between 5.8 and 23.8 °C, following a clear seasonal pattern. Salinity varied between 0 and 9, with low values found both in early summer and late autumn. The low values recorded in June were atypical and were related to heavy rainfall (260% of average values) that also influenced temperature (Fig. 1a).

Chlorophyll-a and pheopigments data were already discussed elsewhere (Santos et al., 1997) thus only a simple description is presented here. The mean annual value of Chl-a was rather low (26.4 mg m<sup>-2</sup>). Though peak values were observed during summer, these were followed by rather low values showing thus high variability during this season. A clear increase was observed during late winter and early spring (Fig. 1b). Organic carbon presented higher values in spring-summer as compared to autumn-winter (Fig. 1b).

The sand content of the sediment was generally very low (< 5%), values varied strongly at short time scales (up to 10% in a single week) and no clear pattern could be observed (Fig. 1c).

The temporal evolution of the developmental stages of *N. palustris* at the intertidal station of the Gironde estuary is shown at Fig. 2. Minimum densities, ranging between 100 and 640 ind 24.6 cm<sup>-2</sup>, were observed during autumn and early winter when almost only adults were present (Fig. 2). Greater densities (values ranging between 250 and 4100 ind 24.6 cm<sup>-2</sup>) were observed during spring-summer as compared to autumn-winter (Fig. 2). A similar pattern was observed for the clutch size with maximum values (20 to 22 eggs per ovigerous female) mainly present during summer (Fig. 3). Clutch size (average of 17.4 eggs per ovigerous females with a standard deviation of 2.6) was strongly related to temperature and salinity (both squared, salinity with a 2 weeks lag phase) (Table 2).

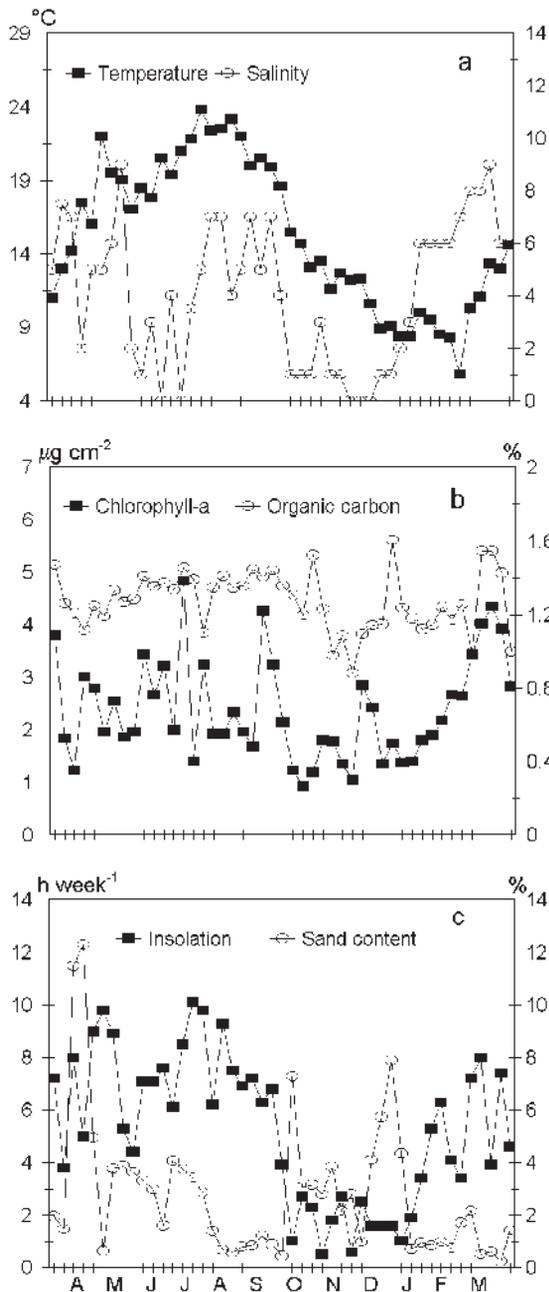
The number of eggs in 24.6 cm<sup>2</sup> (Fig. 2) was obtained by multiplying the number of ovigerous females by the mean clutch size (Fig. 3) for each sampling date. Values increased throughout spring and early summer, attaining maximum

