Impact of egg predation by *Noctiluca miliaris* on the summer development of copepod populations in the southern North Sea

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ABSTRACT· Development of zooplankton in summer and mechanisms that control population dynamics of copepods were studied in the Dutch coastal area of the North Sea with particular attention to the significance of predation as a regulating factor. Among predators the zooflagellate *Noctiluca miliaris*, which is known to feed on copepod eggs, played a major role. During *Noctiluca* blooms in July often high percentages (up to 75 %) of the total number of copepod eggs in the water column were found in this predator's cells. However, the eggs appeared to be digested very slowly and, as a consequence, quantitative estimates of predation pressure by *N. miliaris* (based on abundance, number of ingested copepod eggs per cell and digestion time) came out lower than expected. The importance of this predation was judged by comparing it to daily copepod egg production. The maximum percentage of eggs cleared by *N. miliaris* before hatching was estimated at 50 %. Although the impact of *N. miliaris* predation on the recruitment of nauplii may thus be considerable, large fluctuations in natural egg densities are not likely to be caused by this predation, but may be attributable to changes in individual copepod egg production. Our data suggest that, during deteriorating food conditions in summer, egg production can fall by a factor of at least 7 to 10 and that therefore food should be considered a key factor regulating nauplii recruitment.

INTRODUCTION

The zooflagellate *Noctiluca* is a known predator of copepod eggs. Kimor (1979) reported on the effects of its predation on the density of *Acartia tonsa* eggs off the coast of Southern California, and during a *Noctiluca* bloom found about 50 % of the eggs of this copepod ingested by cells of *N. miliaris*. Sekiguchi & Kato (1976) deduced from their observations in Ise Bay, central Japan, that a *Noctiluca* outburst in May consumed at least 74 % of the eggs produced by *A. clausi*.

Densities of *Noctiluca miliaris* in the North Sea culminate in summer. Over a 14 yr period of continuous monitoring in the German Bight, Uhlig & Sahling (1982) found consistent annual peaks of abundance (on average 200 to 300 cells l^{-1}) in July, with little variation in timing. This mass occurrence in summer has given support to the hypothesis that *N. miliaris* predation on copepod eggs could be of crucial importance to copepod population dynamics in the North Sea.

In the southern North Sea, particularly in the coastal zone, copepod populations show a dramatic decline in June or July (Fransz et al. 1978, Fransz & Gieskes 1984). This phenomenon is not unique to this area. It has also been observed in other coastal waters in temperate regions, e.g. the English Channel (Digby 1950), Narragansett Bay, USA (Hulsizer 1976) and Saanich Inlet near Vancouver, Canada (Huntley & Hobson 1978). In this context the fundamental question was raised, what factors are responsible for the limitation of copepod densities and, in particular, whether predation could play a predominant role. With a view to verifying that this copepod development is not occasional but a periodic annual occurrence, a sampling program was carried out in 1983 in the Texelstroom, the westernmost inlet of the Dutch Wadden Sea. The breakdown of copepod populations was observed as expected and appeared to be preceded by a strong decline in nauplii. From this observation it was deduced that copepod densities are largely regulated by the nauplius stage or by nauplii recruitment. A failing recruitment of nauplii could in turn be due to increased egg predation or to decreased egg production by adult copepod females, which possibly experi-

ence serious food shortage in July (Daro & van Gijsegem 1984).

In the following 2 summers the population developments of copepods, distinguished into different stages from egg to adult, in Dutch coastal waters were recorded in detail. Simultaneously, the numbers of *Noctiluca miliaris* cells and copepod eggs ingested by these were counted. These observations were complemented by experiments on egg predation by *N. miliaris* and on egg production by adult copepods.

The present paper deals with the influence of egg predation by *Noctiluca miliaris* on the recruitment of nauplii. The importance of this predation is evaluated by comparing it to changing daily egg production by the adult copepod standing stock in the southern North Sea.

METHODS

Zooplankton sampling took place from the 'Meetpost Noordwijk' measuring platform situated 13 km off the Dutch coast at Noordwijk, in a water depth of 18 m. Vertical net hauls (opening 32 cm, mesh 50 μm) to a depth of 15 to 18 m were made from the platform at the turn of the tide, so that the weighted net could sink almost vertically to the bottom. Samples were taken twice a day in 1984 and once a day in 1985, except weekends. Volumes filtered ranged between 1.2 and 2.4 m^3. Directly after sampling, a subsample was placed under a projection microscope. In this subsample the quantities of free eggs, *Noctiluca miliaris* cells and eggs ingested by *N. miliaris* were counted. It is important to note that only intact eggs (undamaged and without loss of colour) were enumerated. Under a dissection microscope another subsample was used for counting adult copepods. As a rule males and females were not counted separately, since random checks did not reveal significant deviations from a 1:1 sex ratio.

