



Services du Premier Ministre  
Programmation de la Politique scientifique  
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BELGIQUE



Diensten van de Eerste Minister  
Programmatie van het Wetenschapsbeleid  
Wetenschapsstraat 8  
1040 BRUSSEL  
BELGIE

**ACTIONS DE  
RECHERCHE CONCERTÉES**

**ACTION INTERUNIVERSITAIRE**

**OCEANOLOGIE**

**Rapport final**

**Volume 3**

**GECONCERTEERDE  
ONDERZOEKSACTIES**

**INTERUNIVERSITAIRE ACTIE**

**OCEANOLOGIE**

**Eindverslag**

**Boekdeel 3**

**BIOLOGICAL PROCESSES AND TRANSLOCATIONS**

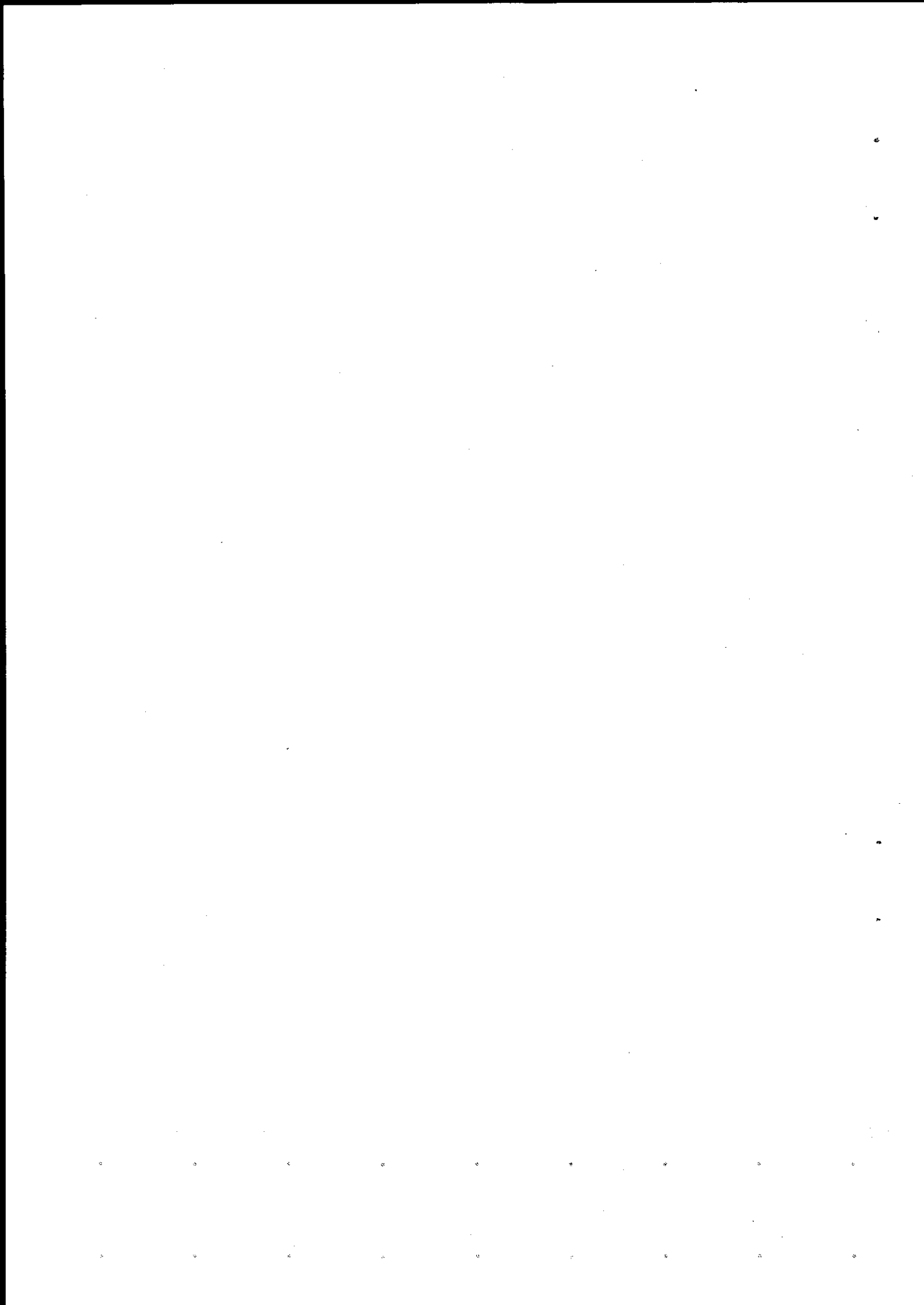
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# **BIOLOGICAL PROCESSES AND TRANSLOCATIONS**

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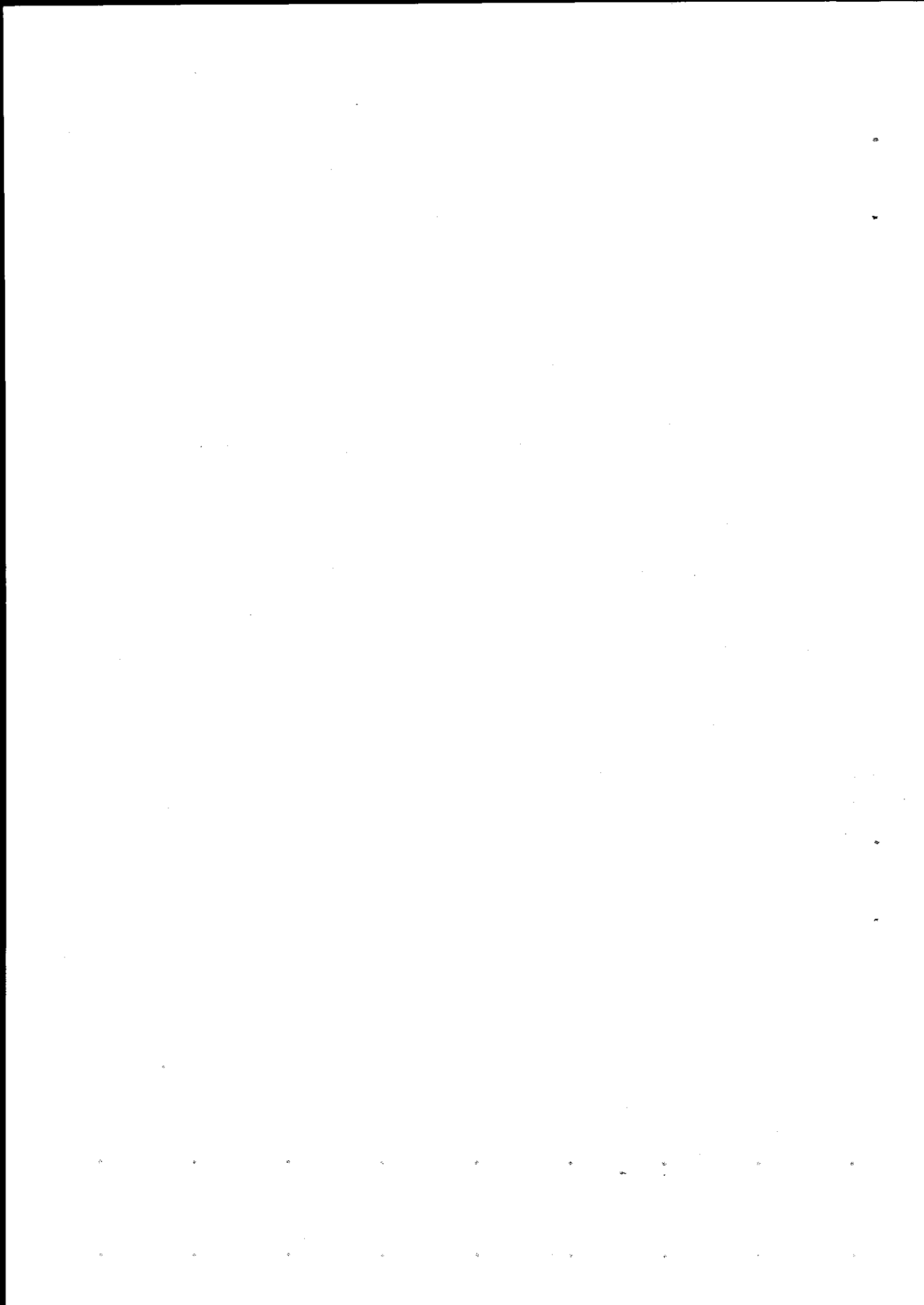
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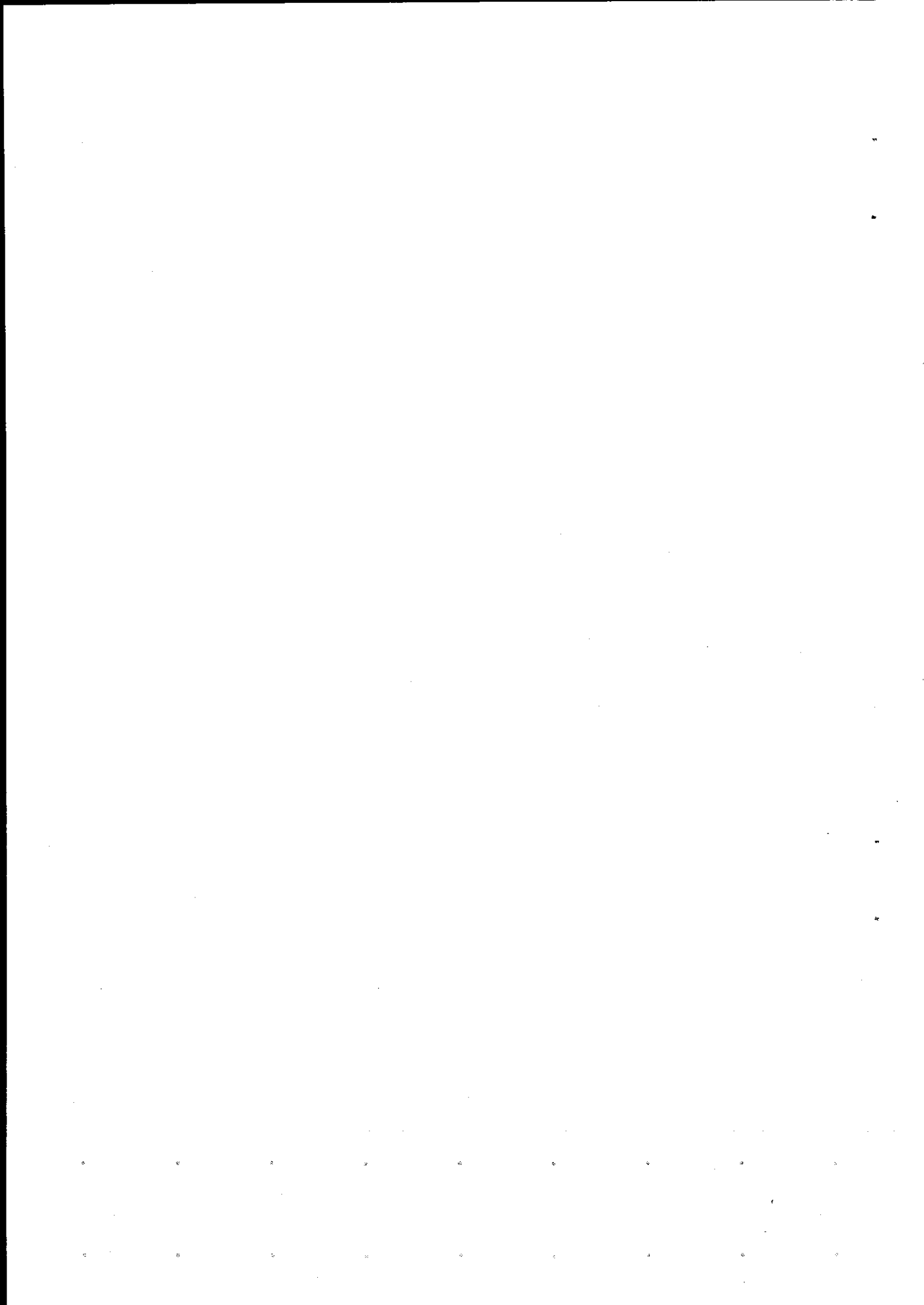
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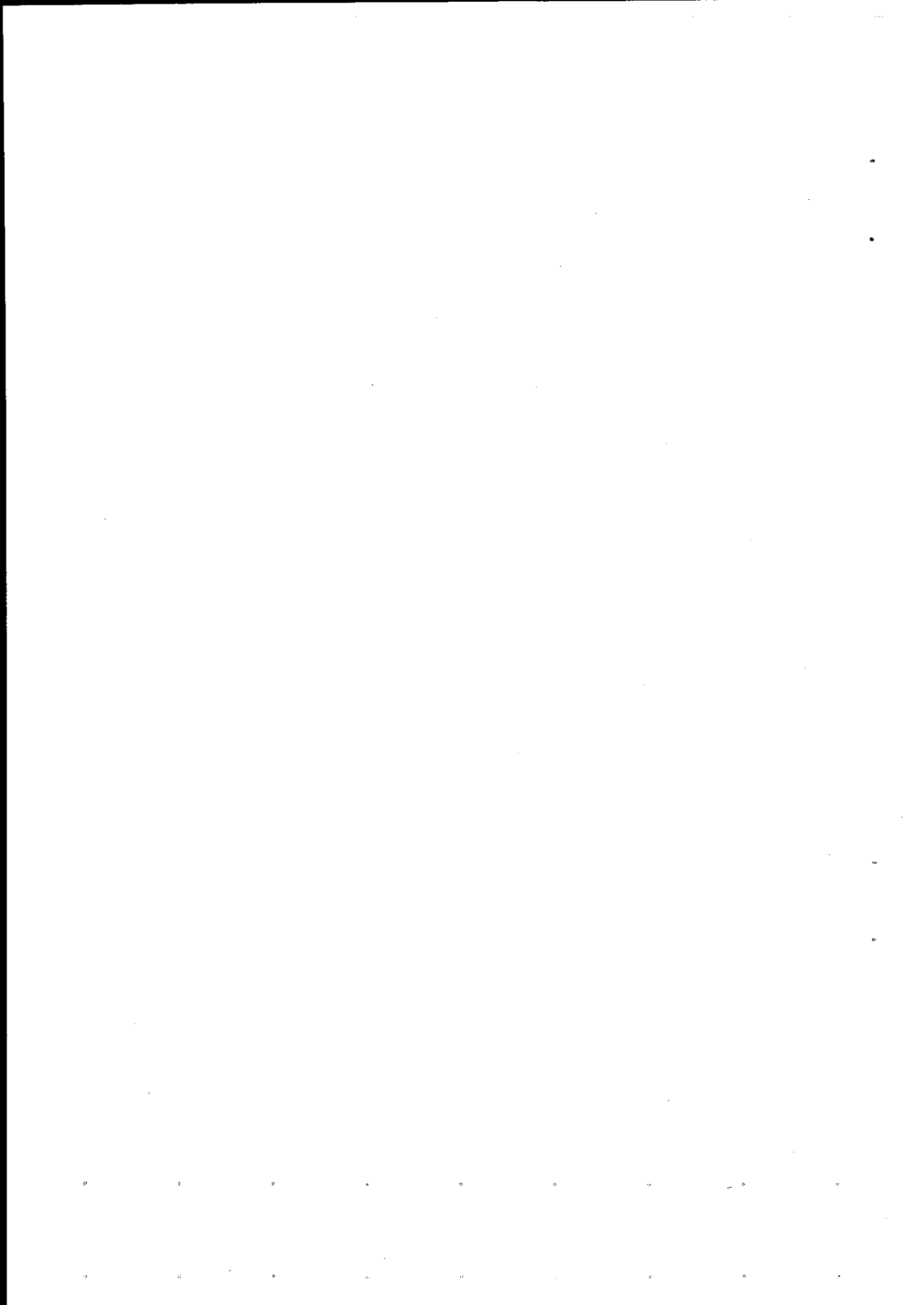
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**BENTHIC STUDIES**  
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**AND ITS ADJACENT CONTINENTAL ESTUARIES**



