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FIELD STUDY OF THE DIET, SELECTIVE AND EFFICIENCY FEEDING OF THE
MARINE COPEPOD TEMORA LONGICORNIS IN THE SOUTHERN BIGHT
OF THE NORTH SEA.

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ABSTRACT

Temora longicornis is the dominant species among the zooplankton during the phytoplankton bloom, being dominated by Phaeocystis pouchetti. Shipboard grazing experiments carried out before and after the bloom showed that Temora feeds very unefficiently on Phaeocystis, as far as the late Copepodites and the adults are concerned. Ivlev Parsons feeding relationships on different size-classes of phytoplankton are given for all developmental stages. When diatoms are blooming (at the beginning of April, before the Phaeocystis bloom) or, when the Phaeocystis develops, and after the bloom when only small flagellates are present, different relations for the same stage were found.

This unefficient feeding occurs when Phaeocystis develops its mucous envelope at the top and in the declining fase of the bloom: colonies of a few mm till few cm diameter - the top of the bloom can represent 20 - 30 mg chlorophyll/m³ and daily ingestions of late Copepodites and adults represent only 15 - 20% of their own weight. Together with the low ingestion rates, day-night feeding rhythms disappear. Discussion is given about the consequence of 24 hours activity (instead of a few hours nightly at high rates) on the energy budget of the animals whose production is declining; this phenomenon is paralleled by increasing temperature on a shallow water column (higher oxygen demand and metabolic rates). Possible surviving mechanisms are discussed (lipid reserves, resistant eggs production, switching to other food diet?).

I. INTRODUCTION

The numerical importance of its individuals makes the Copepod *Temora longicornis* to exercise a potential important action during the phytoplankton springbloom. Grazing experiments, carried out from April to July tended to get an accurate picture of this role during the declining fase of the springbloom and also to emphasize a possible day-night and seasonal variations. It is very well known that grazing is a function of the concentration of phytoplankton and that not all species or size-classes are equally eaten with the same efficiency (Mullin 1963, Frost 1972). It was therefore useful to observe the grazing by different size-classes of particles. During the springbloom most of the biomass is represented by *Phaeocystis pouchetti* (Joiris et al, 1982) which is situated in a size-class larger than 100μ , while the flagellates are in a mucous envelop or isolated in individual cells smaller than 25μ . We chose then to do our measurements of grazing on 3 different phytoplankton size-classes i.e. : smaller than 25μ , between 25μ and 100μ , larger than 100μ .

Following our own experience in the Northern North Sea with *Calanus finmarchicus*, variations within the day-night rythm of feeding can be extremely marked (Daro, 1980) with feeding rates till 20 times higher at night than at day ; it was therefore important to look after possible day and night differences.

We had as third concern to check if the 3 generations of *Temora* succeeding from April to July showed the same efficiency at taking their food comparatively with the succession of different phytoplankton populations during the same period.

II. METHODS

Broadly the method is the one described in a fewer paper (Daro, 1978) which consists in labelling, under natural light, natural phytoplankton with radioactive C^{14} bicarbonate, in presence of natural zooplankton concentrated at a maximal rate of 5 x in flasks of 1 liter. The tracer is then followed in the phytoplankton and the zooplankton during 1 of 2 hours incubation time.

What concerns night experiments, the phytoplankton is prelabelled in artificial light during 1 hour. All experiments are shipboard experiments. When working on different phytoplankton fractions, we proceed as follows :

- a) one set of bottles with a fraction larger than 100μ (Zoo + Phytoplankton) is put together in one liter smaller than 25μ
- b) one set of bottles where the fraction larger than 100μ is put in one liter total water (not filtered)
- c) one set of bottles where the fraction larger than 100μ is put in one liter fresh on 45μ filtered seawater.

The grazing occurs then in c) only on phytoplankton larger than 100 μ, in a), on phytoplankton smaller than 25 μ and larger than 100 μ and in b) on the totality offered.

With simple subtractions of radioactivity traced in the zooplankton (the different development stages having been sorted) in the different sets of experiments one obtains the rates providing from the grazing on the fraction smaller than 25 μ, comprised between 25 and 100 μ and larger than 100 μ.