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Total Development Time model II  
Egg Development Time  
Dn/Dt ratio

$lnTDT = 8.226 - 0.071T - 0.061mT - 5.16L + 2.155L^2$   
 $EDT = 12.823 - 0.944T + 0.016T^2 + 0.781L$   
 $Dn/Dt = 0.559 - 0.187L$

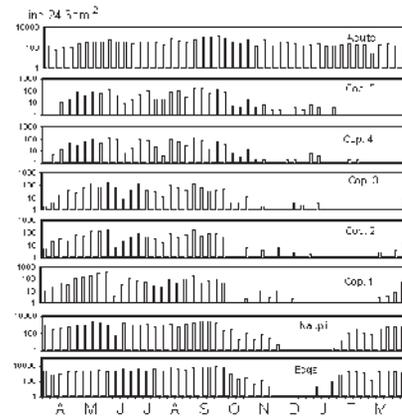
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**Figure 1.** Temporal variation during the study period of the environmental factors at the sampling area. (a) Temperature (°C) and salinity; (b) Chlorophyll-a ( $\mu\text{g cm}^{-2}$ ) and organic carbon content of the sediment (%); (c) Insolation ( $\text{h week}^{-1}$ ) and sand content of the sediment (%).

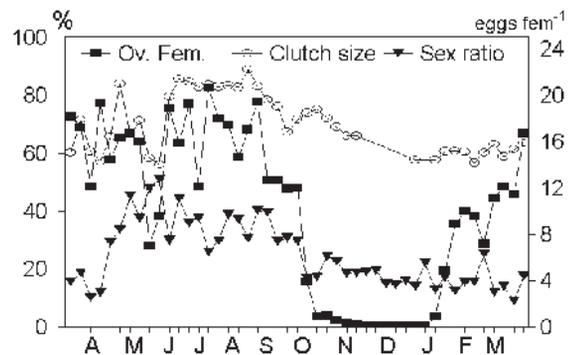
**Figure 1.** Variation temporelle pendant la période d'étude des facteurs environnementaux dans l'aire d'échantillonnage. (a) Température (°C) et salinité ; (b) Chlorophylle-a ( $\mu\text{g cm}^{-2}$ ) et contenu en carbone du sédiment (%); (c) Insolation ( $\text{h semaine}^{-1}$ ) et contenu en sable du sédiment (%).

peaks of nearly 10,000 eggs  $24.6 \text{ cm}^{-2}$  on late summer when a sudden decrease occurred. Since mean clutch size did not



**Figure 2.** Temporal evolution of *Nannopus palustris* eggs, nauplii, copepodites and adults density at the intertidal station of the mudflat during the period April 1992 to April 1993.

**Figure 2.** Évolution temporelle de la densité des œufs, nauplii, copépodites et adultes dans la station intertidale de la vasière pendant la période Avril 1992 à Avril 1993.



**Figure 3.** *Nannopus palustris* clutch size (number of eggs per ovigerous female), sex ratio (male to female ratio) and percentage of ovigerous females variation during the sampling period.

**Figure 3.** Évolution temporelle de la taille de la ponte (nombre d'œufs portés par femelle ovigère), de la sex-ratio (proportion mâle/femelle) et du pourcentage de femelles ovigères de *Nannopus palustris* pendant la période d'échantillonnage.

vary greatly (14 to 22 eggs per ovigerous female), the total number of ovigerous females mainly determined the egg numbers. Factors affecting ovigerous females abundance, i.e. temperature and chlorophyll-a concentration, were thus the same determining egg abundance (Table 3).

The sex ratio (males/females) showed a clear seasonal pattern with a higher proportion of females during winter-spring as compared to summer-autumn (Fig. 3). Females dominate adult density throughout the year, a single exception occurring on 19th June 1992 when males make up

**Table 2.** Stepwise multiple regression analysis for clutch size (eggs per ovigerous female) (both temperature and salinity squared, salinity with lag of 2 weeks) ( $p < 0.05$ ). (for all Tables: C – coefficient; B - beta coefficient).