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### III

## ENERGY FLOW THROUGH THE MEIOBENTHOS

C. HEIP, P.M.J. HERMAN, N. SMOL, D. VAN BRUSSEL and G. VRANKEN

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#### Abstract.

The estimation of energy flow through meiobenthic populations is particularly difficult as only a few measurements on production and respiration, mainly of harpacticoid copepods and nematodes, exist. The use of a single production-biomass P/B-ratio for meiobenthos is still a common practice. However, studies presented in this paper for a variety of harpacticoid copepods, ostracods and nematodes demonstrate that there exists an extreme diversity in life-cycle histories and respiration rates in these groups and that meiobenthic production is in many cases much higher than the value  $P = 9B$  proposed by Gerlach (1971).

#### Introduction.

Energy flow through the benthos is the most important force structuring this system. In the North Sea, without benthic primary production, the input of organic material is by sedimentation from the water column. In the classical model of Steele (1974) this sedimentation was estimated at one third of primary production, which in the northern North Sea amounts to  $90 \text{ g C.m}^{-2}.\text{y}^{-1}$ . In the Southern Bight a similar model was based on primary production estimates of  $110\text{-}187 \text{ g C.m}^{-2}.\text{y}^{-1}$  and a sedimentation rate of  $37\text{-}62 \text{ g C.m}^{-2}.\text{y}^{-1}$ . Energy flow through the benthos was based on very indirect measurement of biomass and literature data on production and respiration (Van Damme & Heip, 1977) ; it was calculated that total benthic production amounted

to  $7.7 \text{ g C.m}^{-2}$ , total benthic respiration (excluding bacteria) to  $11.1 \text{ g C.m}^{-2}$ . Energy consumption by benthic animals should then be about  $31 \text{ g C.m}^{-2}.\text{y}^{-1}$ , amounting to 50-90% of sedimentation. However, when bacteria are added as an additional trophic level between detritus and benthos, with an ecological efficiency of 20%, the required input in the system should be  $150 \text{ g C.m}^{-2}.\text{y}^{-1}$ . Clearly then, when the basic model is accepted some of the 1977 estimates should be revised.

As will be demonstrated in other reports in this volume, primary production and sedimentation in the Southern Bight of the North Sea are indeed higher than previously estimated. The research efforts in our laboratory were concentrated on the production and respiration of meiofauna, as the estimates existing in 1977 were extremely inaccurate, whereas figures of macro- and epifauna were based on much more solid grounds and have been retained in recent calculations.

Despite their numerical abundance in all benthic ecosystems, the functional role of meiobenthos in these systems is still poorly known. Several potentially important roles have been ascribed to the meiofauna : food for higher trophic levels, nutrient regenerators and intermediates in detritus transfer to macrofauna (Coul & Bell, 1979).

None of these roles, however, has been quantified. Even the most basic information on the energy flow through meiobenthic populations is almost entirely lacking : namely how much energy enters the population, and in what form is it subsequently leaving it?

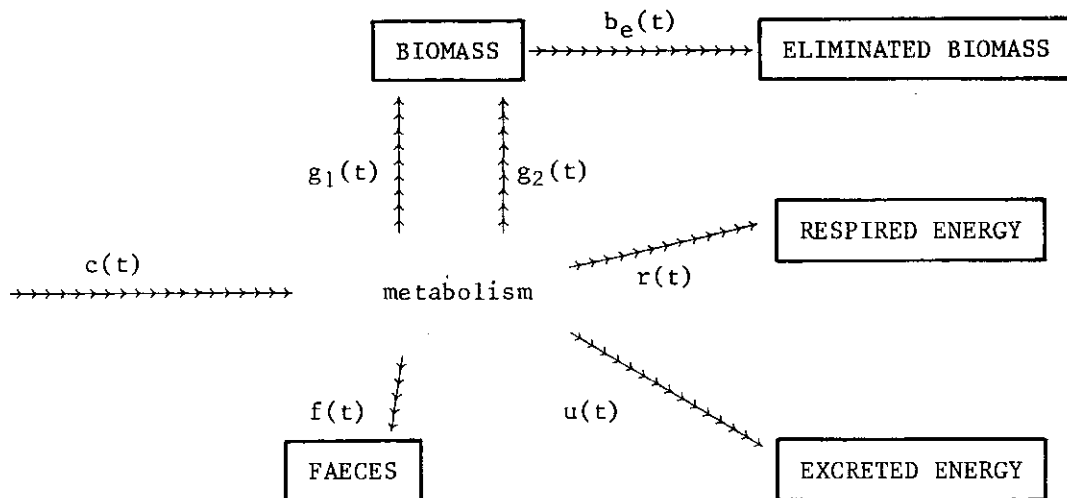


fig. 1.

Energy flow through biological populations

In figure 1 the partitioning by metabolic processes of the energy entering a population as consumption [consumption flux  $c(t)$ ] is shown. Part of this energy is used for somatic growth [flux  $g_1(t)$ ] and reproductive output [flux  $g_2(t)$ ]. Both fluxes increase the biomass (standing stock) of the population which is decreased by the elimination of individuals or parts of individuals from the population. This eliminated biomass goes to higher trophic levels or to the decomposer food chain. It consists of high energy content organic material. The rest of the incoming energy is rejected as faeces  $f(t)$ , lost in low energy content excretion products  $u(t)$  or dissipated as heat in respiratory processes  $r(t)$ . In terms of energy content, conservation principles require that

$$(1) \quad c(t) = g_1(t) + g_2(t) + f(t) + u(t) + r(t)$$

Secondary production of a population is the integration of the fluxes  $g_1(t)$  and  $g_2(t)$  over the interval of time  $t_2 - t_1 = \Delta t$  considered :

$$(2) \quad P = \frac{1}{\Delta t} \int_{t_1}^{t_2} [g_1(t) + g_2(t)] dt$$

Production thus depicts the flow of the ecologically "usefull" energy through the population. Losses of energy in respiratory activity and excretion are the "price" at which this flow-through is realized.

The direct measurement of production involves the use of theoretical models fitted to density and biomass data of the population. These models take a simple form in the case of cohort populations, where reproduction is synchronuous and occurs over relatively short periods. However, when reproduction is continuous, as is the case in most meiobenthic populations, the estimation of production is highly complicated. For different instars or size classes one has to estimate either recruitment and mortality, or the duration of the stage. Alternatively, growth rates determined in laboratory experiments can be used. In either case, the field population must be sampled frequently.

Probably because of these technical difficulties only two production estimates of meiobenthic animals have appeared to date : Feller (1977) (cited in Banse & Mosher, 1980) reports on the production of the harpacticoid copepod *Huntemannia jadensis*, and Fleeger & Palmer (1982) studied the production of *Microarthridion littorale*, another harpacticoid. Although nematodes are the numerically most important meiobenthic taxon, direct production estimations of nematode populations have not yet been reported. In this report we present direct production estimates of some populations from a brackish water habitat : two harpacticoid copepod species, *Tachidius discipes* and *Paronychocamptus nanus*, and one ostracod species, *Cyprideis torosa*.

It is practically impossible to sample marine populations as frequently as needed for direct production estimates. Therefore

indirect methods, approximating the production from easily measurable parameters should be of great practical interest. Two approaches may be useful in this respect : the estimation of the yearly production/biomass ratio from the body weight at sexual maturity (Banse & Mosher, 1980) and the estimation of production from population respiration (McNeill & Lawton, 1970 ; Humphreys, 1979). These (log-log) relationships are purely empirical, so it is necessary that enough data on production, body mass and respiration are available to estimate their parameters accurately. Therefore we measured the respiration of the species mentioned. In addition, these respiration data complete the picture of the energy flow through the populations.

When even less information is available production estimates may be based on an annual P/B-ratio based on the life-cycle turnover (which, according to Waters (1969), lies between two and five with a modal value of 3.5) multiplied by the annual number of generations the populations produces in the field. The annual number of generations itself may be estimated directly from the life history of the species in the field but when this is also impossible laboratory experiments in which the influence of temperature on generation time is measured can be used. In this last case it is clear that the outcome should be treated with caution, but in the case of many marine nematodes cultivation in laboratory conditions is unavoidable when one wants to obtain accurate knowledge about dynamic aspects of their life cycles (e.g. fecundity, embryonic and postembryonic development, mortality, growth).