Following the formula given by us (Daro, 1978) for accurate calculation of the grazing, we measured also in each set of experiment the radioactivity of the different phytoplankton fractions i.e. smaller than 25 μ, smaller than 100 μ and larger than 100 μ.

III. RESULTS

A) Size class selectivity

The fig. 1 abcdef give all results of experiments carried out during April and May for Temora ranging from nauplii to adults, on 3 size classes of Phytoplankton.

a) The nauplii (fig. 1a)

A discrimination was made between nauplii I to III on one hand, and nauplii IV to VI on the other hand.

The grazing on the fraction larger than 100 μ was always equal to zero. No preference could be detected concerning the two other fractions.

The Ivlev Parsons relationship as a function of the chlorophyll concentration comprised between 0 and 100 μ reads as follows :

$$I_h = .32(1 - e^{-.22(p-.2)}) \text{ for the nauplii I to III} \quad (1)$$

$$I_h = .94(1 - e^{-.24(p-.2)}) \text{ for the nauplii IV to VI} \quad (2)$$

Where I_h is the ingestion expressed in $\mu\text{g Chl}a \times 10^{-3}/\text{Animal}/\text{hour}$ and p the chlorophyll concentration in $\mu\text{g Chl}a/l$ for the fraction 0 - 100 μ.

b) The copepodite I - II (Fig. 1 b & 1 c)

As the nauplii they do not feed on the fraction larger than 100 μ. We may here distinct two relationships for either fractions, as follows :

$$I_h = .76(1 - e^{-.71(p-.3)}) \text{ for the grazing on the particles smaller than } 25 \mu \quad (3)$$

$$I_h = 1.4(1 - e^{-.4(p-.2)}) \text{ for the grazing on the particles } 25-100 \mu \quad (4)$$

where I_h in both relationship is the ingestion in $\mu\text{g Chl}a \times 10^{-3}/\text{Animal}/\text{hour}$.