**Tableau 2.** Analyse de régression multiple pas-à-pas pour la taille des pontes (Œufs par femelle ovigère) (température et salinité élevées au carré, salinité avec un décalage de deux semaines) ( $p < 0,05$ ). (pour tous les tableaux : C – coefficient ; B – coefficient beta).

	intercept	Temperature	Salinity	$R_a^2$
C	7.402	0.0065	-0.0184	0.747
B		0.789	0.334	

**Table 3.** Stepwise multiple regression analyses for total egg numbers (eggs  $10\text{ cm}^{-2}$ ) (temperature with lag of 1 week) and for abundance of ovigerous female (ovigerous females  $10\text{ cm}^{-2}$ ) (Chlorophyll-a in natural logarithm) ( $p < 0.05$ ).

**Tableau 3.** Analyse de régression multiple pas-à-pas pour le nombre total d'œufs (œufs  $10\text{ cm}^{-2}$ ) (température avec un décalage d'une semaine) et pour l'abondance de femelles ovigères (femelles ovigères  $10\text{ cm}^{-2}$ ) (chlorophylle-a en logarithme naturel) ( $p < 0,05$ ).

Eggs	intercept	Temperature	Chlorophyll-a	$R_a^2$
C	-3628.1	317	284.5	0.618
B		2.075	0.117	

Females	intercept	Temperature	Chlorophyll-a	$R_a^2$
C	-172.8	15.2	56.66	0.598
B		0.678	0.490	

51% of the adult density. Though significantly lower in abundance as compared to females, males were always present in sufficient numbers to form clasping pairs. The number of clasping pairs was mainly limited by the abundance of female copepodite-5 and clasping males did not surpass 30% of total male abundance. From 72 clasping pairs examined 66 were composed by an adult male and a copepodite-5 female and 6 pairs by an adult male and a copepodite-4 female suggesting that females are fertilized only once during their life-time. Temperature and density of non-naupliar animals strongly influenced the sex ratio (Table 4).

The percentage of ovigerous females (Fig. 3) also displayed a clear seasonal variation, high values occurred during most of the spring and summer periods. A single factor, insolation (with a lag phase of one week), explained more than 84% of the percentage of ovigerous females variability (Table 5).

**Table 4.** Stepwise multiple regression analysis for sex ratio (males percentage) (density excluding nauplius stages ) ( $p < 0.05$ ).

**Tableau 4.** Analyse de régression multiple pas-à-pas pour la sex-ratio (pourcentage de mâles) (densités sans le nombre de nauplii) ( $p < 0,05$ ).

	intercept	Temperature	Density	$R_a^2$
C	0.0307	0.0106	0.0001	0.632
B		4.711	0.403	

**Table 5.** Stepwise multiple regression analysis for percentage of ovigerous females (insolation with lag of 1 week) ( $p < 0.05$ ).

**Tableau 5.** Analyse de régression multiple pas-à-pas pour le pourcentage de femelles ovigères (insolation avec un décalage d'une semaine) ( $p < 0,05$ ).

	intercept	Insolation	$R^2$
C	-0.0916	0.0916	0.842

#### Field development time

The determination of significant peaks on the stage abundance data (Fig. 2) using Bhattacharya's method was not always successful and peaks for adjacent stages occurred frequently at the same sampling date. These results suggest that the sampling interval was not sufficiently short to follow the nauplii recruitment peaks and imply that care should be taken while using these data. Nevertheless, six pulses of nauplii production could be determined with development time estimates (from an average nauplius stage to adult, see Discussion) varying from 12 to 28 days (Table 6).

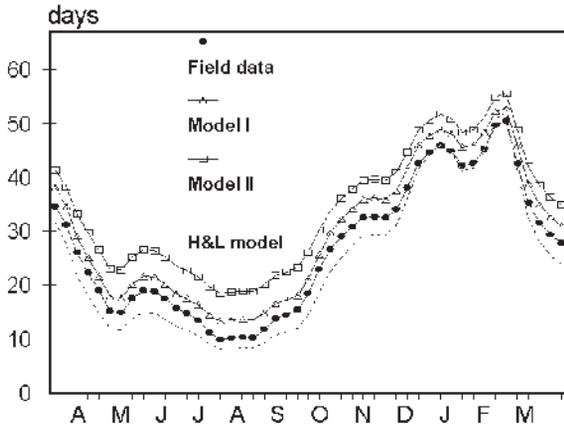
Temperature was the only factor significantly related to these development time data. A very good relationship (hereafter called field development model) was obtained between total development time (**Dt**) and temperature (**T**) when the latter was transformed on its natural logarithm

**Table 6.** Development times (from average nauplius stage to adult) (Time in days) and mean temperature during development (Temperature) of the six growth pulses followed.