Temperature was measured with a reversing thermometer, which was lowered to about 8 m depth in the well-mixed water column (a summer thermocline is absent in this area).

In order to carry out experiments on digestion time fresh *Noctiluca miliaris* were collected with a 150 l water-sampler. Preliminary tests were made with individual cells containing at least one copepod egg. They were put in small beakers (30 ml) and inspected from time to time under a dissection microscope till digestion yielded visible effects on colour or shape of the eggs. Since handling sometimes disturbed the experimental flagellates (e.g. they ejected eggs prematurely), the following statistical method was preferred. The contents of the sampler were transferred through a tube directly into the test jar (Fig. 1) – a polyethylene tank (40 × 30 × 25 cm) with a bottom of 200 μm

plankton gauze – which itself was placed in a larger tank. From the water sample, *N. miliaris* cells, including those which had eaten copepod eggs in the natural situation, were thus concentrated, whereas the copepod eggs (diam. ca 80 μm) fell through the 200 μm gauze, out of reach of the *N. miliaris*. From the test jar samples of about 200 *N. miliaris* were repeatedly taken for analysis of cell contents. Temperature during the experiments was kept within 2 C° of the outside water temperature.

In 1985, copepod egg production experiments were carried out once a week. The experiments were done with freshly caught *Temora longicornis*, *Acartia clausi* and *Centropages hamatus*. In each experiment 20 adult females were kept for 24 h in 5 l buckets filled with 50 μm filtered seawater and kept at *in situ* tem-
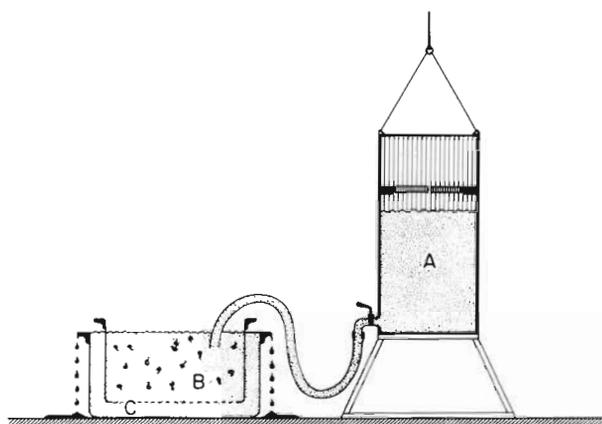

Fig. 1. Schematic drawing of the method used to concentrate *Noctiluca miliaris* cells for determination of digestion time. A: water-sampler; B: inner (test) tank; C: outer tank. For explanation see text
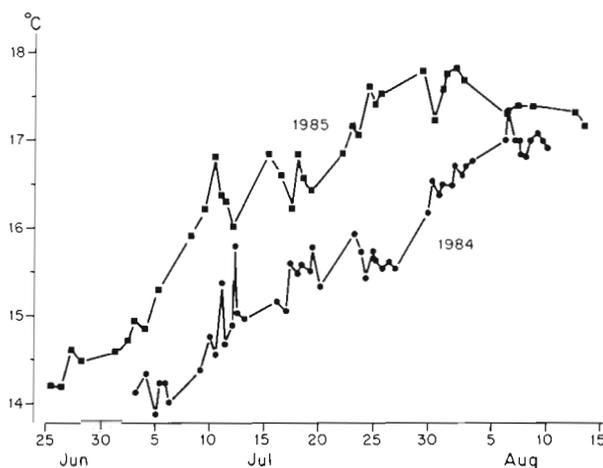

Fig. 2. Sea water temperature at 'Meetpost Noordwijk' in 1984 and 1985

perature. The contents of the buckets were then sieved over 50 μm gauze. After checking the number of females, the eggs produced were counted under a projection microscope.

Similar experiments were carried out to estimate the development rate of the eggs. In these experiments egg production was stopped after 24 h by sieving out the copepods over 300 μm gauze. The eggs were then incubated once more for 24 h allowing a fraction of them to hatch. The total of eggs and Nauplii I after 48 h then represented 24 h egg production, while the frac-

tion of nauplii hatched gave an estimate of egg development time.