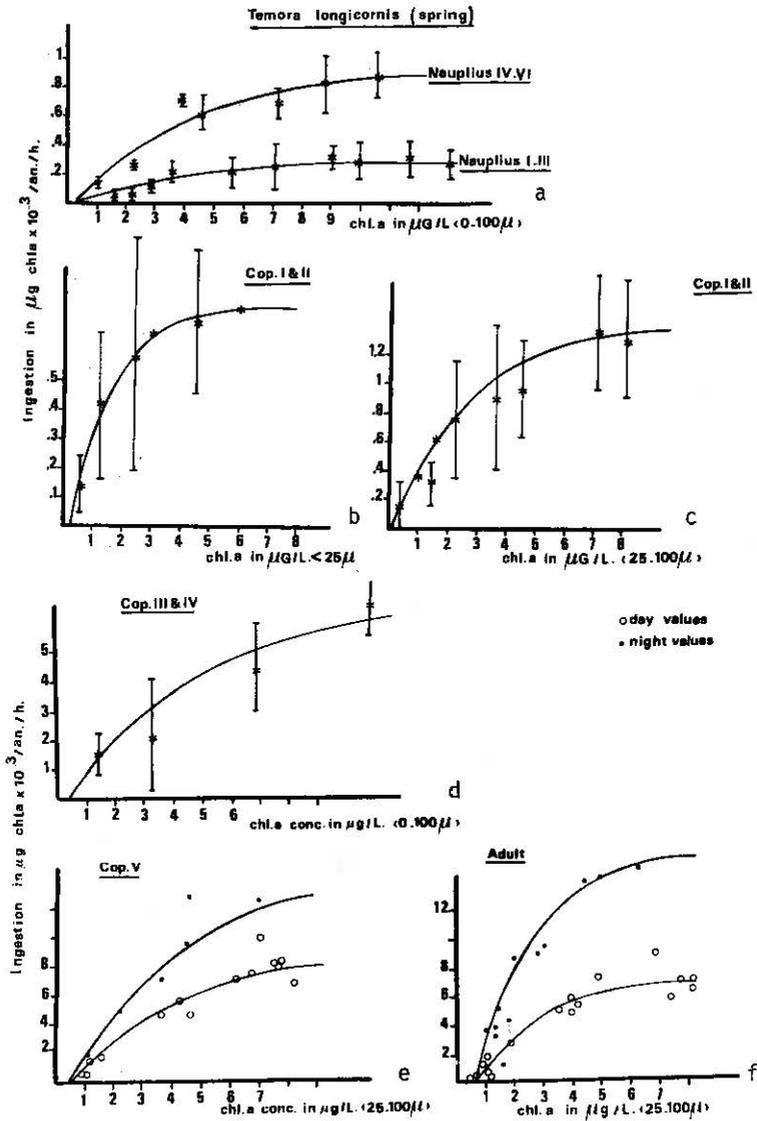


FIG. 1

Fig. 1

Hourly ingestions of different developmental stages of *Temora longicornis* in Spring time as a function of chlorophyll concentration

p in relation (3) is the chlorophyll concentration in $\mu\text{g Chla/l}$ smaller than 25μ .

p in relation (4) is the chlorophyll concentration in $\mu\text{g Chla/l}$ $25 - 100 \mu$.

c) The copepodites III - IV (fig. 1 d)

Their grazing behaviour is the same as nauplii's, in the fact that here also the largest fraction 100μ is neglected. No clear difference could be found between the two other fractions and the Ivlev Parsons relationship can be figured as follows :

$$I_h = 7(1 - e^{-.2(p-.4)}) \quad (5)$$

I_h being the ingestion in $\mu\text{g Chla} \times 10^{-3}/\text{animal/hour}$

p is the chlorophyll concentration in $\mu\text{g Chla/l}$ for the fraction $0 - 100 \mu$.

d) The copepodites V (fig. 1 e)

They are clearly selective on the mean fraction $25 - 100 \mu$. The few non zero values of grazing obtained on either other fractions larger than 100μ and smaller than 25μ did not allow to calculate Ivlev Parsons relationship. The Ivlev Parsons relationship at day time on the fraction $25 - 100 \mu$ is as follows :

$$I_h = 9(1 - e^{-.25(p-.5)}) \quad (6)$$

I_h being the ingestion expressed as $\mu\text{g Chla} \times 10^{-3}/\text{Animal/hour}$ and p the chlorophyll a concentration in $\mu\text{g Chla/l}$ in the fraction $25 - 100 \mu$ at day time.

e) The adults (fig. 1 f)

They show the same grazing behaviour as the copepodites V, with a noticeable preference for the middle fraction $25 - 100 \mu$.

Here again, though we sometimes observed also feeding values on the two other fractions the Ivlev Parsons relationship obtained about the grazing at day time on the mean fraction reads as follows :

$$I_h = 6.8 (1 - e^{-.51(p-.7)}) \quad (7)$$

Where I_h is the ingestion in $\mu\text{g Chla} \times 10^{-3}/\text{Animal/hour}$ and p is the chlorophyll concentration in $\mu\text{g Chla/l}$ for the fraction $25 - 100 \mu$ at day time.

B) The day night feeding rhythm (Fig. 1 e - 1 f)

Concerning the young stages from nauplii up to copepodites IV no difference was observed between day and night ingestions and relationship (1) to (5) take in account all day and night values.

On the other hand, the oldest stages, copepodites V and adults show a clear difference between day and night feeding rates.

The Ivlev Parsons relationships read as follows :

$$I_h = 14.65 (1 - e^{-.25(p-.5)}) \text{ for the copepodites V} \quad (8)$$

$$I_h = 16 (1 - e^{-.25(p-.5)}) \text{ for the adults} \quad (9)$$

where in both relations I_h is the ingestion in $\mu\text{g Chl}a \times 10^{-3}/\text{Animal}/\text{Hour}$ and p the chlorophyll concentration in $\mu\text{g Chl}a/\text{l}$ in the fraction 25 - 100 μ at night.

There are some little differences in the feeding rhythm between these 2 oldest stages : Copepodites V show a higher I_h at day than the adults, when the contrary is occurring at night. In other words, the older the animals are, more pronounced is the feeding rhythm. An adult, at night, feeds 2.35 times more than during the day, when this proportion falls to 1.63 for a Copepodite V. This fact was thus observed during the spring bloom, in April - May.