**Tableau 6.** Temps de développement (du stage nauplius moyen à adulte) (temps en jours) et température moyenne pendant le développement (Température, °C) des six pics de croissance suivis.

Pulse No.	1	2	3	4	5	6
Time	28	13	15	12	15	16
Temperature	15	19	19	23	21	19
Start	April 16 <sup>th</sup>	May 29 <sup>th</sup>	Jun 28 <sup>th</sup>	Aug 04 <sup>th</sup>	Aug 27 <sup>th</sup>	Sept 19 <sup>th</sup>
Final	May 14 <sup>th</sup>	Jun 11 <sup>th</sup>	Jul 13 <sup>th</sup>	Aug 16 <sup>th</sup>	Sept 11 <sup>th</sup>	Oct 05 <sup>th</sup>

following the equation:  $Dt = 124.57 - 36.59 (\ln T)$ ;  $df = 5$ ,  $R^2 = 80\%$ ,  $p < 0.015$ . The total development time values estimated for *N. palustris* with the field development model, those predicted by models I and II from Santos et al. (1999) and a general model for marine planktonic copepods (Huntley & Lopez, 1992) are shown in Fig. 4.



**Figure 4.** *Nannopus palustris* development time values, as a function of observed field temperatures (smoothed by a running mean of three terms), obtained using the field data model, Santos et al. (1999) models I, II and Huntley & Lopez (1992) model (see text for details).

**Figure 4.** Temps de développement de *Nannopus palustris*, en fonction de la température (lissé avec une moyenne mobile de période trois), obtenue avec le modèle des données de terrain, modèles de Santos et al. (1999) I et II, et modèle de Huntley & Lopez (1992) (voir texte pour les détails).

#### Birth and death rates

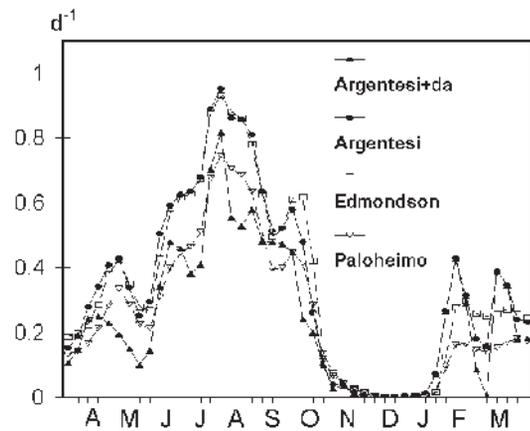
Fecundity attained values of 6 eggs per female per day during summer with a clear seasonal variation that was significantly explained by temperature (squared) and salinity ( $R_a^2 = 86\%$ ) (Table 7).

**Table 7.** Stepwise multiple regression analysis for fecundity (number of hatching/produced eggs per female per day) (Tempsqu = squared temperature) ( $p < 0.05$ ).

**Tableau 7.** Analyse de régression multiple pas-à-pas pour la fécondité (nombres d'œufs produits par femelle par jour) (Tempsqu = température au carré) ( $p < 0,05$ ).

	intercept	Tempsqu	Salinity	$R_a^2$
C	-1.119	0.01	0.135	0.863
B		0.845	0.202	

The instantaneous birth rate estimated from four different methods/calculations are shown in Fig. 5. Only small differences were observed in the magnitude of this rate estimates between the different methods. Birth rates followed fecundity with maximum values occurring during summer.



**Figure 5.** Instantaneous birth rates calculated using the methods of Edmondson (1960), Paloheimo (1974) and Argentesi et al. (1974) (Argentesi+da - calculated considering that eggs death rate equals adults death rate; see Methods).