RESULTS

Temperature

The seasonal trends of subsurface temperatures in both years (given in Fig. 2) show that the July water temperature was significantly higher (1.5 C°) in 1985 than in 1984.
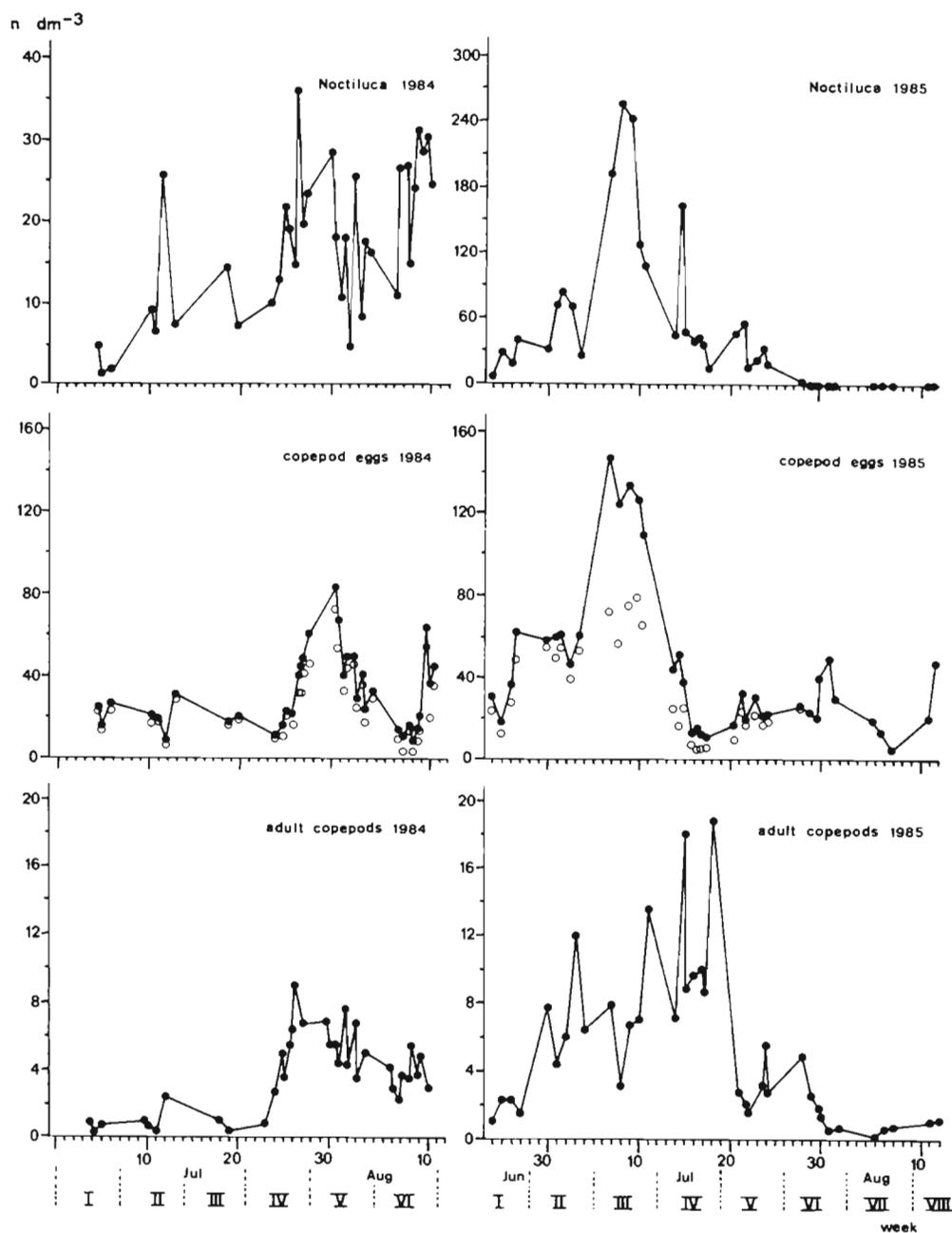

Fig. 3. Densities of *Noctiluca miliaris* and eggs and adults of *Temora longicornis*, *Acartia clausi* and *Centropages hamatus* in 1984 and 1985. Densities for eggs: (●) total numbers; (○) numbers of free eggs

Population developments

Noctiluca miliaris densities in the summers of 1984 and 1985 together with those of copepod eggs and adult copepods are given in Fig. 3. There was a distinct difference between the 2 yr. In 1984, the population of *N. miliaris* grew steadily until the end of the sampling period. In 1985, there was a marked peak in the first 10 d of July, after which the population dwindled and disappeared before the end of July. Maximum density was by far higher in 1985 (note the scale difference).