We, though, shall see further in this paper, that this proposal is not always true.

C) The feeding efficiency

Different phytoplankton populations succeed one another in the course of the season. After the big bloom of *Phaeocystis* which practically disappears at the middle of May, the small naoflagellates are prevailing. The Fig. 2 shows the seasonal evolution of the chlorophyll values among the different fractions, where generally the june values are very low in all fractions, but where also the fraction smaller than 25 μ is, as a rule, dominating, while the mean fraction 25 - 100 μ is practically absent. It was, therefore, interesting, to observe the way *Temora* adapts to this period, where its preferred size-class food is missing.

Chlorophyll variation West - Hinder

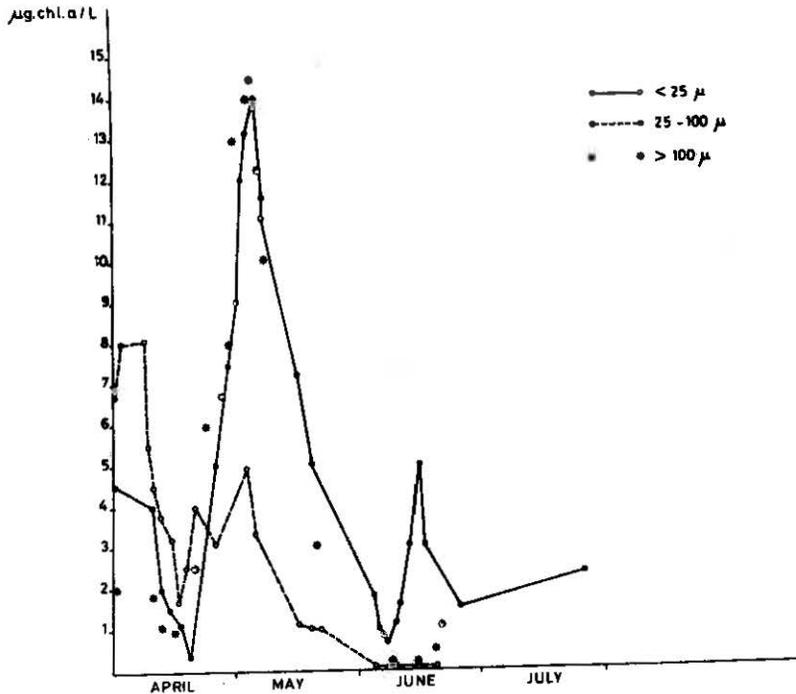


Fig. 2

Seasonal variation of chlorophyll in three different size classes $< 25 \mu$
 $25 - 100 \mu$ $> 100 \mu$

The Fig. 3 shows all results of experiments carried out in June.

Different remarks can be done :

- There is no difference to detect between day and night feeding rates, even by oldest stages.
- All relationships between ingestion and chlorophyll concentrations are linear we are drawing attention to the fact that by working with very low concentrations (between 5 and 3 $\mu\text{g Chl a / l}$) it is impossible to detect relationships other than linear ones.