#### Material and methods.

The Southern Bight area has been described in our first progress report (Heip *et al.*, 1979) where also the field methods were explained in detail. Production estimates of North Sea subtidal meiobenthos are all based on density and biomass data from a number of stations sampled in principle four times a year. The detailed results of these cruises will be published later and only a synthesis of some of the more important results will be given in Herman *et al.* (this volume).

The populations used in direct production estimates, were studied in the "Dievengat", a very shallow (about 10 cm) brackish water pond, situated in a polder in north-western Belgium, also described in Heip *et al.* (1979).

Samples were taken with a glass core (surface area 6.06 cm<sup>2</sup>) to a depth of 5 cm. After being transferred to the laboratory, they were fixed in a neutralized isotonic 4% formaldehyde solution, heated to 70°C. The animals were extracted according to



the method described by Heip *et al.* (1974), except that centrifugation was done with LUDOX, a silica-gel, instead of sucrose (De Jonge & Bouwman, 1977). For *Cyprideis torosa*, samples were taken fortnightly from 1970 through 1974 ; for *Tachidius discipes*, every three days during the spring of 1979 ; for *Paronychocamptus nanus*, every five days from March to November 1980.

In the same habitat two nematode species were studied taking monthly samples during four years. Both are members of the order Enoplida. *Oncholaimus oxyuris* Ditlevsen, 1911 is the dominant predator in the habitat and of primary importance in terms of biomass (it makes up for the largest part of the total biomass over the year) ; *Viscosia viscosa* Bastian, 1865 is an important euryhaline species and member of a cosmopolitan genus. Both are regarded as omnivorous species.

For cultivation of marine nematodes we used bacto-agar. The great advantage of this material is that the animals can be observed individually during their entire life. Sixteen species belonging to thirteen genera were cultured over the last four years. This paper contains an extensive study of the influence of temperature on the postembryonic development of four brackish water species : *Paracanthochus caecus*, *Monhystera microphthalma*, *Monhystrella parelegantula* and *Chromadora nudicapitata*.

*Monhystrella parelegantula* was collected from the Sluice Dock of Ostend, a shallow brackish water pond with yearly salinity fluctuations between 24 ‰ and 37 ‰ (see Thielemans *et al.*, this volume), the other species from the Dievengat.

Meiobenthic organisms and detritus were extracted from the sand by the method of Barnett (1968) and collected on a sieve (mesh width = 38  $\mu$ m) after which the animals were removed and placed into petri-dishes containing 0.8% bacto-agar. After a few weeks, nematodes, harpacticoids and other organisms penetrate into the transparent agar. In this way, it is possible to maintain the stocks for several months (Vranken *et al.*, 1981).

Monospecific cultures were set up by transferring a number of gravid females on enriched agar plates. The enrichment was realized by adding 1% medium of Vlasblom and 15 g/l silica (= medium used for *Monhystera microphthalma* and *Monhystrella parelegantula*). The constitution of this medium is as follows :

0.278	g	FeSO <sub>4</sub> .7H <sub>2</sub> O
3	g	NaH <sub>2</sub> PO <sub>4</sub> .2H <sub>2</sub> O
30	g	NaNO <sub>3</sub>
0.47	g	MnCl <sub>2</sub> .4H <sub>2</sub> O
50	g	glycine per liter distilled water.

For the other two species (*Paracanthochus caecus* and *Chromadora nudicapitata*), we used a mixture of phosphorus modified Walne medium and Provasoli medium (ratio 5/1).

The salinity of the cultures was kept constant and was controlled with a Goldberg T/C refractometer.

The experiments were carried out in incubators, without light, at temperatures ranging from 5°C to 30°C. Per temperature a minimum of two replica's was examined and per replica a

known number ( $\pm 30$ ) of gravid females deposited eggs during maximal 24 hours. Time zero was taken 12 hours before removing the animals. After this period the adults were transferred, whereupon the number of eggs produced was counted. A daily check enabled us to observe at which time the eggs hatched and the juveniles became sexually mature.

Dry weights were determined on a Mettler ME22 microbalance to a precision of  $\pm 1 \mu\text{g}$ , using batches of about 100 individuals. Before weighing the animals were washed in bidistilled water, and dried for 2 h at  $110^\circ\text{C}$ . Only the soft parts (excluding shells) were weighed for *C. torosa* (Herman & Heip, in press).

Respiration was measured with a stoppered diver Cartesian Diver respirometer (Klekowski, 1971). The divers had a gas volume of  $1 \mu\ell$  or  $2 \mu\ell$ ; each diver contained one animal.

## Results.

### *Direct production estimates.*

#### *C. torosa.*

The ostracod *C. torosa* produces only one generation in the Dievangat (Heip, 1976), but there is considerable overlap between successive generations, due to overwintering of older larvae. Reproduction occurs in late spring and throughout the summer: some of the early larvae become adult before winter, whereas others overwinter in different larval stages. During winter there is no development and maturation is postponed until the next spring.

In the course of their development, the animals pass through eight moults. At each moulting, they shed their calcareous shells and build new ones. As the sediment is slightly alkaline, the shells are well preserved in it. The distribution of the preserved shells over the instars contains information on the mortality pattern in the population: an animal dying e.g. in stage V will leave shells of the stages I-V in the sediment. Thus one expects to find more shells of younger stages than of older ones in a sediment sample, and this is exactly what is observed. Combining this information with density estimates of the stages from the five-year sampling period allowed the calculation of recruitment, the duration of the stages, and the stage-dependent mortality rate. These results are summarized in Table 1. An increment-summation production estimation could be made giving a value of  $9.69 \text{ g dwt.m}^{-2}.\text{y}^{-1}$ . Mean biomass was  $3.55 \text{ g dwt.m}^{-2}$ , hence the annual P/B equalled 2.73.

Table 1

Summary of the data for the production estimate of *Cyprideis torosa*

The survival values were determined from the shell countings : they express the fraction of the animals entering the stage that survive till the next stage. Recruitment data are expressed as numbers per 10 cm<sup>2</sup> per 5 years.

Stage	Survival	Duration (days)	Recruitment	dwt (µg)
IV	0.7478	9.38	4119	0.925
V	0.8521	24.86	3080	1.5
VI	0.8681	56.85	2625	2.9
VII	0.8400	85.94	2278	5.3
VIII	0.9048	76.10	1914	10.3
AD	0.8641	111.88	1732	19.9

The size-frequency method for production estimation (Menzie, 1980 and references therein) was also used to calculate the production of this population. It basically consists of the fitting of a simple (but robust) population dynamical model to the data, and the subsequent calculation of production from the estimated recruitment into the stages. Some information is needed on the relative duration of the stages, and although these were roughly calculated assuming a constant mortality, the resulting production estimate,  $P = 9.24 \text{ g dwt.m}^{-2}.\text{y}^{-1}$ , is in good agreement with the results obtained with the more elaborated model.

The dependence of respiration on body mass and temperature can be expressed (Herman & Heip, in press) as :

$$\log R = 9.7055 - \frac{2785.122}{T_{\text{abs}}} + 0.746 \log w$$

where  $R$  = respiration ( $\text{nl O}_2 \text{ hr}^{-1} \text{ ind}^{-1}$ )

$W$  = body mass ( $\mu\text{g dwt ind}^{-1}$ )

$T_{\text{abs}}$  = absolute temperature (K).

The oxygen consumption of the population is  $20.38 \text{ l O}_2 \text{ m}^{-2}.\text{y}^{-1}$ ; giving a production efficiency,  $P/(P+R)$ , of 0.382 and 0.372 for both production estimates resp.

#### *Tachidius discipes.*

The harpacticoid copepod *T. discipes* is a dominant species in many European and North-American brackish waters. Its size, form and epibenthic life style make it a representative species for an important part of the North Sea harpacticoid fauna. The data from the frequent sampling program (three days intervals) in

the spring of 1979 show that there are most probably three generations. These generations are clearly distinguishable in the younger stages, but show increasing overlap in older copepodite stages and adults (Fig. 2). In order to resolve the generation peaks from these compound curves, we assumed that the peaks take the form of Gaussian distributions. Then a statistical method for the resolution of frequency distributions into Gaussian components (Bhattacharya, 1968) could be used. Fig. 3 shows the fit of the summed Gaussians on the density data of copepodite 3.

T. discipes : N / sample

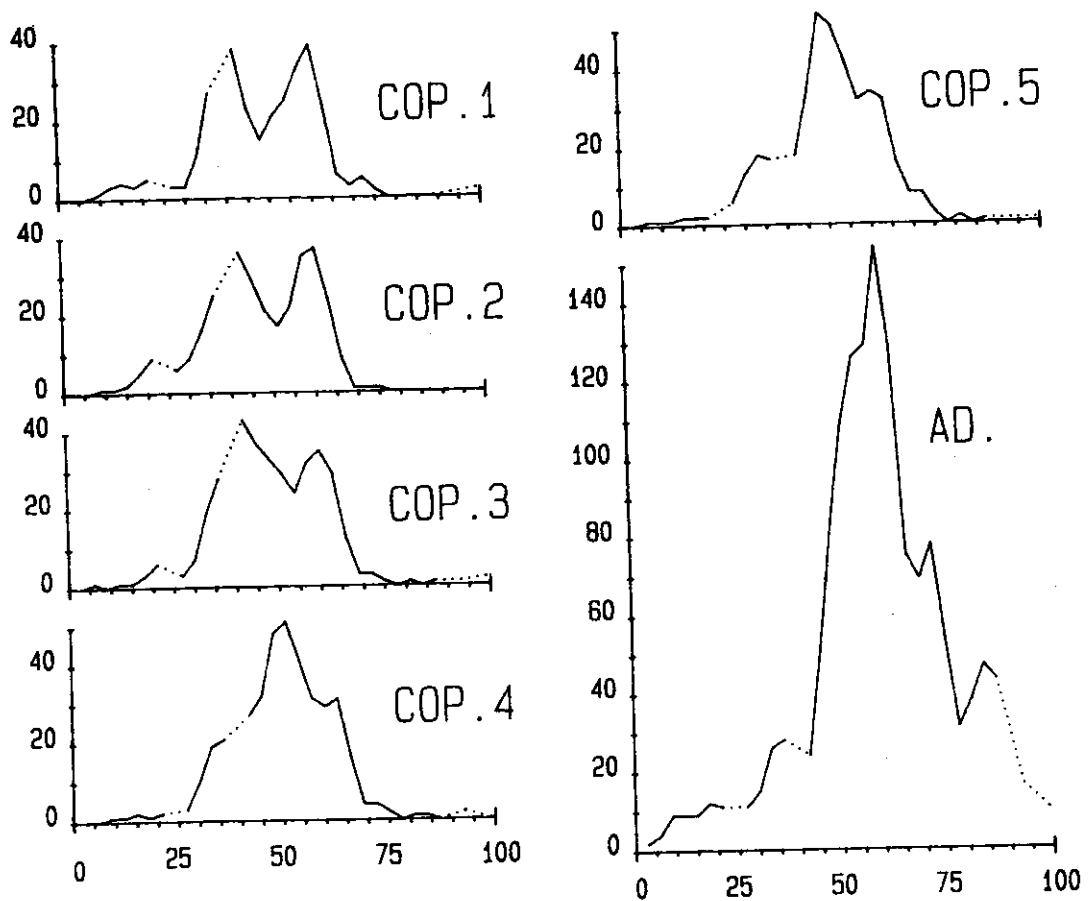


fig. 2.

*Tachidius discipes* : densities (N/sample of 6.06 cm<sup>2</sup>)  
of the different stages during spring 1979  
(Day 0 : 27-03-1979)

# Tachidius discipes

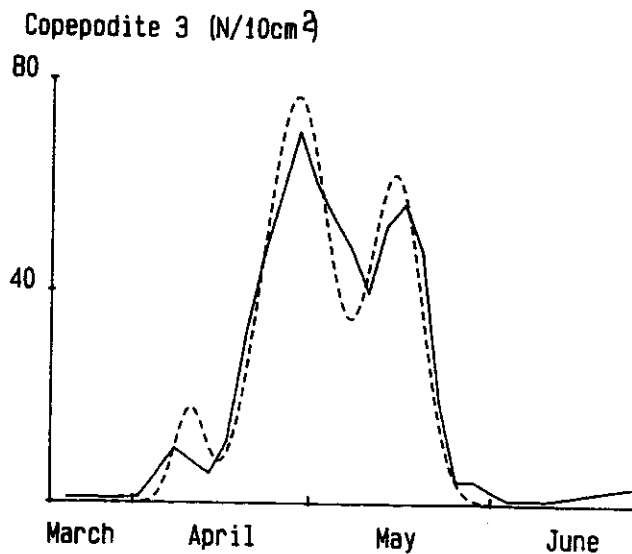


fig. 3.

