

Cannibalism in omnivorous calanoid copepods

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ABSTRACT: During a study on population dynamics of copepods in the southern North Sea some semi-in-situ experiments were performed on predation by adult copepods on co-occurring nauplii. In a period with a strong decline in naupliar abundance, experimental naupliar mortality by cannibalism amounted to 35% of the standing stock per day. Simultaneous observations on chlorophyll *a* and diatom concentrations in situ and on egg production by adult females suggested poor food conditions for adults. There appeared to be a tendency for increased predatory behaviour in the absence of other food, indicating the possible importance of cannibalism as a factor in naupliar mortality. Microscopic observations and a series of experiments on laboratory cultured *Temora longicornis* revealed adult female predation on stages N I through N V. Rates of capture declined with ascending developmental prey stage. Prey-specific predation rates increased continuously with prey density, but were significantly depressed in the presence of alternative algal food. Estimates of naupliar mortality in situ due only to cannibalism, based on experimentally determined predation rates, explained 5 to over 100% of the estimated total naupliar mortality. It is suggested that cannibalism may act as a major factor in naupliar mortality and may contribute significantly to a rapid fall in naupliar densities in periods of algal food shortage.

INTRODUCTION

In descriptions of the structure and function of marine planktonic communities, calanoid copepods have often been divided into herbivores and carnivores. However, this concept has been challenged, particularly with respect to the existence of true herbivores (e.g. Paffenhöfer & Knowles 1980). Studies on the feeding of calanoid copepods, which traditionally were called 'herbivores' and were considered as the main secondary producers in marine pelagic food chains (e.g. Steele 1974), have shown that all common genera include omnivorous species. In addition to algae, their diet includes heterotrophic flagellates and ciliates (e.g. Klein Breteler 1980), but also crustacean larvae, mainly nauplii of copepods belonging to the same order. Predation on nauplii by adult omnivores, both inter- and intraspecific, has been established in several neritic genera, like *Acartia* (Heinle 1970, Landry 1978a, Lonsdale et al. 1979, Uye 1982), *Temora* and *Centropages* (Paffenhöfer & Knowles 1980, Conley & Turner 1985) and *Sulcanus* (Hodgkin & Ripplingale 1971), but also in the oceanic genus *Calanus* (Landry 1981).

Although omnivorous feeding in marine copepods has long been known (Lebour 1922), the role of canni-

balism (in the context of this paper referring to both inter- and intraspecific predation in copepods) became a subject of interest from a population dynamic point of view only during the past 2 decades. Heinle (1970), who found 20 to 60% mortality per day in the first 9 stages in laboratory cultures of *Acartia tonsa*, suggested 'cannibalism to act as a mechanism for regulating populations when (alternative) food is scarce and densities of populations are high'. Gabriel (1985) concluded on the basis of a demographic model on cyclopoid copepods that cannibalism could prevent extinction of populations in periods of food limitation.

In the Southern Bight of the North Sea, where neritic copepod species are predominant, copepod populations increase during spring, reaching maximum densities in early summer. In June or July a decline in population abundance is often observed (see Fransz et al. 1978, Bossicart 1980, Fransz & van Arkel 1983), announced initially by a strong decrease in naupliar densities. The decrease may, at least partly, be explained by a diminished recruitment of nauplii in this period, primarily due to low egg production by adults and, secondarily, to flourishing of egg predators (Daan 1987). However, the question remains to what extent naupliar mortality contributes to this break in the production of new generations. A possible cause of

enhanced naupliar mortality might be found in a higher predation pressure exerted by adult copepods: since shortage of algal food for adult copepods is likely to occur in summer in the North Sea (Klein Breteler et al. 1982, Daro & van Gijsegem 1984, Klein Breteler & Gonzalez 1986, Daan 1987), a switch to cannibalism as an alternative foraging strategy (see Landry 1981) is conceivable.

During a frequent sampling program, carried out in the southern North Sea in the summer of 1985, we conducted semi-in-situ experiments over 6 consecutive weeks to find evidence for cannibalism among natural copepod populations and, possibly, a link with algal food shortage. In addition a series of laboratory experiments was performed on *Temora longicornis*, to determine which stages are exposed to predation by adults, how prey density and presence of alternative algal food affect cannibalistic feeding, and, finally, to obtain an estimate of naupliar mortality by cannibalism in situ. In the present paper the experimental results are discussed with special reference to the significance of cannibalism in copepod population dynamics.