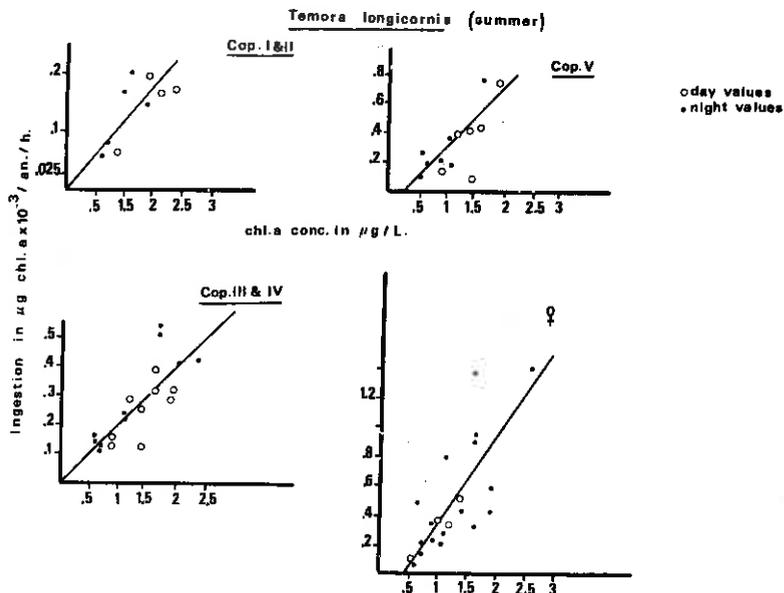


Fig. 3

Hourly ingestions of different developmental stages of *Temora longicornis* in the summer time as a function of chlorophyll concentration.

Nevertheless, there was for the animals no other choice than feeding on it, a situation which represents the true natural conditions.

As follows, the relationships which are found out

$I_h = .12 p$ for the copepodites I-II

$I_h = .20 p$ for the copepodites III-IV

$I_h = .46 - .16$ for the copepodites V

$I_h = .59 - .22$ for the females

where I_h is the ingestion in $\mu\text{g Chl a} \times 10^{-3} / \text{Animal/Hour}$

p is the chlorophyll concentration in $\mu\text{g Chl a/l}$ for the fraction 25μ .

Let us point out that our samples did not contain nauplii and males in sufficiency to produce correct values of grazing.

If we now compare the ingestion values from the Ivlev Parsons relationship for the period April-May with the linear ones put in evidence for June, we observe that, with the same concentration chlorophyll, these values are much lower in June than in April-May.

It is more realistic to express the values in Carbon units, since we know that the carbon/chlorophyll equivalences are not constant, but vary following the

species and the physiological conditions.

We adopted the chlorophyll/carbon equivalences given by Lancelot (1980) for the same area as being 32 in the spring and 74 in the summer.

As for example, the daily grazing of an adult at the concentration of 2 $\mu\text{g Chla/l}$ will be during the spring $132.6 \times 10^{-3} \mu\text{g Chla}$ or 4.24 μgC (from 16), and in summer $23.4 \times 10^{-3} \mu\text{g Chla}$ or 1.70 μgC from (20) multiplied by 24. So that even if the carbon contents are much higher in the summer, the ingested food is much lower ; in other words the feeding efficiency decreases during the summer for *Temora* which probably is not able to feed on very small particles.

Finally we put all results together, obtained in April, May and June and we obtained on the Fig. 4 different relations following *Temora* feeds on the prebloom of diatoms in early April (the highest values) or in May when *Phaeocystis* colonies are abundant and June when only small flagellates dominate the phytoplankton.