*Tachidius discipes* : density (N/10 cm<sup>2</sup>) of copepodite 3 during spring 1979 with the summed Gaussians (dotted line) superimposed

The means of these Gaussians correspond to the mean pulse time of the generation peaks used in the model of Rigler & Cooley (1974). Their absolute heights correspond to the surface under the abundance curves (number of animal.days). Using Rigler & Cooley's model enabled the estimation of the duration of the stages and of their recruitment : it provided the necessary parameters for a production estimation. The production of copepodites and adults amounted to 1.1 g dwt.m<sup>-2</sup> in the spring period when the species was present.

Production of nauplii and eggs was based on the number of egg sacs produced and the duration of naupliar development as determined in the laboratory (Smol & Heip, 1974 ; Heip & Smol, 1976). It is 1.3 g dwt.m<sup>-2</sup>, and thus a very important part of total production. The P/B ratio for the total population was P/B = 9.34 over the sampling period. This amounts to 3.11 per generation.

The dependence of respiration rate on body weight is shown in Fig. 4. As body weight the mean weight of the stage that that the experimental animal belonged to was taken, since length measurements proved to be inaccurate due to the telescoping of the body segments. The relationship can be expressed as :

$$\log R = 1.12 + 0.82 \log W$$

where R = respiration in nl O<sub>2</sub> ind<sup>-1</sup> hr<sup>-1</sup>  
W =  $\mu$ g dwt ind<sup>-1</sup>

## Tachidius discipes

Log respiration ( $\text{nl O}_2\text{h}^{-1}$ )

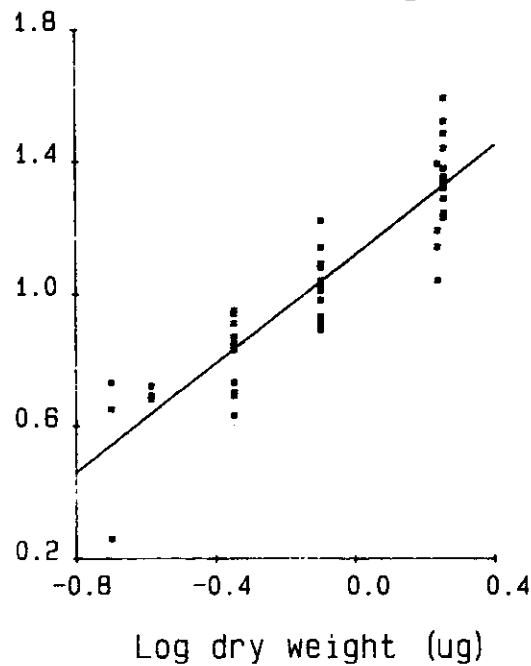


fig. 4.

*Tachidius discipes*

log - log relationship between dry weight and respiration

Assuming that temperature dependence of the respiration rate can be expressed by Krogh's normal curve, the respiration of copepodites and adults amounts to  $3.3 \text{ l O}_2\text{m}^{-2}$  during the sampling period. Production efficiency is then 0.302.

### *Paronychocamptus nanus*.

The production of copepodites and adults of this harpacticoid species was estimated with the size-frequency method. This requires the estimation of the generation time and of the proportion of the life cycle spent in each stage.

Smol & Heip (1974) estimated the dependence of generation time on temperature from laboratory cultures of this species. Their equation  $D = 528 T^{-1.05}$  was used to establish a physiological time scale. One unit on this time scale corresponds to one

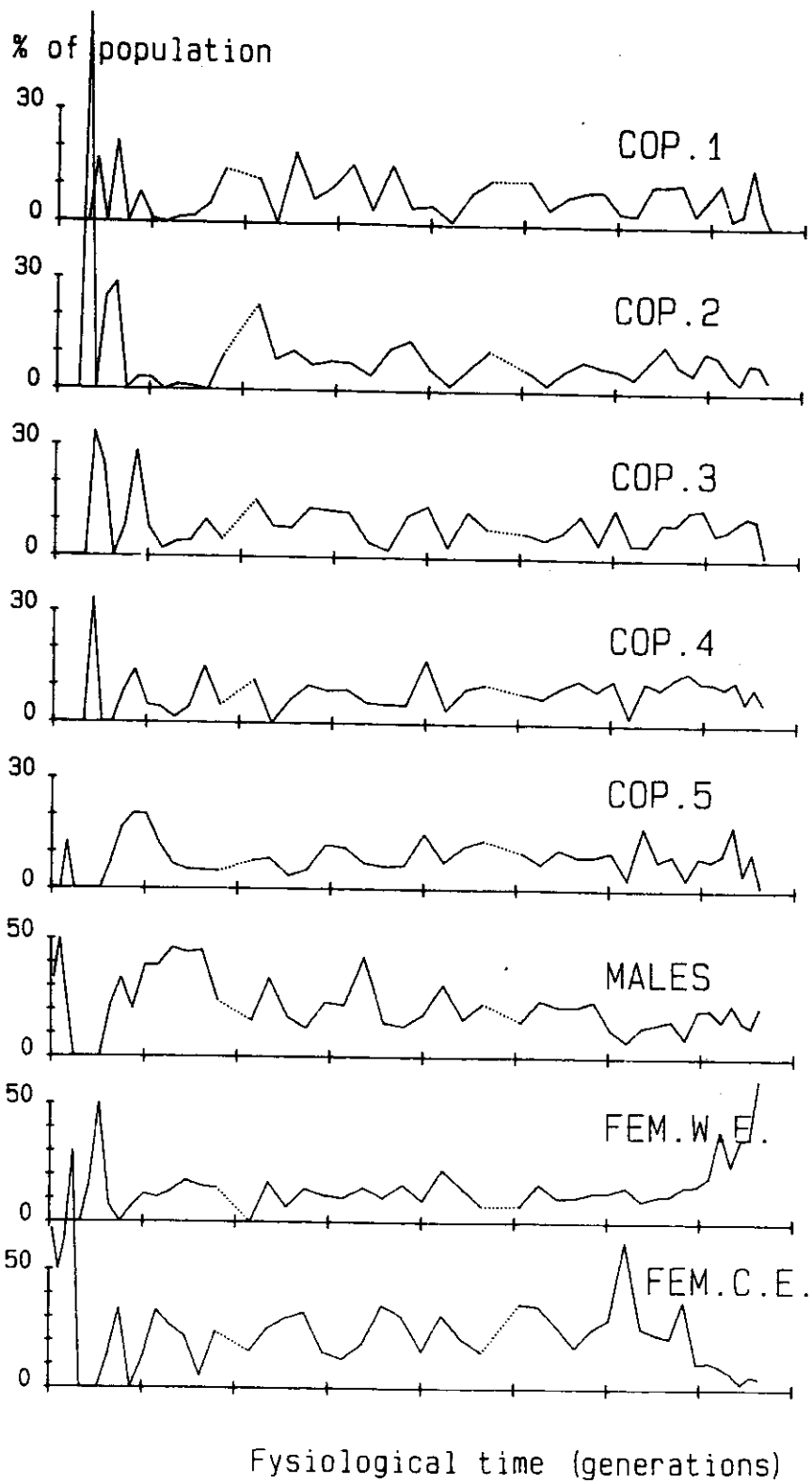


fig. 5.

*Paronychocampus nanus* : procentual composition of the population during 1980  
on a physiological time scale

generation time, and it can be seen from Fig. 5 that there occurs one peak per time unit in most stages, giving support to the use of the laboratory values.

The proportion spent in each stage was calculated assuming a uniform mortality. This is a rough estimation, but the method does not seem to depend critically on it (Benke, 1979). Production of copepodites and adults thus calculated amounted to 1.92 g dwt.m<sup>-2</sup> during the sampling period (March-November).

The production of eggs and nauplii, estimated in the same way as for *T. discipes*, is 2.31 g dwt.m<sup>-2</sup>.

The P/B ratio for the total population is 24.45, or 3.20 per generation.

### Paronychocamptus nanus

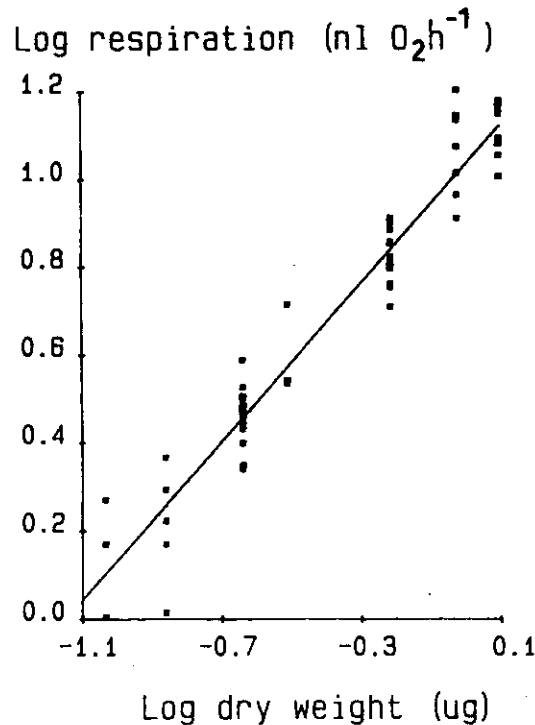


fig. 6.

*Paronychocamptus nanus*  
log - log relationship between dry weight and respiration

The regression of respiration rate on body weight is shown in Fig. 6. It is expressed by

$$\log R = 1.03 + 0.90 \log W$$



The respiration of the copepodites and adults amounts to  $7.2 \ell \text{ O}_2 \text{ m}^{-2}$  during the sampling period. The production efficiency of copepodites and adults is 0.27.

#### *Indirect production estimates.*

As the number of annual generation is the critical parameter in indirect production estimates, the life cycle of the species in the field has been studied for two nematode species.

#### *Oncholaimus oxyuris.*

Density fluctuations of this species are characterized by bimodal annual curves for all age-classes, with an important peak in spring or summer and winter. Minima occurred during February or March. Because on the average 70% of the population is represented by juveniles, we have a nearly similar curve for the juveniles. The lowest densities of juveniles occur each year during spring, from March till June, a period in which their part in the population is reduced to below 50%. It is clear that most of them moult into adults (Fig. 7).

In winter we note a second but less distinct period of low abundance, but the contribution of juveniles to the population remains high, only few of them have moulted into adults.

An analysis of density of the two sexes (Fig. 8 demonstrates that males are present throughout the year ; they mature earlier and live longer than the females. They constitute a large part of the adult population, with a mean value of 75% and a sex-ratio of 40:60.

The presence of females is restricted to distinct periods. A main peak of high abundance occurs during spring with numbers nearly equal to the males. They appear again during winter, but in much lower numbers. During the rest of the year females are absent, providing a mean sex-ratio of 1:4 over the whole year. When females are present, more than 50% and often 100% of them are gravid.

Summarizing, we find a reproductive period in spring extending from March until June ; the first juveniles then produced are able to complete their life-cycle before winter, whereas the juveniles born later, have to overwinter to attain adulthood next spring. The juveniles that become adults in late summer are able to reproduce so that the overwintering juveniles belong to two generations (Fig. 9), but their offspring are produced during the same main reproductive period in the following spring. Whether these generations remain distinct or not is not clear.