METHODS

Field observations. Field studies on the population development in copepods were made at the measuring platform 'Meetpost Noordwijk', situated 7 miles off the Dutch coast at Noordwijk (water depth 18 m). In this area *Temora longicornis* (Müller), *Acartia clausi* Giesbrecht, *Centropages hamatus* (Lilljeborg) and *Pseudocalanus elongatus* (Boeck) are the dominant species. Densities of 'typical' carnivorous copepods are negligible.

In situ zooplankton composition and density were recorded by quantitative sampling with a vertical 50 µm mesh net (Daan 1987). Subsamples, containing at least 50 nauplii and 50 adult copepods, were taken for microscopic determination and enumeration. In the period 15 to 23 July, however, naupliar abundance appeared too low to count more than about 25 specimens in even relatively large subsamples.

Chlorophyll *a* concentrations were determined (according to the method described by Lorenzen 1967) from watersamples (1 l) taken at 10 m water depth, to obtain a rough measure of algal food conditions.

To reduce the risk of sampling different populations at the permanent station, samples taken during each week were collected at the same high or low tide, alternating the next week. For the same reason our conclusions on mortality and relations with chlorophyll concentrations and adult abundance are based on estimates obtained from samples collected within the short period of less than 1 wk, leaving space to long-

term changes in population densities due to weather conditions and tidal and residual currents.

Field experiments. For field experiments on cannibalism zooplankton was collected at 10 m depth with a 150 l water sampler. Separate size fractions were obtained, each in its natural density, by filtering 50 l of the catch through a column of sieves with mesh sizes of successively 1000, 400, 200, 100 and 50 µm. The column was placed in a jar filled with sea water, to keep the animals immersed in the water, and to prevent them from injuries during sieving. The fractions retained on the 400, 100 and 50 µm sieves were liberated into barrels, each filled with the original volume of 50 l of 50 µm filtered sea water. The 400 to 1000 µm fraction contained the adult copepods and sometimes a few C IV and C V stages, while pelagic predators like fish larvae and Hydromedusae had been removed by the 1000 µm sieve. The 100 to 200 µm fraction appeared to contain copepod eggs and all naupliar stages, whereas in the 50 to 100 µm fraction only eggs, N I and N II were present. Control of the 200 to 400 µm fraction (not used in these experiments) revealed that herein the subadult copepodite stages predominated and that nauplii and adults were almost absent.

After careful stirring, from each of the barrels holding the 50 to 100 µm and the 100 to 200 µm fraction, 2 containers (5 l) were filled. One served as a control, whereas to the other a natural number of adults (obtained by a 5 l aliquot from the 400 to 1000 µm barrel) was added. Subsequently, from each of the barrels holding the naupliar fractions a 5 l sample was taken, to determine prey concentrations at the start of the experiment. The control and experimental containers were incubated for 24 h at ambient sea water temperature, after which nauplii and adults were counted. In this way cannibalistic predation by adults could be derived from the difference in naupliar numbers between control and experimental container. However, the experiments were only suitable to detect predation on nauplii of *Temora longicornis*, *Acartia clausi* and *Centropages hamatus*. Predation on nauplii of *Pseudocalanus elongatus* had to be left out of consideration, since adult females of this species carry eggs, in all developmental stages, along in egg sacs, thus potentially introducing new offspring in the experimental containers. In the other species freshly spawned eggs do not hatch within the experimental period of 24 h. The experiments were performed weekly from 25 June to 30 July.

Laboratory experiments. Intraspecific predation by adult copepods on nauplii was determined in the laboratory both in the presence and in the absence of alternative (algal) food. For that purpose laboratory cultured *Temora longicornis* (adults and nauplii) were used (see Klein Breteler 1980). To minimize effects of