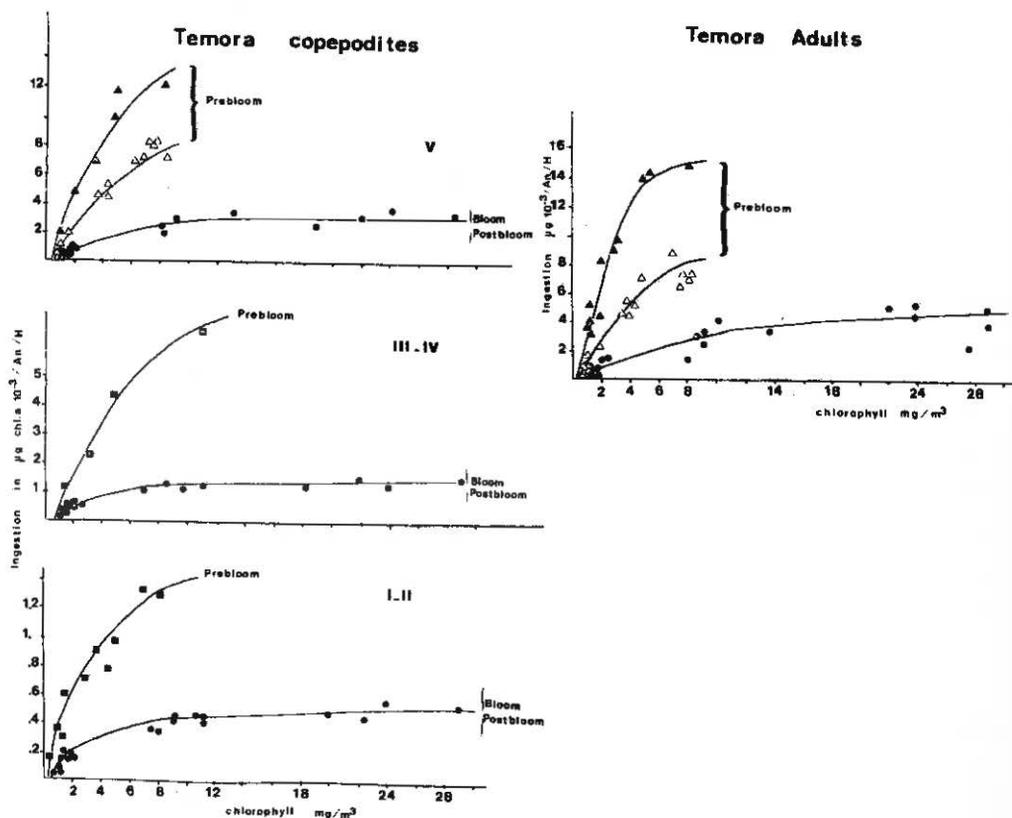


Fig. 4

Hourly ingestions of different development stages of *Temora longicornis* as a function of chlorophyll concentration. All results together.

D) Feeding of Temora through 3 generations.

The question which now arises is to put in evidence the consequences which differences in feeding selectivity and efficiency could entail during the life of the succeeding generations from April to July.

The successions were detailly studied in the same area by Bossicart (1979) so that we know accurately the development times, which we used for our calculations.

Taking into account all results produced in this paper and the evolution of the chlorophyll concentration in the different fractions, we were able to calculate the grazing of an animal in its natural conditions through its all life.

The results expressed in $\mu\text{gC}/\text{Animal}/\text{Day}$, taking the conversions factors of Lancelot (1980), for 3 generations and for different hatching times (see fig. 5).

The food ingestion of the animals of the first generation, born on the first of April does increase through all their life. At the end of the life of the animals born on the 10 th of April, one observes a decreasing food ingestion, though not drastic. The animals born on the 20 th of April endure difficulties and scarce feeding conditions when reaching the adult stage.

This trend is more and more pronounced at the second generation, the young copepodites only disposing of good feeding conditions. As one comes to the third generation, one can speak of true shortage, in any case concerning the latest born animals.

We already mentioned (Daro & Van Gijsegem 1984) these increasing bad feeding conditions, which are responsible for low or absent egg production, with its immediate consequence : the decreasing number of Temora population. We also stated the hypothesis that Temora could at this period change its food diet and we did not exclude that they might become carnivorous.

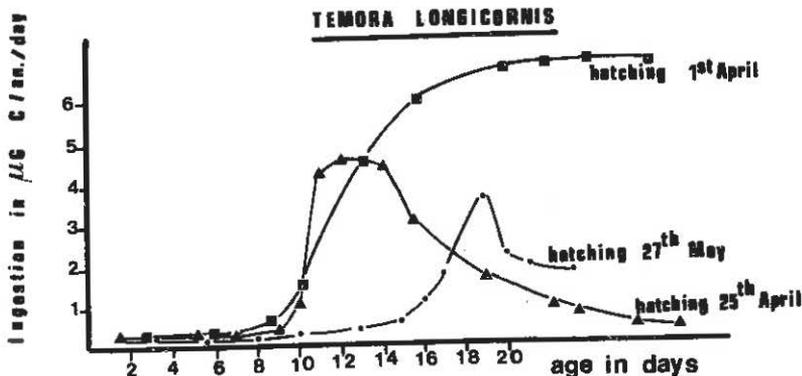


Fig. 5

Daily ingestion of *Temora longicornis* as a function of age of individuals at 3 generations.