O. OXYURIS

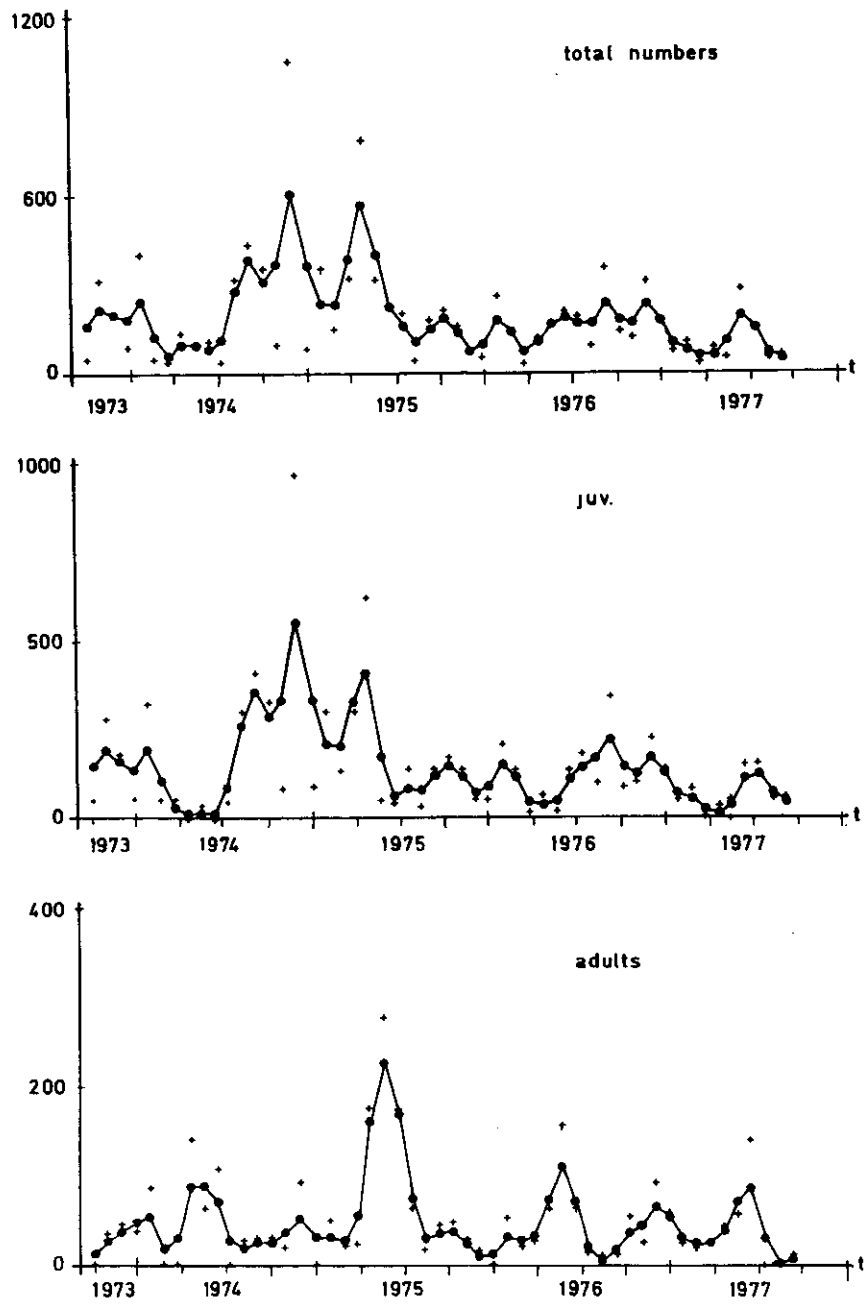


fig. 7.

Density fluctuations of the *Oncholaimus oxyuris* population over four years

O. OXYURIS

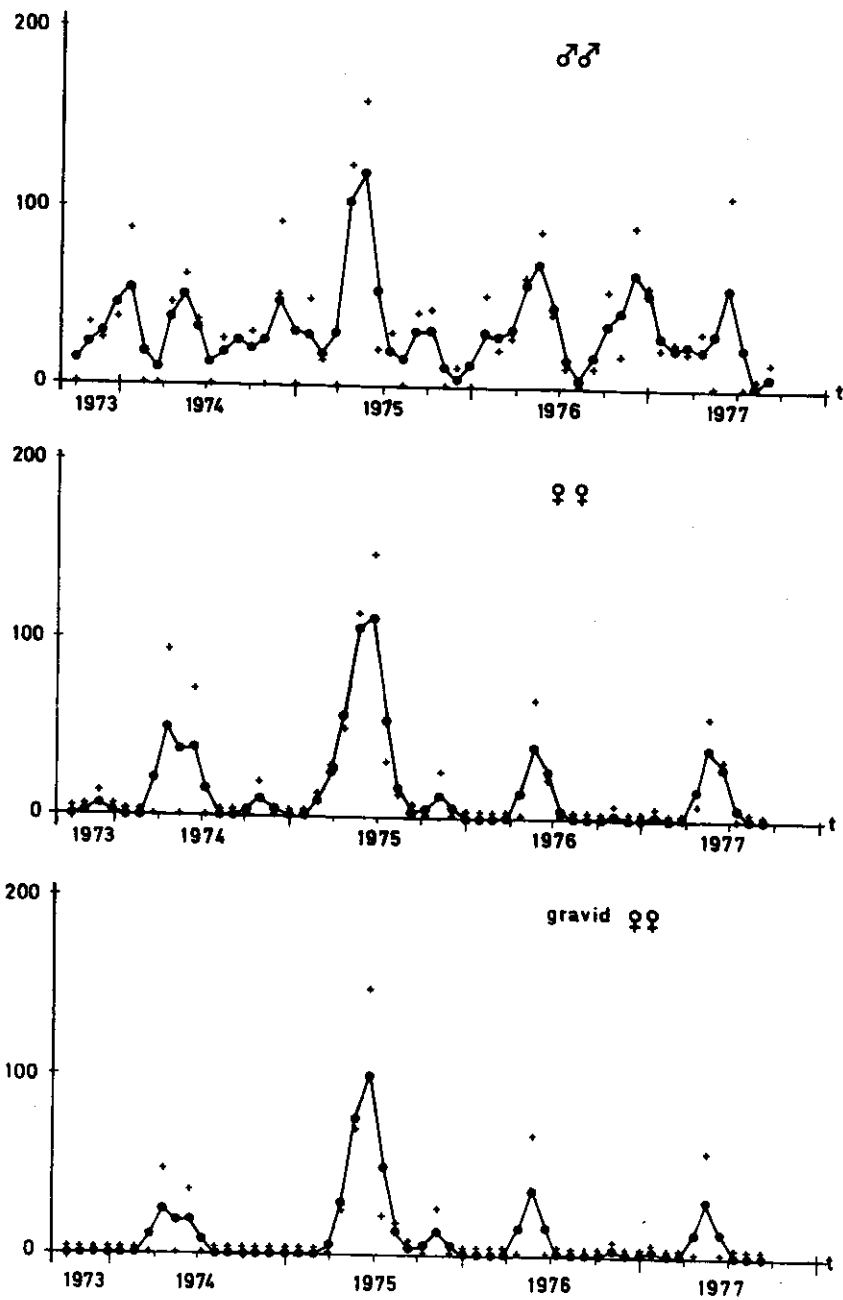


fig. 8.

Density fluctuations of the males, females and gravid females of *Oncholaimus oxyuris* over four years

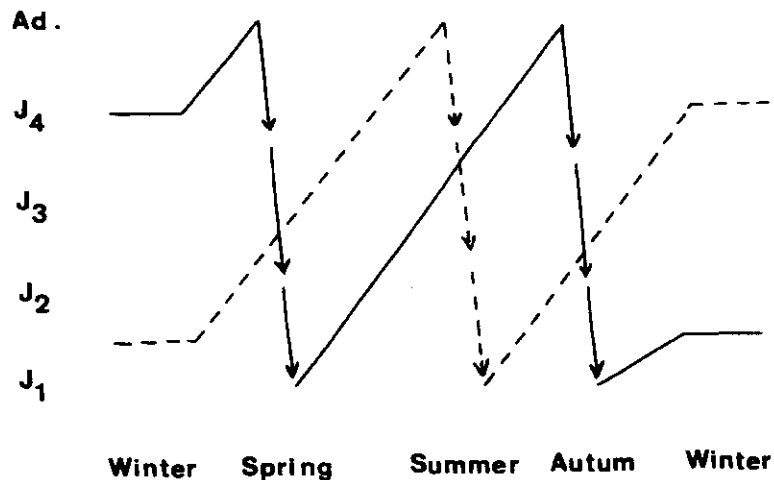


fig. 9.

Scheme of post-embryonic development  
of two cohortes of *Oncholaimus oxyuris* over one year

We may thus have either two generations, one in spring and one in autumn, or more complicated an alternation of two generations in one year and one in the next year, in this case we have three generations in two years of 1.5 per year. This slightly complicated scheme (Fig. 9) may nevertheless represent the most exact picture of the life cycle of *O. oxyuris* as is substantiated by the laboratory experiments (Heip *et al.*, 1978).

#### *Viscosia viscosa*.

Density fluctuations of this species are also characterized by bimodal annual curves in all age-classes (Fig. 10). Maxima occur in spring-summer and in winter. Adults predominate in the population with an annual mean of 60%. Males and females are present all over the year. The number of females is nearly half the number of the males, and *Viscosia viscosa* clearly has two generations each year.

# VISCOSIA VISCOSA

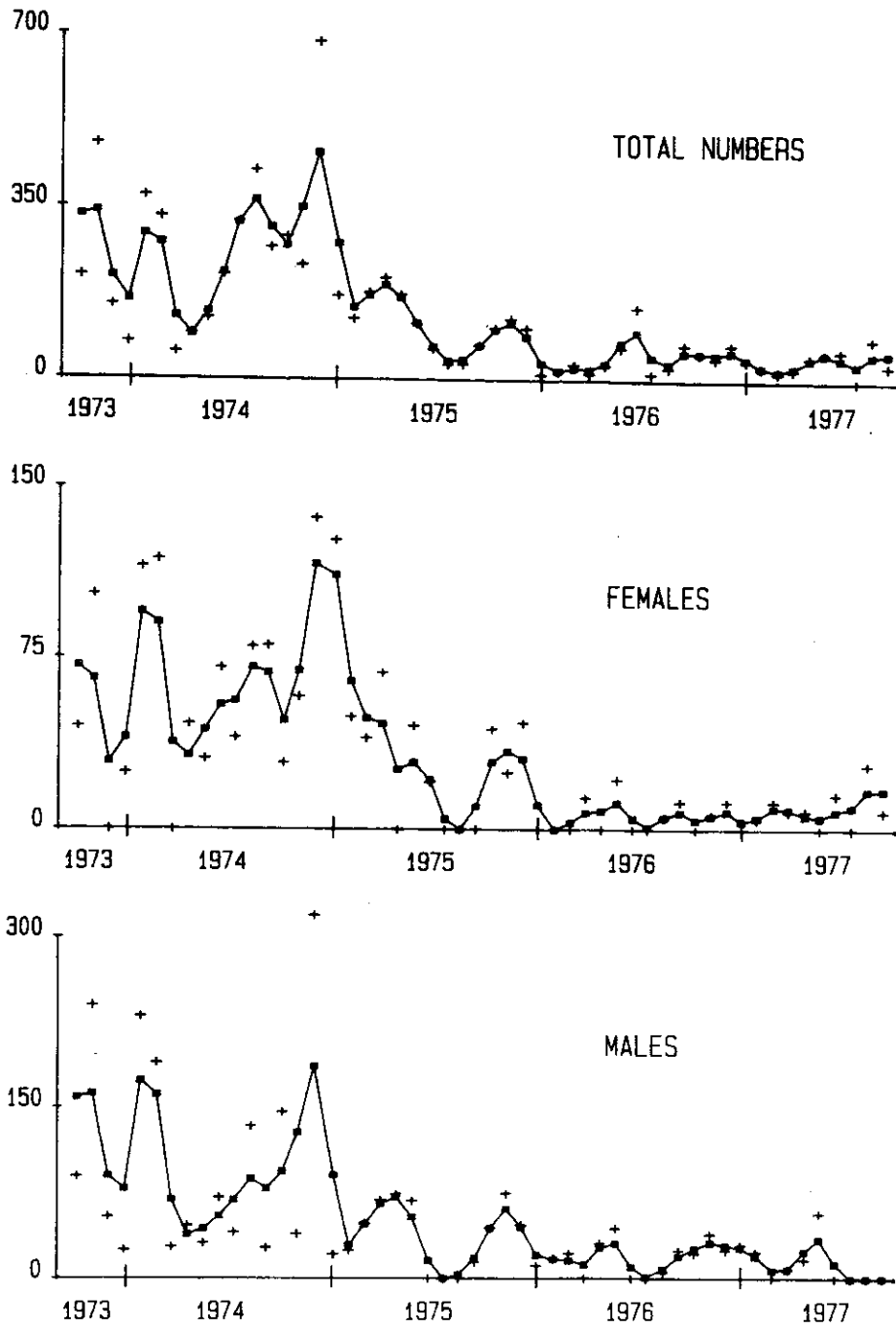


fig. 10.