variance in individual consumption due to age differences, only cultures were used in which a cohort of copepods had moulted from C V to C VI no more than 2 wk before. The copepods were anaesthetized with MS 222 to select adult females of equal size. For each experiment 5 females were put in a beaker filled with 250 ml of 2 μm -filtered sea water or with water from the copepod culture, containing a mixture of *Rhodomonas* sp. (7 μm mean spherical diameter), *Isochrysis galbana* (5 μm) and the heterotrophic dinoflagellate *Oxyrrhis marina* (13 μm) in optimum concentrations (about 460 $\mu\text{g C l}^{-1}$, see Klein Breteler & Gonzalez 1986). The experiments were started by adding 5, 11, 21, 42, 63 or 84 nauplii of a single developmental stage to the beakers, which were kept at 15°C under dimmed light conditions during 24 \pm 2 h. After recovering with a 50 μm sieve, number and condition of the adults was checked, nauplii were counted, and their stage was determined again to check for development during the experiments. Of all 130 experiments only in 1 case was an adult female missed; this indicates that losses due to handling procedure were negligible and, hence, that probably any loss in nauplii could be attributed to predation by adults. Dead nauplii with marks of damage were considered to be eaten. In the bottles with alternative food, the concentrations of *O. marina* cells were determined at the beginning and at the end of the experiments: pronounced changes in cell concentration did not occur.

Predation was calculated as the number of nauplii disappeared: 110 experiments were performed with N I, II or III, and 20 with N IV, V or VI. For statistical analysis of predation rates at different prey concentrations, the *initial* prey concentration was used as the independent variable (Marin et al. 1986). Clearance rates were calculated according to the commonly used formula:

$$F = \frac{(\ln n_0 - \ln n_t) \cdot V}{P \cdot t} \quad (1)$$

where F = clearance rate (l cop $^{-1}$ d $^{-1}$); n_0 = initial number of prey; n_t = final number of prey; V = experimental volume (l); P = number of adult copepods; t = duration of experiment (d). For 2 experiments, in which all nauplii were found to be consumed, we arbitrarily awarded n_1 a value of 0.1 to keep the equation resolvable. In 5 experiments (4 without and 1 with alternative food) one of the adult females died during the experiments. In these cases predation was completely attributed to the 4 surviving copepods.

Estimation of total naupliar mortality in situ. To evaluate the impact of cannibalism on naupliar survival, an estimate of in-situ naupliar mortality is required. Since stage-specific densities of nauplii were not determined in the field we are confined to estimates of mean mortality in the total naupliar stock.

The calculations are based on the principle that mortality may be estimated from an instantaneous density (D) of a stage, when recruitment rate (r) to the stage and development time (T) of the stage are known, and that mortality theoretically induces an exponentially declining curve in the age distribution of individuals within the stage. In a stable situation the instantaneous mortality coefficient (m) of the stage is then related to D , r and T (r and m constant) according to:

$$D = r \frac{(1 - e^{-mT})}{m} \quad (2)$$

(see Taylor & Slatkin 1981).

To calculate the average instantaneous mortality coefficient of all naupliar stages together (m_N) in this way, estimates are required of D_N , T_N , and r_N . D_N was obtained from field data by taking weekly means of observed naupliar densities. The duration (T_N) of total naupliar development at ambient temperatures (15 to 17.5°C) is about 200 to 240 h in *Temora longicornis* (Klein Breteler & Gonzalez 1986) and approximately 240 h in *Acartia* spp. (Landry 1978b). We used the longer time of 250 h to be careful not to underestimate total mortality and, thus, not to overestimate the importance of cannibalism as a factor in total mortality. Estimates of the recruitment rate (r_N) were derived from data on egg density (D_E), experimental egg production (r_E) and egg development time (T_E), collected in the same period (Daan 1987), and from the instantaneous mortality coefficient (m_E) for eggs, the latter determined by applying Eq. (2) to the egg stage.

Using these data 2 methods were applied for estimation of r_N . In the first method r_N was determined from the surviving fraction (s_E) of the eggs produced (r_E):

$$r_N = s_E \cdot r_E \quad (3)$$

in which

$$s_E = e^{-m_E \cdot T_E} \quad (4)$$

(see Gulland 1969).