IV. DISCUSSION

There is already long time that it was showed that most of the calanoid Copepods do not feed either a very small or very large particles (smaller than 5μ and larger than 100μ) (Gauld 1966). The grazing behaviour of *Temora* do not anything else but confirms once again this observation. On the other hand, considering the range between these class-sizes, food efficiency is believed to increase when increases the size of particles (Boyd, 1976 ; Nival & Nival 1976). There is also to be mentioned that the amount of food ingested as Carbon is higher - as absolute rate - when the Copepods are feeding on larger sizes (Mullin 1963, Frost 1972, O'Connors et al 1976, Paffenhöfer & Knowles 1978). This general scheme, though, is not relevant to all species. *Calanus pacificus*, for example, was found to feed at similar rates regarding Carbon ingestion on different class-sizes of diatoms, when the concentration in food carbon exceeds a high, critical value which was inversely related to cell size (Frost 1972).

O'Connors, Biggs & Ninivaggi (1970), working with natural assemblages of particles found that the maximal grazing rate of *Temora longicornis* adults increased with a factor 3.5 as the diameters of particles forming the peak of the food size distribution increased from 5 to 30μ .

Poulet (1978), working in the Bedford Basin, also on natural occurring particulate matter found a similar feeding behaviour for the dominant Copepods, among them *Temora longicornis*, the maximal food ingestions - between 5 and 40μ - taking place during the month of June, a schedule which almost totally corresponds to the natural size distribution and concentrations : he pointed out for September a Dimodal food distribution on small particles of about 2μ , on the one hand, and, on the other hand, on larger particles of about 50μ , which again echoes accurately the natural occurring, size-classes distribution. Poulet's conclusion was that all species were opportunistic filter feeds, non selective as regards particles size but well as concerns particles biomass, in which their behaviour distincts itself from that of passive fixed sieves.

Many authors have described chemoreceptors of several planktonic crustaceans (Elofson 1971, Fleminger 1973, Friediman & Stricker 1975) locating them on the antennae, feeding appendages, anterior tip.

Moreover, Copepods search for food (Kittredge et al 1974). So it is likely that the shifting in mechanisms by marine copepods as well as the searching and tracking for biomass peaks (Poulet 1973- 1974 , Richman et al 1977) may depend upon chemoreceptors (Poulet x Marsot 1978).

The capability of switching food ingestions from one to another size-class was shown by Poulet (1973) for *Pseudocalanus* when fitting the model of energy maximization of Lehman (1976) and Lam & Frost (1976), where the animals shift their maximal food ingestion to certain size-classes when the energy gain would be higher, so they would not only behave along a pure mechanistic model *Calanus finmarchicus* was also shown switching very efficiently to other size-class particles when phytoplankton composition is modifying (Gamble 1978). We have in our case to deal with mechanisms of an other sort which apparently do not fit with mechanistic models nor energy maximization models. Indeed all events proceed as if *Temora*'s feeding behaviour was induced at the first (and the most numerous) generation, where the mean fraction of phytoplankton (25-100 μ) is the most abundant. This behaviour seems to have dramatic consequences for the further development of the second and the third generation. As stresses by many authors the shelf seas, enclosed seas and coastal areas all over the world are doomed to an increasing "pollution", the latter very often going together with a development to small forms of phytoplankton (Greve & Parsons, 1977). More and more authors mention on the other hand the cosmopolitan development of *Phaeocystis pouchetti*.

The Belgian coastal sea seems to deal with a transitional phenomenon where the herbivorous zooplankton, far as *Temora* is concerned, has not adapted, yet, to the phytoplankton species appearing massively during the springbloom. Regarding the day-night feeding rhythm it is also obvious that there is a threshold of phytoplankton concentration where feeding stops, a matter which is clearly established for the oldest stages but which occurs no more in June when food is becoming scarce.

But we have to point out that in laboratory experiments, on the contrary colonies of *Phaeocystis pouchetti* from the German Wadden Sea off Sylt were ingested by *Temora longicornis* (Weize 1983).

From own experience in the field, we know that the colonies are very difficult to conserve intact, and that only transport in a vessel modify totally the size distribution pattern. Perhaps the *Temora* off Sylt had another size colonies to feed in these laboratory experiments, and that could be the explanation of the divergent results.

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