In broad terms the wax and wane of *Noctiluca miliaris* seems to coincide with the trend in densities of copepod eggs. The graphs in Fig. 3 represent eggs and adults of *Temora longicornis*, *Acartia clausi* and *Centropages hamatus*. These species together always contributed more than 75 % of the total copepod standing stock. *Pseudocalanus* was not considered, because this genus carries its eggs adhering to the urosome, thus withdrawing them from *N. miliaris* predation (Sekiguchi & Kato 1976). In Fig. 3, numbers of free eggs and total numbers, i.e. free eggs plus those ingested by *N. miliaris*, are both represented. Though the trends in egg densities are rather different in the 2 yr, there is in both cases a peak followed by a strong decline, which cannot be attributed to a decline in the numbers of egg-producing adults.

Maximum egg density in 1985 was about twice as high as in 1984. This difference is in accordance with the difference in adult densities in both years. How-

ever, the maximal concentrations of free eggs in 1985 hardly exceeded those of 1984, because during the 1985 peak about 50 % of the total number of eggs present had been ingested by *N. miliaris*.

Numbers of copepod eggs found in a single *Noctiluca miliaris* cell were generally low, although sometimes surprisingly high values were found, as shown in Table 1: one cell had ingested 27 spiny eggs of *Centropages hamatus*! Fig. 4 gives weekly means of eggs ingested per cell. On average the cells contained more eggs in 1984 (0.36 eggs cell^{-1}; 2561 cells inspected) than in 1985 (0.23 eggs cell^{-1}; 3269 cells inspected).

Digestion time

Actual predation by *Noctiluca miliaris* can be estimated from mean cell contents and digestion time. Fig. 5 shows the results of 6 digestion experiments. Five experiments were carried out according to the statistical method, in which numbers of ingested eggs at each control were determined in 100 to 300 *N. miliaris* cells; one line represents the decrease of undigested eggs in 15 individual cells. The figure shows percentual decrease of the number of ingested eggs per cell during the experiments, in which cell contents at the beginning of incubation were regarded as 100 %. If it is assumed that the eggs present as cell content at the start of the experiment had been ingested at random during the preceding time, a linear decrease would be expected. Although the results do not permit an accurate estimate of digestion time, they do provide rough limits of the time range within which digestion must occur. Since halving of the number of ingested eggs took at least 15 h at ambient temperatures, 30 h may be considered to represent a lower limit; likewise 80 h can be accepted as an upper limit.

Egg production

Egg production by adult copepod females was experimentally determined during 6 wk in 1985. Results are given in Table 2. Values for *Acartia clausi* and *Centropages hamatus* are combined, because mixtures
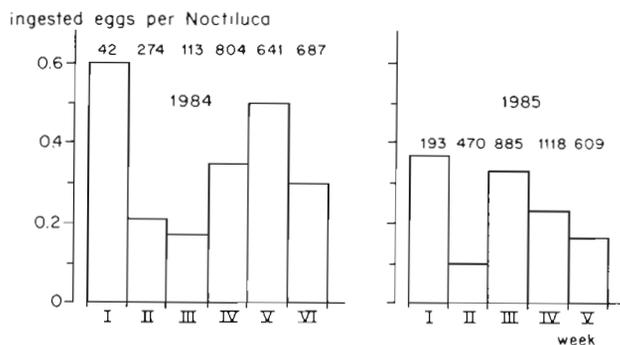

Fig. 4. Weekly determined mean cell contents (number of ingested eggs per *Noctiluca miliaris* cell) in 1984 and 1985. (Numbers of cells inspected are given above bars)

Table 1. Frequency of occurrence of copepod eggs in cells of *Noctiluca miliaris* in 1984 and 1985