The second method provides an estimate of the maximum r_N and consequently leads to a maximum estimate of naupliar mortality at observed naupliar densities. In this method all eggs found are assumed to hatch after normal development time at ambient temperature, so:

$$r_N = D_E \cdot T_E^{-1} \quad (5)$$

The 2 methods of estimating r_N result in 2 different estimates of m_N , which will be referred to as Estimate I of real mortality and Estimate II of maximum mortality. From both estimates of m_N the absolute naupliar mortality M_N , i.e. the number of nauplii dying per liter per 24 h, could be calculated from:

$$M_N = D_N \cdot (1 - e^{-24 \cdot m_N}) \quad (6)$$

RESULTS

Field observations

In the first 3 wk of observations the natural densities of nauplii fluctuated without a clear trend, while adult numbers increased steadily (Fig. 1). However, between 10 and 15 July, remarkably low naupliar densities were

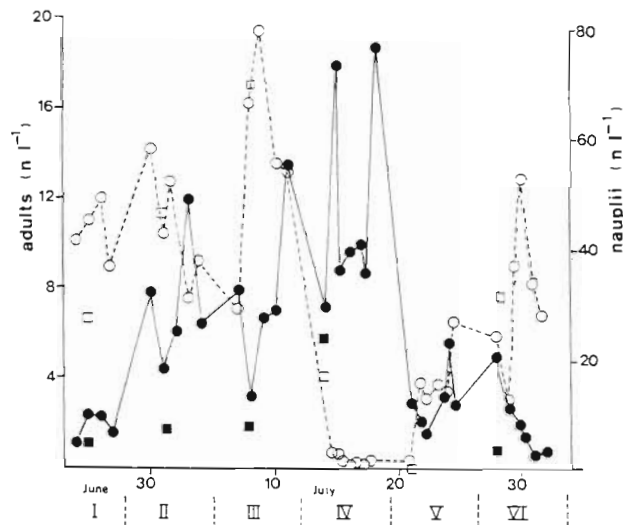


Fig. 1. *Temora longicornis*, *Centropages hamatus*, *Acartia clausi*. Field densities of nauplii (○) and adults (●) in the Southern Bight of the North Sea (July 1985). Squares give concentrations of nauplii (□) and adults (■) in field experiments

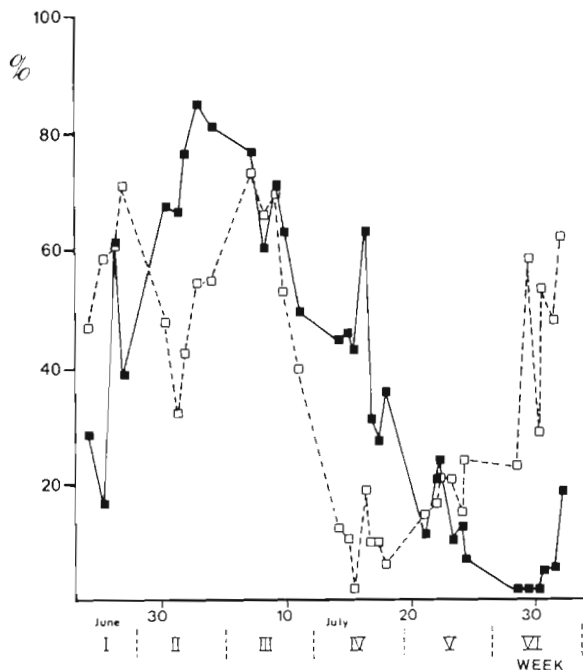


Fig. 2. *Temora longicornis*. Relative abundance in adult (■) and naupliar (□) stocks in the Southern Bight of the North Sea (July 1985)

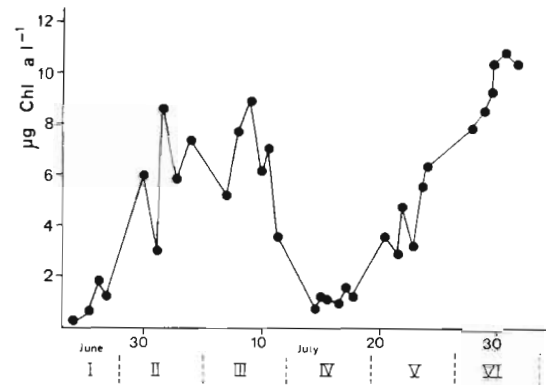


Fig. 3. Chlorophyll a concentrations in the Southern Bight of the North Sea (July 1985)

found. Adults were still abundant then. A decline in adult numbers was observed about 10 d later, coinciding with a partial recover of the stock of nauplii.