**Figure 5.** Taux instantanés de natalité calculés avec les méthodes de Edmondson (1960), Paloheimo (1974) et Argentesi et al. (1974) (Argentesi+da - calculé en considérant que les oeufs ont un taux de mortalité semblable à celui des adultes; voir Méthodes).

Death rates for nauplii did not change very much independently of the model or  $Dn/Dt$  ratio. Even if we use the development time models that gave the most different results (field and II models), nauplii death rates did not vary strongly (Fig. 6a). The same did not occur for copepodites and adults. Using different development models can double the estimated mortality at several sampling times (Fig. 6b and 6c).

Table 8 clearly shows that the mean mortality rate is much higher in nauplii as compared to both copepodites and adults, and that copepodites suffered higher mortality rates than adults.

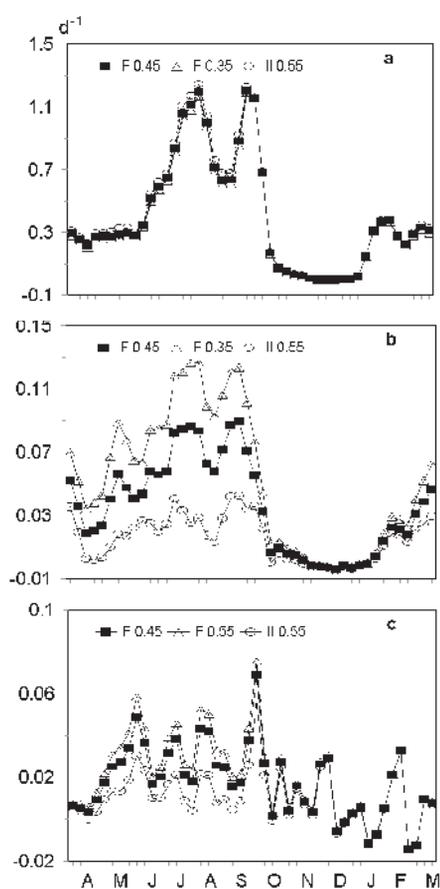
The comparison of the estimated mortality rates based on the different development models, independent of  $Dn/Dt$  ratios, shows that model II (slower development time) increases nauplii mortality and decreases both copepodites and adult mortality rates (Table 8). Compared to the  $Dn/Dt$  ratio, the choice of the development model is more important for the estimation of adult mortality rates. Copepodite rates however react strongly to the  $Dn/Dt$  ratio (Table 8).

Stage specific death rates, obtained using the field development model and a  $Dn/Dt = 0.45$ , were always significantly correlated with the previous stage abundance ( $r = 0.817$   $p < 0.001$  for nauplii death rate x number of eggs;  $r = 0.798$   $p < 0.001$  for copepodites death rate x nauplii and;  $r = 0.603$   $p < 0.001$  for adults death rate x copepodites).

**Table 8.** Mean mortality rates ( $\text{day}^{-1}$ ) of nauplius, copepodite and adult calculated using the field development model, model I and II from Santos et al. (1999) and using a  $\text{Dn/Dt}$  ratio of 0.45 and its confidence limits 0.35 and 0.55.

**Tableau 8.** Taux de mortalité moyennes ( $\text{jour}^{-1}$ ) des nauplii, copépodites et adultes calculés avec le modèle des données obtenues sur le terrain, modèles I et II de Santos et al. (1999) et en utilisant une proportion  $\text{Dn/Dt}$  de 0,45 et ses limites de confiance 0,35 et 0,55.

Stage	Nauplius			Copepodite			Adult		
$\text{Dn/Dt}$ Model	Field	I	II	Field	I	II	Field	I	II
0.35	0.394	0.404	0.416	0.052	0.044	0.035	0.015	0.013	0.011
0.45	0.405	0.413	0.422	0.035	0.030	0.024	0.018	0.015	0.012
0.55	0.409	0.416	0.423	0.023	0.019	0.015	0.021	0.018	0.015



**Figure 6.** Death rates estimated using the different development models (F – field model, and II – model II from Santos et al. (1999)) and  $\text{Dn/Dt}$  ratios (0.35, 0.45 and 0.55). Dark plots are for the field model with a  $\text{Dn/Dt} = 0.45$  and the others are for those which gave the highest and lowest mortality rate results. (a) nauplius; (b) copepodite; (c) adult.