Density fluctuations of the *Viscosia viscosa* population over four years

**Laboratory experiments.**

Development times until adulthood, at different temperatures, are listed in Table 2 and shown in Figs 11-14. Separate data are given for both sexes, except for *M. parelegantula*.

Table 2

Development times of four brackish water nematodes at different temperatures (T) and fixed salinity (S). Mean duration in days (D) with standard deviation; number of experiments (n) and number of females, respectively males (N) studied during the experiments.

Species	S %	T	D (females)	D (males)
<i>M. microphthalmalma</i>	20	15	27.8± 2.20(n=7; N=123)	28.1± 1.67(n=7; N=96)
		20	10.2± 0.92(n=11; N=113)	11.2± 0.90(n=11; N=107)
		25	7.8± 1.18(n=15; N=174)	8.0± 1.10(n=15; N=160)
		30	6.6± 1.31(n=10; N=137)	6.4± 1.02(n=10; N=86)
<i>M. parelegantula</i>	30	15	54.3± 5.74(n=2; N=30)	-
		20	18.1± 1.52(n=5; N=275)	-
		25	7.9± 0.57(n=6; N=539)	-
		30	6.3± 0.48(n=5; N=467)	-
<i>C. nudicapitata</i>	20	5	84.5± 8.20(n=2; N=52)	87.0± 9.0(n=2; N=48)
		10	52.5± 3.80(n=3; N=96)	51.1± 3.4(n=3; N=79)
		15	24.9± 2.70(n=3; N=64)	23.3± 3.1(n=3; N=53)
		20	14.0± 1.40(n=3; N=108)	14.1± 1.6(n=3; N=76)
		25	16.9± 1.70(n=3; N=44)	15.2± 2.1(n=3; N=49)
<i>P. caecus</i>	20	10	131.9±14.7(n=2; N=93)	124.0±13.0(n=2; N=35)
		15	65.7± 3.6(n=3; N=82)	65.7± 3.8(n=3; N=68)
		20	51.1± 4.8(n=4; N=66)	47.0± 4.9(n=4; N=60)
		25	41.9± 4.2(n=4; N=92)	37.6± 4.9(n=4; N=87)

From these results we can conclude that there is an important influence of temperature on development. Previous studies (for a summary see Kinne, 1977) did already reach the same conclusion. Another aspect of development studies that has received some attention in literature, is the nature of the relationship between temperature and the duration of development time (MacLaren, 1963 ; Heip, 1974 ; Botrell, 1975 ; Heip & Smol, 1976 ; Sarvala, 1979 ; Palmer & Coull, 1980). Several equations have been investigated, but two equations, namely the simple power equation :  $D = at^b$  (Heip, 1974 ; Heip & Smol, 1976 ; Sarvala, 1979 ; Warwick, 1982 ; Heip *et al.*, 1982) and the semilogarithmic quadratic equation  $\ln D = \ln a + T \ln b + T^2 \ln c$  (Botrell, 1975 and Sarvala, 1979) have been proposed and used as models to describe this relationship. Both equations give a reasonable fit to the experimental data. The semilogarithmic quadratic equation has the advantage that after logarithmic transformation, the heteroscedacity among variances can disappear (Sarvala, 1979), although this is not always the case. The function can describe

longer development times at higher temperatures, but the power equation is preferred by several authors due to its simplicity.

Table 3

Curvilinear regressions relating development time (D) in days and temperature (T) in °C, for four species of brackish water nematodes. Parameter values (= constants) are given for two equations. The variance ratio (F) tests the significance of the regression. The coefficient of determination ( $r^2$ ) estimates the amount of variance of the dependent variable (D) explained by the independent variable (T).

	D = aT <sup>b</sup>				D = a + bT + cT <sup>2</sup>					
	a	b	F <sub>s</sub>	r <sup>2</sup>	a	b	c	F <sub>s</sub>	r <sup>2</sup>	
<i>M. microphthalma</i>										
females	4679	-1.96	126****	0.75	115	-8.13	0.15	86****	0.81	
males	7270	-2.10	209****	0.84	116	-8.05	0.15	116****	0.85	
<i>M. parelegantula</i>	208053	-3.11	241****	0.94	241	-17.40	0.32	248****	0.97	
<i>C. nudicapitata</i>										
females	607	-1.16	102****	0.90	134	-10.92	0.25	479****	0.99	
males	684	-1.22	148****	0.93	138	-11.40	0.26	563****	0.99	
<i>P. caecus</i>										
females	2357	-1.28	92****	0.89	304	-22.40	0.48	79****	0.94	
males	2252	-1.29	131****	0.92	275	-19.90	0.42	98****	0.95	

In this paper we used two equations, the power equation and the untransformed quadratic equation,  $D=a+bT+cT^2$ . Table 3 gives the values of the constants a and b for the power equation (equation I) and the coefficients a, b and c for the quadratic equation (equation II). Furthermore this table contains the statistic F which is ratio between the mean square due to linear regression and the residual or the unexplained mean square. The coefficient of determination ( $r^2$ ) which can be considered as a measurement of the variation of the dependent variable (D) explained by the independent variable (T) is also listed. From Table 3, we can conclude that for all the regressions the F value is highly significant ( $P<0.001$ ,  $\beta=0$ ). The coefficient of determination ( $r^2$ ) is always larger for equation II than for equation I. Calculated predictions of the development times for the females, as results of the application of both functions are listed in Table 4. Both functions give a reasonable fit and can be used for descriptive or predictive purpose, this without giving any theoretical meaning to the fitted equations (Figs. 11-14). Both functions can then be used to obtain an estimation of the number of annual juvenile periods (i.e. approximately the number of generations) produced by the species in the field. Juvenile periods are intervals where the development accumulation  $D(t) = 1$ .

Table 4

Observed development time ( $D_{obs}$ ) at different temperatures compared with predicted values ( $D_{pred}$ ) obtained by application of equation (I) :  $D = aT^b$  and equation (II) :  $D = a + bt + cT^2$  for female individuals.

	Temperatures (°C)					
	5	10	15	20	25	30
<i>Monhystera microphthalmma</i>						
$D_{exp. I}$	-	-	23.2	13.2	8.5	6.0
$D_{exp. II}$	-	-	26.8	12.4	5.5	6.1
$D_{obs.}$	-	-	27.8	10.2	7.8	6.6
<i>Monhystrella parelegantula</i>						
$D_{exp. I}$	-	-	45.8	18.7	9.3	5.3
$D_{exp. II}$	-	-	52.0	21.0	6.0	7.0
$D_{obs.}$	-	-	54.3	18.1	7.9	6.3
<i>Chromadora nudicapitata</i>						
$D_{exp. I}$	93.8	42.0	26.2	18.7	14.5	-
$D_{exp. II}$	85.7	49.8	26.4	15.6	17.3	-
$D_{obs.}$	84.5	52.5	24.9	14.0	16.9	-
<i>Paracanthochus caecus</i>						
$D_{exp. I}$	-	123.7	73.6	50.9	38.3	-
$D_{exp. II}$	-	128.0	76.0	48.0	44.0	-
$D_{obs.}$	-	131.9	65.7	51.1	41.9	-

$$D(t) = \int_0^t R[T(t)] dt$$

where  $R$  is the development rate and  $T$  the temperature, is the total amount of juvenile development that takes place in a given interval of time. To calculate  $D(t)$  we have to know the water temperature of the habitat. Water temperature in the Dievangat and the Sluice Dock can be described as simple sinusoidal functions of time  $t$ ; for the Dievangat the equation is

$$T(t) = 11.2 + 8.3 \sin(t - 117)$$

(Heip & Smol, 1976); for the Sluice Dock the mean daily temperature can be estimated with the equation provided by Podamo (1975)

$$T(t) = 11.5 + 8.5 \sin(t - 120)$$



# Monhystrella parelegantula

Development time (days)

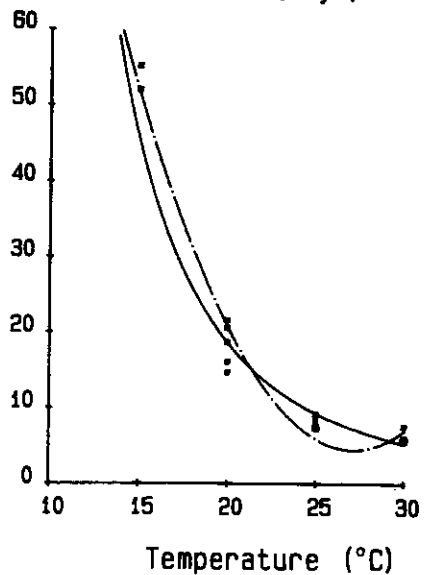
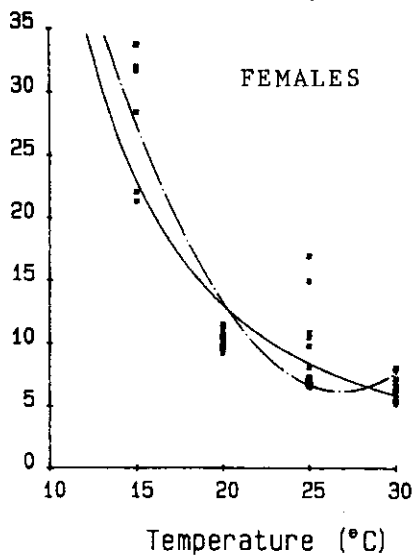


fig. 11.

*Monhystrella parelegantula*  
 Relation between development time (days) and temperature (°C)  
 at 30 % salinity  
 (Data obtained from cultures of female individuals)

# Monhystera microphthalma

Development time (days)



Development time (days)

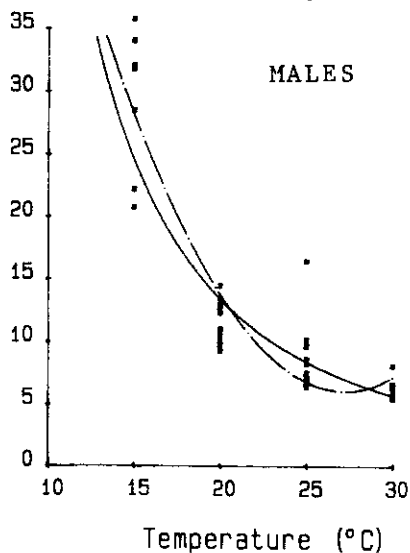
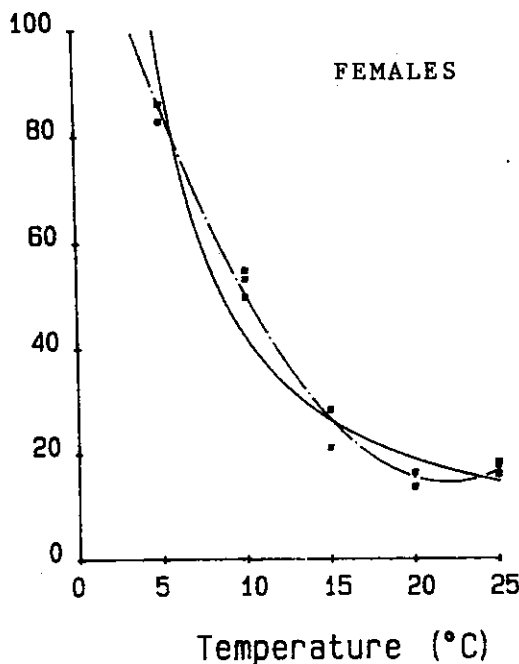


fig. 12.