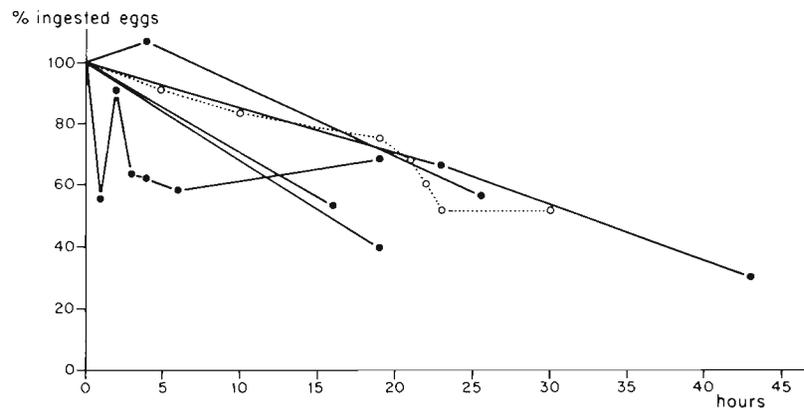| Year	No. of cells inspected	No. of ingested eggs per cell														
		0	1	2	3	4	5	6	7	8	9	10	11	12...	17 ..	27
1984	2561	1906	500	104	29	12	4	2	1	1	1	0	0	1	0	0
1985	3269	2717	452	63	19	7	4	1	1	1	1	0	1	0	1	1

% ingested eggs

Fig. 5. Percentage decrease of ingested eggs per *Noctiluca miliaris* cell. The intersection of a line with the time axis should denote digestion time. (O····O) observations of individual cells; (●——●) statistical experiments

Table 2. Numbers of eggs produced in 24 h by individual females of the commonest copepods (1985)

Week	*Temora longicornis*	*Centropages hamatus* & *Acartia clausi*	Mean egg production per adult female copepod *in situ*
II	9.0	37.3	14.3
III	18.5	42.5	26.1
IV	2.8	2.2	2.5
V	1.0	3.8	3.4
VI	4.6	16.0	15.8
VII	2.3	1.0	1.7

of adult females of both species were used in some experiments.

Cannibalistic feeding on eggs during the experiments was assumed to be negligible. Microscopic observation of *Temora longicornis* females offered eggs and nauplii showed that nauplii were taken readily, whereas eggs were never ingested (Gonzalez pers. comm.). A remarkable decrease in individual egg production in all species was observed between Weeks III and IV. Total daily egg production per litre in the natural situation was estimated from mean densities of adult females of the 3 different species and their individual experimental egg production rates. In order to compare these production estimates with actual mean egg concentrations, both are given in Fig. 6. Since development time of eggs is more than 1 d (see next paragraph), actual densities should be higher than daily productions. The very similar trends shown by both curves support the usefulness of experimental egg production data.

Egg development rate

The availability of eggs to *Noctiluca miliaris* predation is determined by egg production rates and hatch-

ing time. Hatching time was estimated on the assumption that eggs were continuously produced during 24 h. This assumption is justified by previous studies finding no diurnal periodicity in egg production (Dagg 1978, Parrish & Wilson 1978, Uye 1981). We also assumed that 100 % of the eggs produced were viable and not damaged during sieving or in any other way impaired in their development. Therefore, experimental estimates of development time are maximum estimates. Results of the method (Table 3) are well within the range of data given in the literature. According to Corkett & McLaren (1970) development time of eggs of *Temora longicornis* is 42.5 h at 15 °C and 35 h at 17.5 °C. Landry (1975) found in *Acartia clausi* 45 h at 15° C and 37 h at 17.5 °C. Uye & Fleminger (1976), reporting on the same species, gave 1.5 to 2 d at temperatures between 15 and 17.5 °C.
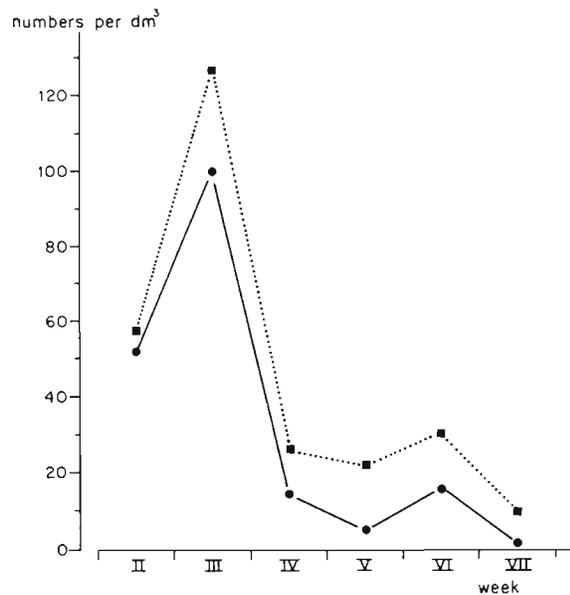
numbers per dm³