**Figure 6.** Taux de mortalité calculés avec différents modèles de développement (F – modèle pour les données obtenues sur le terrain, et II – modèle II de Santos et al. (1999)) et différentes proportions  $\text{Dn/Dt}$  (0,35, 0,45 et 0,55). Les carrés noirs montrent le modèle F avec  $\text{Dn/Dt} = 0,45$  et les autres symboles donnent les résultats les plus hauts et les plus bas des taux de mortalité. (a) nauplii ; (b) copépodites ; (c) adultes.

## Discussion

The density of the different stages, as well as the basic parameters measured directly from the *Nannopus palustris* field population (clutch size, percentage of ovigerous females and sex ratio) showed clear seasonal variations. Similar patterns, with a spring-summer density peak, have been consistently documented for this species in estuaries (Bodin, 1972; Fleeger, 1985; Phillips & Fleeger, 1985). The timing varying with latitude, both high densities and percentage of ovigerous females occurring between January and May in a Louisiana estuary ( $29^{\circ}10'N$ ) (Fleeger, 1985) and between March and October in the Gironde estuary ( $45^{\circ}32'N$ ), suggests that temperature/light may have an important influence over this species population dynamics. The good relationships found between clutch size, number of ovigerous females or sex ratio and temperature support this view.

Percentage of ovigerous females and clutch size were lowest during autumn and winter (from October to January). Several authors have used these indices as indicators of food limitation (e.g. Van Dolah et al., 1975 and references therein) but results from the stepwise multiple regressions better suggest temperature as the main factor affecting *Nannopus palustris*.

Total numbers of ovigerous females and eggs were significantly related to food availability (as expressed by chlorophyll-a concentration). Nevertheless, this effect is very slight as compared to that of temperature according to the regression coefficients beta. Also, no lag phase was observed for ovigerous female numbers, mainly suggesting that the animals were responding to chlorophyll-a, in a similar way as does the ovigerous female number to temperature and thus indicating that food was not limiting during most of the study period.

Salinity also affected clutch size but with a lag phase of two weeks. This is a very long lag phase since 15 days approximate the total development time during most of the spring-summer period. Thus, it is reasonable to suppose that

the salinity effect may be a result of its influence on previous life-cycle phase (naupliar or copepodite stages). This hypothesis can be related to a similar long-term effect (referring to a single generation period) of simulated perturbation (crowding) on egg production observed by Walker (1979).

Sex ratios generally favoured females, a situation normally occurring in field samplings (see Hicks & Coull, 1983). The factors that affected this ratio, temperature and population density, are within the most common (Hicks & Coull, 1983) and suggest a labile population oriented sex determination since males were always available in sufficient numbers to inseminate females even when they represent only 20% of the adult population. A similar situation was observed by Dinet (1972) for *Halectinosoma herdmani*, males representing less than 15% just before the reproductive period.

The development time data obtained for the field population of *Nannopus palustris*, though including values obtained mainly with high field temperatures could be significantly related to temperature. Though the development time was calculated from a mean nauplius age (since we have not determined nauplius stages), which would suggest that the calculated development time was underestimated, the high mortality rate calculated for nauplii (independently of the development time model used) suggests that this was a reasonable procedure since most of the animals should be from the younger naupliar stages. The model developed with this field data compared well with the predictions of the literature models for harpacticoid copepods, especially with the one based on the equiproportional rule (Santos et al., 1999).

From the three models considered for *N. palustris*, the field development model was more similar to the model developed by Huntley & Lopez (1992; equation 15) for planktonic copepods on non-limiting food conditions (see Figure 3). Nevertheless, the three models for *N. palustris* indicate longer development times at higher temperatures compared to planktonic copepods.

Fecundity, or egg production rate, showed strong variation throughout the year with maximum values of about 6 eggs Fem<sup>-1</sup> day<sup>-1</sup>, far from the value of 4.75 obtained for *Coullana canadensis* by Gupta et al. (1994). The pattern of variation was similar to that of *Eurytemora affinis*, a planktonic copepod studied by Castel & Feurtet (1992) in the same estuary. The influence of temperature on fecundity rate was pronounced and can be easily explained by its influence on egg development time (Santos et al., 1999), clutch size and total number of ovigerous females.