*Monhystera microphthalma*  
 Development time (days) at different temperatures (°C)  
 and a constant salinity of 20 % under laboratory conditions

# Chromadora nudicapitata

Development time (days)



Development time (days)

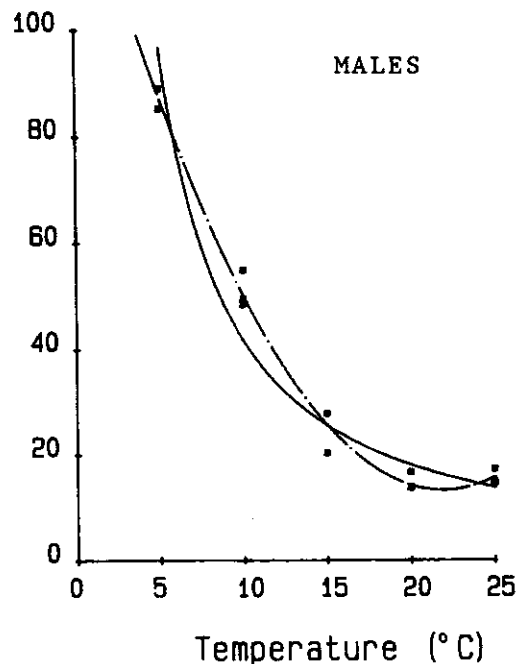


fig. 13.

*Chromadora nudicapitata*

Relationship between temperature (°C) and development time (days)  
at 20‰ salinity under laboratory conditions

Knowing the annual temperature regimes in both habitats, we now are able to estimate the development rate  $R$  (the reciprocal of the development time  $D$ ) as a function of temperature. For example for *M. microphthalma* we can give estimations of the development rate  $R$  at any time  $t$  using the following equations

$$(3) \quad R[T(t)] = \frac{1}{4679} [11.2 + 8.3 \sin(t - 117)]^{-1.96}$$

for the power equation and (4)

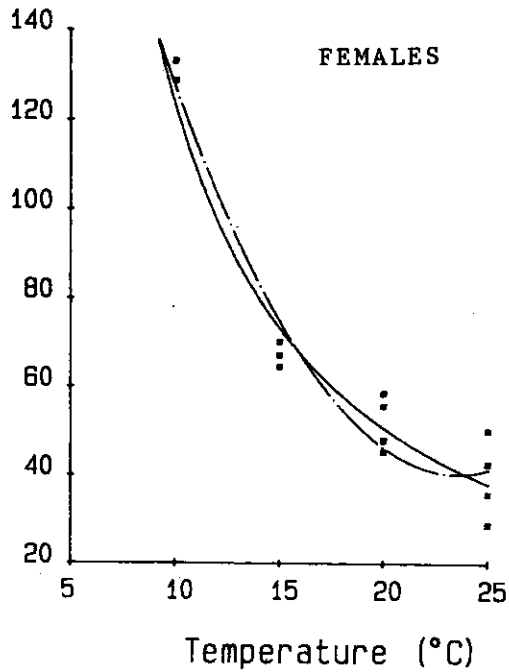
$$R[T(t)] = \frac{1}{115} - 8.13[11.2 + 8.3 \sin(t - 117)] + 0.15[11.2 + 8.3 \sin(t - 117)]^2$$

for the quadratic equation. The development rate of the three other species can be obtained by using analogous equations. The constants of this equations can be found in table 3.

For *M. microphthalma* the annual development accumulation  $D(365)$  can now be estimated by integrating the development rate obtained by application of (3) or (4) over a period of one year.

# Paracanthonchus caecus

Development time (days)



Development time (days)

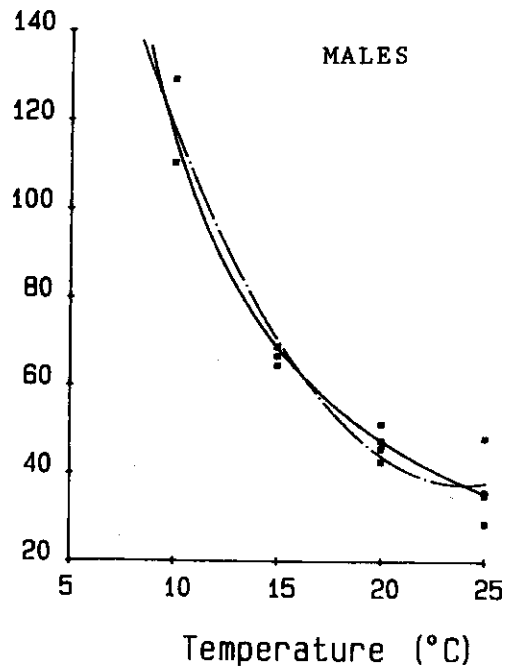


fig. 14.

*Paracanthonchus caecus*  
Duration of development time (days) until adulthood  
in relation with temperature (°C) at 20 ‰ salinity  
under laboratory conditions

We have calculated this integral

$$\int_0^{365} R[T(t)] dt = D(365)$$

using Simpson's method for discrete intervals. The results of these computations are given in table 5, from which we can see that the number of annual juvenile periods for any one species is very similar whether using the power (A) or the quadratic equation (B).

These results (Table 5) have to be regarded with some caution, because they are based on development times (= minimum generation times) and not on mean generation times; the latter have to contain the mean duration of the egg production period. Furthermore these estimations are biased because they do not account for the basal temperature (the temperature below which development stops).

Table 5

Number of juvenile periods during one year for four brackish water nematodes (females); using Simpson's approximative method with development rates predicted by the power equation (A) and the quadratic equation (B); (A)\*, (B)\* yearly juvenile periods after correcting for the basal temperature.

Species	(A)	(A)*	(B)	(B)*
<i>M. microphthalma</i>	11.0	9.9	11.6	9.3
<i>M. parelegantula</i>	6.6	6.4	6.7	5.7
<i>C. nudicapitata</i>	10.1	10.1	10.8	10.8
<i>P. caecus</i>	3.5	3.4	3.8	3.5

Observations on life history of the species in laboratory conditions gave the following values for the basal temperature : 10°C for *M. microphthalma* ; ±10°C for *M. parelegantula* ; 5°C for *P. caecus* and less than 3°C for *C. nudicapitata*. When these biological zero's are accounted for the computations result in the numbers indicated with an asteriks (Table 5). The largest difference, 2.3 juvenile periods, occurs for *M. microphthalma*, the discrepancy between the other values is rather small. From this, it is also obvious that the quadratic equation gives more weight to the lower temperatures. Nevertheless the bias introduced when basal temperature is not accounted for moderate ; only for those species where basal temperature is high, precautions are necessary.

The annual number of generations (Table 5) is somewhat less than previously published values : 15 for both *Chromadorina germanica* (Tietjen & Lee, 1977) and *Monhystera denticulata* (Tietjen & Lee, 1972) and 17 generations for *M. disjuncta* (Gerlach, 1971), but considerably higher than the modal value of three proposed by Gerlach (1971) for marine meiobenthos, except for *P. caecus*, the largest species. At the time being we can only confirm the statement of Heip *et al.* (1982) that it is too early to give a modal value for nematodes, because development data exist only for opportunistic species belonging to a few genera.

## Discussion.

The available results of direct production estimates of meiobenthic populations (Table 6) already indicate that the use of a single annual P/B value for meiofauna (Gerlach, 1971) is inappropriate. In fact the annual P/B values show a considerable range, and the high diversity in life histories of meiobenthic populations is clearly reflected in the diversity of annual P/B values. In this respect, it is interesting to note that the P/B per generations annually is the most important factor in determining annual P/B-values (Waters, 1969).

Table 6  
P/B ratio's per year and per generation for meiobenthic species  
for which direct production estimates are available

Species	(P/B) <sub>a</sub>	(P/B) <sub>g</sub>	Source
<i>Huntemannia jadensis</i>	3.8	3.8	Feller, 1977
<i>Microarthridion littorale</i>	18.0	?	Fleeger & Palmer, 1982
<i>Tachidius discipes</i>	9.3*	3.1	This paper
<i>Paronychocamptus nanus</i>	24.5	3.2	id.
<i>Cyprideis torosa</i>	2.7	2.7	id.

\* The annual P/B for *T. discipes* is calculated over the period of presence in the habitat.

In nematodes, both field observations and culture experiments show that the generation times range between a few days and a whole year. Since generation P/B is relatively constant, the range of annual P/B values will be much wider than the results of direct production estimation indicate to date. On the basis of our laboratory experiments on the four nematode species, and assuming a life cycle P/B of three, we can give a rough approximation of the annual (indicated  $\text{yr}^{-1}$ ) P/B,  $28.8 \text{ yr}^{-1}$  for *M. microphthalma*;  $18.2 \text{ yr}^{-1*}$  for *M. parelegantula*;  $31.4 \text{ yr}^{-1*}$  for *C. nudicapitata* and  $10.4 \text{ yr}^{-1}$  for *P. caecus*. As *M. parelegantula* and *M. microphthalma* do not reproduce and occur only sporadically during approximately half a year, annual mean biomass will be much lower and the annual P/B-ratio consequently much higher than these figures, which are based on the period that the species actually occurs ( $\text{yr}^{-1*}$ ). On the other hand, the large *O. oxyuris* and *V. viscosa* are expected to have a P/B of between three and six.

The use of a single P/B for the meiobenthos is clearly unrealistic. However, other shortcut methods may prove more useful. The data presented here indicate that the production efficiencies are rather constant, implying that respiration data may be used to estimate production. Humphreys (1979) analysed 235 field populations and found significant log-log relationships

between annual production and annual respiration for a number of species groups. For non-insect invertebrate detritivores he found  $\log P = -0.601 + 1.069 \log R$  (P and R in  $\text{cal m}^{-2}\text{y}^{-1}$ ). Table 7 compares the productions estimated from this equation to the productions directly measured for the three populations studied in this paper. The rather close agreement between these values encourages further research along this line.

Table 7  
Comparison between observed production  
and production predicted from respiration  
for three meiobenthic crustaceans

	log R	(log P) <sub>pred.</sub>	(log P) <sub>obs.</sub>
<i>Cyprideis torosa</i>	4.950	4.691	4.741
<i>Paronychocamptus nanus</i>	4.499	4.208	4.038
<i>Tachidius discipes</i>	4.160	3.846	3.797
(R and P in $\text{cal m}^{-2}\text{y}^{-1}$ )			

Table 8  
Respiration per unit body weight ( $\text{nl O}_2 \cdot \text{dwt}^{-1} \cdot \text{h}^{-1}$ )  
of meiobenthic Crustacea

Species	Respiration	Source
<i>Asellopsis intermedia</i>	3.8	Lasker <i>et al.</i> , 1970
<i>Hastigerella leptoderma</i>	3.42	Vernberg <i>et al.</i> , 1977
<i>Nannopus palustris</i>	4.99	id.
<i>Thompsonula hyaenae</i>	10	Sellner, 1976
<i>Paraleptastacus spinicauda</i>	4.2	Laserre & Renaud-Mornant, 1973
<i>Enhydrosoma propinquum</i>	2.0	Coull & Vernberg, 1970
<i>Longipedia helgolandica</i>	6.6	id.
Harpacticoids brackish water		
"class I" (9.0 $\mu\text{g}$ dwt)	4.0	Laserre <i>et al.</i> , 1975
"class II" (1.5 $\mu\text{g}$ dwt)	10.0	id.
Ostracods	3.0	id.
<i>Hirschmannia viridis</i>	2.0	Hagerman, 1969
<i>Cyprideis torosa</i>	0.8-1.0	this paper
<i>T. discipes</i>	11.8-17.4	id.
<i>Paronychocamptus nanus</i>	10.5-13.7	id.
Marine planctonic copepods	30	Ivleva, 1980

The available data show that a considerable range exists in the respiratory activities of meiobenthic animals. Data for nematodes are reviewed by Warwick & Price (1979). Table 8 summarizes data on crustaceans. In nematodes the variation is one

order of magnitude ; it is somewhat less, but still important in meiobenthic crustaceans. Several attempts have been made to correlate the observed variation to ecological variables such as feeding type of the species or oxygen content of the habitat (Teal & Wieser, 1966 ; Schiemer & Duncan, 1974 ; Warwick & Price, 1979), but although there appear to be some tendencies, the results are not very conclusive. Therefore, it remains difficult to forecast the respiratory rate of a population unless it has been measured.

Furthermore, a comparison between the respiration rates of *T. discipes* in the Dievengat (this paper) and in an English estuary (Teare & Price, 1979) makes clear that important differences can exist between two populations of the same species. In the Lynher estuary, reproduction is continuous throughout the year. The modal volume of adult animals (value read from a figure) is about 8.25 nl and the respiration rate per unit body volume of animals from the field population is almost 2.5 times lower than for the Dievengat animals. In the Dievengat the population is only present in the spring, the modal body volume of an adult is 12.5 nl, and the respiratory rate is higher. At least a part of these differences can be attributed to differences in feeding conditions. In their laboratory reared population, Teare & Price (1979) had adults of modal body volume = 10.0 nl, with a respiration rate per unit volume twice as high as in the animals taken from the field.