Fig. 6. Computed daily egg production per dm³ by copepods in the field during Week II to VII (●——●) and weekly means of actual egg densities (■····■) in the same period (1985)

Table 3. Results of experiment on development time of copepod eggs in 4 consecutive weeks in 1985

| Week | Species | n | Temperature (°C) | | Eggs produced in 24 h | Hatched after 48 h | Development time |
			Experiments	In situ			
IV	Temora longicornis	20	16.1 (15.5–16.5)	16.2–16.8	57	7	45 h
	Acartia clausi/ Centropages hamatus	20			43	6	45 h
V	Temora longicornis	20	16.5 (16.0–17.6)	17.0–17.6	20	7	40 h
	Acartia clausi/ Centropages hamatus	37			142	96	32 h
VI	Temora longicornis	50	17.0 (16.5–17.5)	17.2–17.8	234	80	40 h
	Acartia clausi/ Centropages hamatus	40			640	276	38 h
VII	Temora longicornis	40	17.5 (17.2–18.0)	17.2–17.4	95	72	30 h
	Acartia clausi/ Centropages hamatus	20			(20)	?	?

Quantitative estimation of egg predation by *Noctiluca miliaris*

A simple model is presented which provides an estimate of the survival rate of copepod eggs with *Noctiluca miliaris* as the only predator. It is based on the ratio of instantaneous densities of free and ingested eggs. Variables in this model are listed in Table 4.

If p and m are constant, the age distribution of free and ingested eggs has the general shape given in Fig. 7. If so, the next equations are valid:

$$D_{free} = \int_{-T_d}^{0} p\, e^{mt}\, dt = \frac{p\,(1 - e^{-m\,T_d})}{m} \qquad (1)$$

and

$$N_{ing} = T_i \times (p - p\, e^{-m\,T_d}) = T_i\, p\, (1 - e^{-m\,T_d}) \qquad (2)$$

From Eqns (1) and (2) can be deduced that:

$$m = \frac{1}{T_i} \frac{N_{ing}}{D_{free}} \qquad (3)$$

The survival rate now can be computed as:

$$s = \frac{p\, e^{-m\,T_d}}{p} = e^{-m\,T_d} \times 100\,\% \qquad (4)$$

When T_i and T_d are known, s can be estimated from Eqns (3) and (4). As discussed above T_d values are approximately 45 h at 15 °C and 35 h at 17.5 °C; T_d values at ambient temperatures found by linear interpolation between those values are regarded as estimates lying within 5 h from the actual T_d. Estimation of T_i is more difficult, but 48 h seems a plausible

intermediate between 30 and 80 h as lower and upper limits. Table 5 was composed using these values. During the third and fourth week of 1985 only 44 and 54 % of the eggs respectively survived the *Noctiluca* bloom. Although *N. miliaris* thus considerably diminished the number of eggs that could develop into nauplii, a dramatic decline in nauplii recruitment was not likely to be expected, since densities of adults increased to a maximum level precisely during these crucial weeks. If egg production by individual females had remained constant, an even higher recruitment would have been possible.

Table 2 shows a strong decrease in individual egg production between Weeks III and IV in 1985. There is another way to obtain an estimate of individual egg production. This method is, like the computation of m, based on field densities. After calculation of m according to Eqn (3) and substitution of m in Eqn (1), one can

Table 4. Variables used in egg-predation model

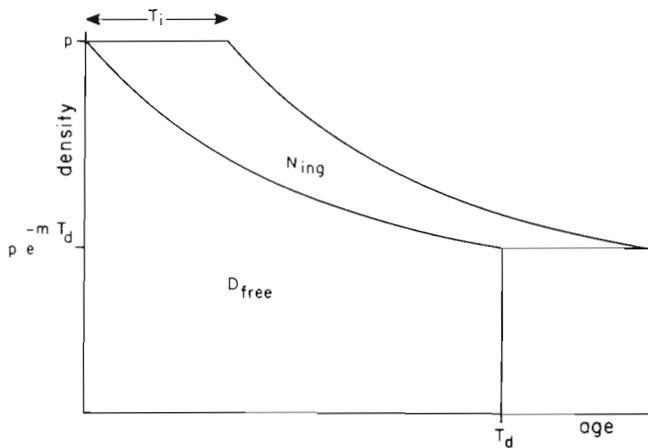| Symbol	Definition
D_{free}	Density of free eggs (n dm^{-3})
N_{ing}	Number of ingested eggs (n dm^{-3})
p	Recruitment rate of eggs (n dm^{-3} h^{-1})
m	Mortality rate of eggs due to *Noctiluca miliaris* predation (h^{-1})
T_d	Development time of eggs (h)
T_i	Digestion time of eggs ingested by *Noctiluca miliaris* (h)
s	Survival rate of eggs (%)