Instantaneous birth rates varied from about 0.2 to 0.8 day<sup>-1</sup> during the reproductive period (late winter to late summer). Similar values were observed for the harpacticoids *Microarthridion littorale* and *Stenhelia bifida*,

studied in a South Carolina salt marsh by Fleeger (1979). Mistri & Ceccherelli (1992) also observed similar values, peaks of about 0.3 to 1.5 day<sup>-1</sup> for several benthic harpacticoid species in the muddy embankment of the Po River Delta. Nevertheless, a peak of about 6 day<sup>-1</sup> was observed for *Canuella perplexa* (Mistri & Ceccherelli, 1992) this value being explained by the very large clutch size (80 eggs per ovigerous female) and numbers of ovigerous females in the population.

The different models used to estimate birth rates all resulted in similar birth rate patterns and magnitudes. Taylor & Slatkin (1981), as well as Linch (1982), suggested that the Paloheimo model provides quite good approximations of the population birth rates (though its assumptions are rarely met). Linch (1982) further suggested that a more critical factor than the model used in the analysis of instantaneous rates is the development of accurate sampling techniques to estimate better population densities. This observation is supported by the similarity of the results obtained applying different models to the same data set.

In this study, for the first time, specific mortality rates for nauplius, copepodite and adult animals were estimated for a benthic harpacticoid copepod [but see Morris & Coull (1992) for the calculation of *Microarthridion littorale* minimum copepodite mortality and Webb (1991) for adult mortality of three harpacticoid copepods calculated as area specific values].

The pattern of variation of stage-specific mortality rates was almost the same for each stage independent of the development model or **Dn/Dt** ratio used. Furthermore, all combinations of development models and **Dn/Dt** ratios (Table 8) indicate that nauplius stages suffer higher mortality as compared to copepodite stages or adults. This pattern is very different from the laboratory based mortality patterns. Most of the laboratory studies that describe survival curves of harpacticoid copepods (e.g. Bergmans, 1981 (and references therein); Pinto et al., 2001; Souza-Santos et al., 1999; Williams & Jones, 1994) showed low mortalities of nauplius and copepodite stages, with between 70 to 98% of the animals attaining the adult stage. However, Hicks (1984) demonstrated that juvenile flatfishes preyed mainly on nauplii of a *Parastenhelia megarostrum* field population and, Morris & Coull (1992) also suggested that the recruitment of *Microarthridion littorale* population is regulated by predation pressure during the hot season.

The pattern of variation of mortality rates for each stage was not clearly related to measured environmental parameters. Stepwise multiple regressions were made but these seldom explained even half the data variability, and temperature had always a major contribution to the coefficient of determination. Since temperature is highly involved in the calculation of mortality rates (being the major determinant factor in all development models) we did not consider these relationships.

On the other hand, stage-specific mortality rates were significantly correlated with the previous stage abundance and the first half of the graphics (Figure 6) clearly show waves or peaks of mortality (especially for copepodites and adults) that can be easily related to the progression of the nauplii pulses. Cyclic patterns of both copepodite and adult recruitment and adult mortality were determined for *Microarthridion littorale* by Morris & Coull (1992). The authors suggested delayed naupliar development or periodic waves of predators (different fish species) entering the estuary at different times of year.

The density data of *Nannopus palustris* nauplii does not support the first hypothesis [see also Bergmans (1981) for a criticism of naupliar delayed development] but we cannot exclude the second one, since both Castel (1985) and Coull (1990) considered this species a prey item for fishes.

The strong peak of nauplii mortality rate (more than 1 day<sup>-1</sup>) occurring during late summer as well as the strong decrease of ovigerous females and the variation of the sex ratio were clearly related to the major decrease of temperature (3.1°C decrease in one week) that occurred during this period, showing once again the major influence of temperature over the population dynamics of this species.

The results of fecundity, development time and mortality rates of *Nannopus palustris* all suggest that this species is not food limited during the year. The population increase is mainly temperature related and the waves of mortality rates could be determined by predation, both results suggesting a “top down” control of this species population dynamics.

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