Apart from stressing the difference between local populations, this example illustrates that food availability, and hence productivity in the habitat may be an important factor in determining the respiratory activity of a population. Therefore, looking for a general value for the respiratory activity of meiofauna may be as spurious as looking for one overall P/B figure.

#### Acknowledgments.

C. Heip and P. Herman acknowledge a grant from the Belgian National Science Foundation N.F.W.O. G. Vranken and D. Van Brussel acknowledge a grant from the Institute for Scientific Research in Industry and Agriculture (I.W.O.N.L.). Part of this research was sponsored through grant 2.0010.78 from the Fund for Collective Fundamental Research F.K.F.O. We thank Wies Gijssels for assistance in the laboratory.

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## IV

# MEIOFAUNA OF THE BELGIAN COASTAL WATERS : SPATIAL AND TEMPORAL VARIABILITY AND PRODUCTIVITY

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### Abstract.

Density, biomass and diversity of meiobenthic assemblages have been studied in the Belgian coastal waters of the North Sea since 1972. Near-shore sediments east of Ostend show an extremely poor meiofauna, with nematodes extremely dominant. West of Ostend muddy sand and sands exist with a richer fauna. These zones are clearly delimited on the basis of nematodes, whereas they are more uniform when either macrofauna or harpacticoids are studied (Govaere et al., 1980). This is also true for off-shore sediments. Besides species diversity also trophic diversity, as expressed by the number of feeding types, increases towards off-shore sandy sediments.

The study of density and biomass of nematodes and harpacticoids permits estimations of production of these groups. The total carbon requirements of the meiobenthos can be estimated at 8-9 g C/m<sup>2</sup>.year in the coastal zone and a minimum of 5-6 g C/m<sup>2</sup>.year on the Kwinte bank, a subtidal sandbank, although sedimentation is very much lower in the sandbank. This indicates that when energy flow is lower a much larger part of it passes through the meiobenthos.

## Introduction.

Meiobenthos of the Southern Bight of the North Sea has been investigated on a large spatial scale from 1971 to 1976 (see maps in Govaere *et al.*, 1980) whereas a smaller area covering the Belgian near-shore waters has been sampled regularly from 1978 onwards. A survey of the meiofauna of the greater grid area was given by Van Damme & Heip (1977) and Govaere *et al.* (1980). These earlier papers were based mainly on harpacticoid copepods as far as the meiofauna was concerned and the sampling programme was very heterogenous in time which made detailed studies of temporal variation impossible. In the present report these gaps have been filled as it presents a detailed analysis of the nematodes of the larger area and data on density, biomass and diversity of nematodes and harpacticoids in the coastal area.

## Material and methods.

From 1971 to 1975 350 samples from 74 stations were analysed for meiofauna (Govaere *et al.*, 1980). All samples were taken with a 0.1 m<sup>2</sup> Van Veen grab. The material was collected in a bucket and fixed in 7% neutralised formalin on board of the ship. Meiobenthos samples were taken from the bucket with a core (sandy sediments). In the laboratory they were elutriated by decantation or a sugar-flotation technique was used (muddy sediments).

Eighteen coastal stations were sampled seasonally during ten cruises from June 1977 till September 1979. The coordinates are listed in table 1.

In the first three cruises (June 77, September 77 and March 78), meiofauna was collected by subsampling a Van Veen grab. From April 78 onwards all sampling was done by a modified Reineck box corer (sample surface : 170 cm<sup>2</sup>). Each box core was subsampled by four plastic cores (surface : 10.2 cm<sup>2</sup>). Two replicates for meiofauna were fixed with warm formalin (70°C) to a final concentration of 4%. The other cores for chemical and sediment analysis were frozen immediately. All stations were sampled during April, June, September, December 1978 and April, June, September 1979, except st. 10061 and st. 10500 which were not sampled in April 1978 due to bad weather conditions.

Sediment analysis and mathematical methods are as described in the first paper of the series (Heip *et al.*, 1979).

Table 1

Coordinates of the eighteen coastal stations and sediment characteristics (average per station over the entire study period) : mean % mud and sand, mean median grain size (in  $\phi$ -units and mm) and mean sorting ( $\phi$ -units) of the sand fraction.

Stat.	Latitude	Longitude	% mud	% sand	Grain size		Sorting
					Md $\phi$	Md <sub>mm</sub>	
10061	51°08'21"	02°31'40"	2.95	97.04	2.461	0.191	0.357
10080	51°07'10"	02°31'00"	0.28	98.24	2.168	0.227	0.401
10481	51°12'20"	02°50'14"	20.75	79.10	2.722	0.152	0.385
10500	51°11'06"	02°42'04"	16.28	81.91	2.499	0.177	0.432
10791	51°14'35"	02°55'25"	49.28	49.52	2.627	0.164	0.499
11121	51°16'40"	03°00'30"	9.09	90.90	2.529	0.174	0.370
11150	51°16'32"	02°51'08"	2.03*	97.73*	1.890	0.270	0.459
11312	51°19'10"	03°06'00"	58.76	36.53	2.600	0.165	0.588
11315	51°19'30"	03°03'00"	56.26	43.60	2.540	0.172	0.526
11331	51°19'01"	02°56'50"	44.81	55.18	2.820	0.142	0.521
11672	51°21'00"	03°14'00"	26.71	71.23	2.383	0.192	0.458
11851	51°23'02"	03°22'56"	44.93	55.27	2.643	0.160	0.575
11860	51°22'38"	03°18'41"	30.93	69.30	2.440	0.184	0.437
11880	51°22'00"	03°09'15"	64.53	34.93	2.600	0.165	0.613
12300	51°26'55"	03°23'24"	25.22	72.90	2.280	0.206	0.449
12501	51°27'17"	03°31'33"	2.29	97.56	2.181	0.221	0.418
12510	51°26'55"	03°21'45"	9.34	91.32	2.381	0.192	0.390
12830	51°29'49"	03°25'45"	18.80	80.91	2.492	0.178	0.461

\* March 78 is not considered due to the aberrant value of 76 % mud.

## Results and discussion.

### *The distribution of sediments in the area.*

The sediment composition of the sea bottom varies from 100% silt, over silty fine sand to clean fine sand from the NE to the SW along the coast and from predominantly muddy in the coastal water to very pure sandy sediments offshore. Due to the decreasing tidal currents a clear gradient from coarse sands in the south to fine sands in the north of the area is a very significant feature of the Southern Bight.

Gullentops *et al.* (1977) gave some data on the origin, transport and on the behaviour of the fine sediments along the Belgian coast. The material along the Belgian coast is from two different origins ; the western part of the coast is influenced by the IJzer, French coast and by the Channel, the eastern coast is influenced by the Western Scheldt estuary. Based on sedimentological arguments and hydrodynamic indications, transport out of the Western Scheldt goes to the SW, probably till Ostend. The silt on the east side of Ostend has its origin in the Western Scheldt ; the silt between Nieuwpoort and Ostend is derived from the Channel, the French coast and from the IJzer.

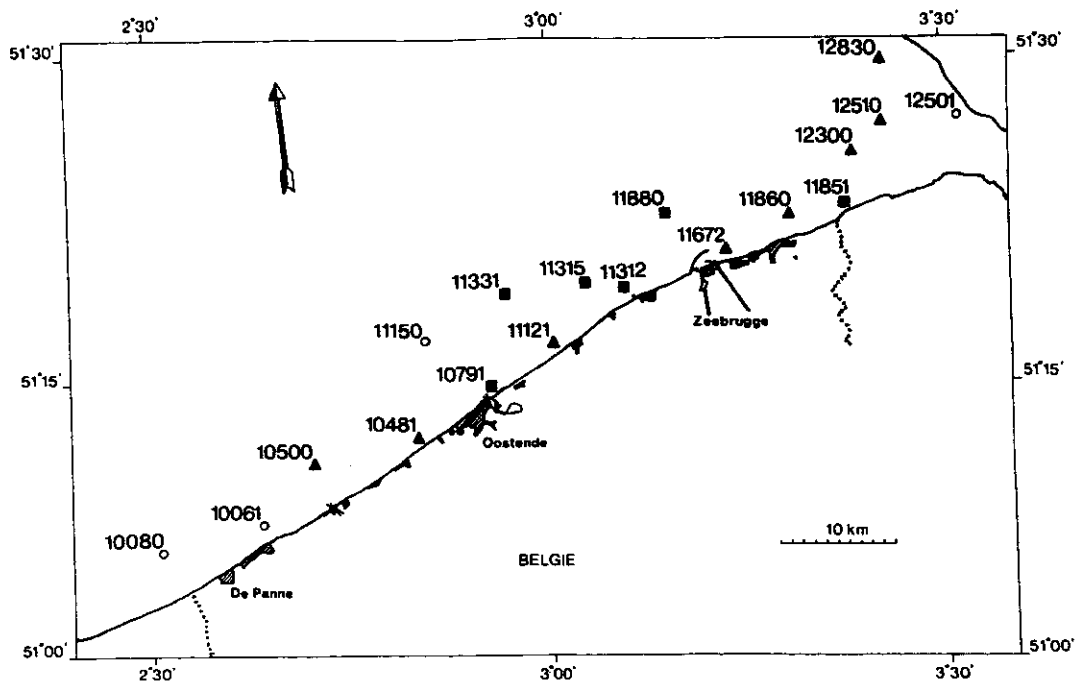


fig. 1.

Localisation of the eighteen coastal stations and their characterisation according to three sediment groups

- sand stations (< 5 % mud)
- ▲ muddy sand stations (5 % < < 32 %)
- mud stations (> 32 % mud)

The characteristics of the sediments in the coastal stations are listed per station in table 1. The overall median grain size of the sand fraction here is 0.186 mm. The eighteen coastal stations can be classified into three groups (Fig. 1). Those stations where the mud content remains below 5% of the sediment over the ten cruises are called sandy stations: 10080, 10061, 11150 and 12501. The mean grain size is 0.226 mm for the whole sampling period. There is no difference between summer and winter samples. Also the percentage mud is quite stable both in space and time. Except for a peak value of 75.75% mud (st. 11150, March 78), the mean mud content is approximately 2% (Table 2). The muddy sand stations with a mud content between 5% and 32% are: 10500, 10481, 11121, 11672, 11860, 12300, 12510 and 12830.

Although the mean grain size is equal for summer and winter samples there is often a great fluctuation in mud content in both station groups. These differences are not only seasonal, but factors such as weather condition, current velocity, fisheries and public work activities may be important.

Table 2  
 Mean and summer-winter values of median grain size ( $Md_{mm}$ ),  
 percentages mud and sand in the three station groups

	Eighteen stations	Sand stations	Muddy sand stations	Mud stations
<b>Median grain size</b>				
mean $Md_{mm}$	0.186	0.228	0.184	0.163
summer	0.187	0.228	0.183	0.164
winter	0.186	0.229	0.184	0.161
<b>% mud (&lt;63 <math>\mu</math>m)</b>				
mean %	27.52	1.75	19.70	53.85
summer	28.64	2.01	21.05	56.36
winter	25.85	1.25	17.67	50.08
<b>% sand</b>				
mean %	72.06	95.79	79.85	45.87
summer	70.94	97.47	78.53	43.14
winter	73.75	93.28	81.84	49.96

#### *Spatial distribution of nematodes in the Southern Bight.*

280 species of nematodes from 121 genera and 28 families have been found, which means a mean number of 20 species per station. Because families group species which are morphologically very similar, an analysis on family basis was attempted. Diagnostic characteristics for families are buccal structures (which reflect feeding preferences) and position and structure of sense organs (which allow reactions to environmental conditions).

Spatial variability was examined from samples obtained during summer 1972, a period in which nearly all stations were sampled. A mean density of 1500 ind./10 cm<sup>2</sup> was found over the whole region. This value should be considered as minimal as the material was subsampled out of a Van Veen grab.

The similarity (Sørensen-index) between the stations was examined. All the families were used for cluster analysis. The matrices of similarity thus obtained were subjected to flexible sorting (Lance & Williams, 1967), with the cluster intensity coefficient  $\beta$  set at -0.25.

The region can be divided into six zones, which are a very good representation of the sediment composition (Fig. 2).