Fig. 7. Theoretical age distribution of free eggs and eggs ingested by *Noctiluca miliaris* (for explanation of symbols see Table 4)

compute p. An estimate of daily egg production per adult female (P_{adf}) is now given by:

$$P_{adf} = \frac{24 \times p}{D_{adf}} \tag{5}$$

where D_{adf} = density of adult females.

Egg production rates determined in this way are given for both years in the last column of Table 5. A remarkable decrease in individual egg production was seen in Week IV of 1984, i.e. after 20 July; nevertheless, an increase of total egg production was possible, since adult population densities were increasing. This is in accordance with observed densities of eggs (Fig. 3). An even more dramatic decrease in individual egg

production took place in Week IV of 1985, this time after 12 July. The trend in egg production from Week II to VII as estimated from field densities was the same as determined experimentally (cf. Table 2). The fall in individual egg production in 1985 was so drastic that even a high density of adults (5.79 adult females l^{-1}) could not prevent a steep decline in egg density (Fig. 3).

DISCUSSION

The changes in population densities as observed at the sampling station do not strictly reflect real developments *in situ*. Tidal currents transport different watermasses past the measuring platform. As a consequence, systematic differences were sometimes observed between HW and LW samples. This may explain part of the sometimes strong short-time fluctuations (e.g. Week V in 1984, Fig. 3).

In general, the watermasses passing the platform move northward along the Dutch coast. According to Veley (1960) and Kautsky (1973) the average residual current velocity in this direction may be roughly estimated at 2 to 5 km d^{-1}, but it is subject to high variability due to meteorological conditions, by which daily residual currents can sometimes amount to 9 km, become zero, or even turn southward. Due to temporal differences between developments of plankton densities in different watermasses, the observed pattern of changing densities may have been biassed by water movements. However, each sample itself represents instantaneous absolute and proportional densities of different planktonic organisms and life

Table 5. Computed survival rates (s) of copepod eggs during *Noctiluca miliaris* blooms in 1984 and 1985, and an estimate of *in situ* egg production by individual copepod females, based on field densities. Lower limits for the range of s are computed at $T_i = 30$ h and $T_d + 5$ h, upper limits at $T_i = 80$ h and $T_d - 5$ h. (See Table 4 for definitions)

Week	N_{ing} (n dm^{-3})	D_{free} (n dm^{-3})	Density of adult females (n dm^{-3})	s at $T_i = 48$ h	Range of s	Estimated daily egg production per adult female
1984						
I	1.5	20.3	0.79	93	88–96	13.0
II	1.4	18.8	0.79	93	88–96	13.6
III	1.8	19.5	0.55	92	86–96	20.5
IV	6.3	26.6	2.40	81	69–89	6.8
V	8.5	39.8	2.77	84	73–91	9.5
VI	7.2	18.1	1.86	74	57–85	7.3
1985						
I	9.3	28.5	0.90	73	57–84	18.9
II	6.0	50.6	3.65	90	82–94	8.0
III	62.7	64.3	3.83	44	23–65	14.7
IV	11.5	15.0	5.79	54	32–72	2.1
V	5.6	18.0	1.51	79	65–89	8.9
VI to VIII No *Noctiluca miliaris* predation						

stages, which may be expected to occur in other passing watermasses also, even though temporal differences do occur. Still there is no reason to expect that in broad terms the observed densities were not representative for this coastal area of the North Sea.

The density curve of *Noctiluca miliaris* as found in 1985 resembles very closely the curves described by Uhlig & Sahling (1982) in the German Bight. Maximum abundance agreed closely with their 'average maximum'. In this respect, the development observed in 1984 may be considered an aberrant one. Possibly the low seawater temperatures in July 1984 (mean 15.1 °C) tempered the *Noctiluca* outburst. Mean temperature in July 1985 (16.5 °C) was in the range of average temperatures (16.0 to 16.5 °C) for this area and time of year (Höhn 1973). In 1984, the decrease in egg densities was observed 3 wk later than in 1985. In both years this decrease took place when the water temperature had risen to about 16.5 °.

In 1984, the percentage of total number of eggs ingested by *Noctiluca miliaris* was particularly high in the last week of the sampling period, immediately after the decline of egg numbers. In one sample over 75 % of the eggs were found in *N. miliaris* cells. Nonetheless, an increase in density of free eggs could be observed during this week. In 1985, the highest percentages of ingested eggs were found in Weeks III and IV. Again in one sample over 75 % was ingested. It must be emphasized that *N. miliaris* predation was most harmful in Week IV when recruitment of nauplii had already declined due to low egg concentrations. Kimor (1979), who reported on *N. miliaris* predation on *Acartia tonsa* eggs off the coast of California, found at much lower *N. miliaris* densities (maximally 13 dm^{-3}) that comparable percentages of eggs had been ingested. However, his quantitative data on free eggs may be underestimates, since he used 73 µm mesh nets, which may not have retained all the 75 to 80 µm size eggs of *A. tonsa*.

A reliable estimate of digestion rate for eggs in *Noctiluca miliaris* has not yet been possible. Therefore, it is still difficult to quantify predation exactly. Nevertheless, it has become obvious that digestion takes considerably more than 1 d, which means that numbers of ingested eggs cannot be directly converted into daily egg predation and compared to egg production, as Sekiguchi & Kato (1976) did. If digestion time is estimated at 2 d, which seems a more realistic assumption (Uye 1982), their estimate of predation would be halved. Moreover, in their paper they did not discern between intact and more or less digested eggs. Kimor (1979) also did not mention whether or not partly digested eggs, which can be seen on his photographs, were included in his counts. It they were, one should take into account an even longer digestion time than

2 d for such egg counts and, as a consequence, lower predation pressure.

The experiments performed in 1985 revealed a steep decline in individual egg production by copepods between Weeks III and IV. Although these experiments were conducted in seawater filtered through a 50 µm screen, so that larger algae were removed, the rates of egg production in Weeks II and III correspond with rates found under optimal food conditions (*Temora longicornis:* Harris & Paffenhöfer 1976; *Acartia tonsa:* Parrish & Wilson 1978, Durbin et al. 1983; *A. clausi:* Sekiguchi et al. 1980; *Centropages typicus:* Dagg 1978). The extremely low values for egg production in the following weeks suggest that food had become limiting for adult copepods. This experimentally observed tendency was confirmed by the estimates of production rates derived from field densities (Table 5), and by the observed field densities themselves (Fig. 6).

Predation pressure on copepod eggs by *Noctiluca miliaris* has been expressed in terms of its effect on the survival rate of these eggs. In fact, we should consider this survival rate as the *potential* daily recruitment of nauplii after normal hatching time in relation to daily egg production, when other factors affecting this recruitment, such as other predators or possible production of dormant eggs, are left out of consideration. Among remaining pelagic egg predators the Hydromedusa *Phialidium haemisphaericum* was found to be the only serious competitor. However, the daily consumption of this species never exceeded 20 % of the maximum number of eggs taken by the *N. miliaris* population. A factor still unknown is the loss of eggs which sink to the bottom, where they possibly suffer high mortality due to consumption by benthic fauna.

The severest predation was exerted by *Noctiluca miliaris* in 1985 during the third and fourth week of observation. A strong decline of egg densities was observed in the same period, which could suggest a causal correlation. However, from Table 5 one can see that, based on individual egg production and density of adult copepod females, in Week III $3.83 \times 14.7 = 56.3$ eggs dm^{-3} d^{-1} were produced, and, if 44 % of this production escaped *N. miliaris* predation, potential recruitment would amount to 25 nauplii dm^{-3} d^{-1}. At the same individual egg production and maximum predation pressure, this recruitment in Week IV would have resulted in 38 nauplii d^{-1}, which is higher than any value that can be computed for all other weeks. In other words, *N. miliaris* predation cannot be considered to act as a major regulating mechanism in the recruitment of nauplii. Although for a short time the considerable fraction of over 50 % of the eggs is lost by this predation, this effect on potential recruitment is small compared to the effect of changes in individual

egg production by adult females. These changes are apparently mainly responsible for the large fluctuations observed in egg densities and recruitment of nauplii respectively.

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