Temora longicornis had a considerable share in the copepod stock, contributing up to 80% of the adult populations in Week II (Fig. 2). Thereafter their relative abundance decreased gradually to less than 25% in Weeks V and VI. In the species composition of nauplii *T. longicornis* represented on average 50% of total densities during the first 3 wk. In Weeks IV and V *T. longicornis* nauplii occurred in relatively low numbers (less than 25%), but in Week VI the share of this species in the naupliar stock rose to about 50% again. Because of its numerical abundance compared to the other single copepod species, *T. longicornis* was chosen to test the possible impact of copepod cannibalism in further experiments.

Chlorophyll a concentrations, initially low, amounted to values near $7 \mu\text{g l}^{-1}$ in Weeks II and III and decreased after Week III to values below $2 \mu\text{g l}^{-1}$ (Fig. 3). During Weeks V and VI the concentrations recovered gradually to values even higher than before.

Field experiments

Six experiments on predation on nauplii in each of the 2 size fractions (50 to $100 \mu\text{m}$ and 100 to $200 \mu\text{m}$) have been accomplished: 3 during the period of steady naupliar abundance and 3 during the declining and recovery phase.

Initial naupliar numbers were generally similar to numbers found afterwards in the controls, indicating that mortality due to the sieving procedure played no important role (Table 1). Densities of nauplii in the controls were similar to mean densities measured over the whole water column (Fig. 1). However, adult densities in the experiments were generally lower than mean total column densities, possibly due to accumula-

Table 1 Predation by adult copepods in field experiments; numbers of nauplii at the start of the experiments ($t = 0$) and after 24 h incubation in containers without (controls) and with adult copepods

Week	$t = 0$	Control	Number of adults in experiments									
			1	2	3	4	5	6	7	9	18	25
Fraction 50–100 μm (naupliar stages NI and NII)												
I	92	82				80				53		
II	56	69						58				
III	93	120				99						
IV	23	26									13	
V	(<5)	(<5)										
VI	57	73	65									
Fraction 100–200 μm (naupliar stages NI through N VI)												
I	57	47		66						45		
II	153	150				147						
III	161	196		162								
IV	57	61										12
V	(<5)	(<5)										
VI	84	95				40						

tion of adults in water layers other than the 10 m depth where the copepods were collected.

In 11 of the 12 experiments the final numbers of nauplii in the containers with adults were lower than in the controls (Table 1). Since adult copepods were the only predators in the experiments, the significantly (sign test, $p < 0.05$) lower numbers of nauplii in the experimental containers are attributed to cannibalism.

When the mean predation on both size fractions, as appeared in the above experiments, is expressed as the percentage of the daily naupliar standing stock (Fig. 4),

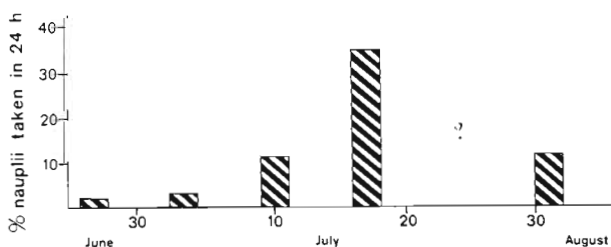


Fig. 4. *Temora longicornis*, *Centropages hamatus*, *Acartia clausi*. Percentage daily mortality in natural nauplii stocks as a result of predation by adults in the Southern Bight of the North Sea in 6 consecutive weeks (July 1985). In the 5th week mortality could not be determined because of too low naupliar densities

less than 5% of the nauplii were eaten during the first 2 wk of the experimental period. However, in the following 2 wk ± 12 and 35%, respectively, and in the last week $\pm 15\%$ of the nauplii were lost in the presence of adults. Although these results do not allow for

reliable quantitative estimates of cannibalism in situ, they indicate the occurrence of cannibalism among natural copepod stocks and support a possible correlation between enhanced cannibalism and shortage of algal food (compare Fig. 3).

Laboratory observations

The occurrence of cannibalism in *Temora longicornis* was affirmed by microscopic observation. In a drop on a slide we saw an adult copepod female generating a water current towards the mouth, in which an added nauplius was carried along, in spite of its attempts to escape, till it neared the feeding appendages and was swallowed within a few seconds. During a 3½ h period of observation one *T. longicornis* female thus caught and devoured 37 N I. Another female took 8 N II in 2 h and a third one 9 N III in 4½ h. Of course such findings cannot lead to any quantitative estimate of cannibalism in the natural situation, since the circumstances would imply a prey density of some 10000 l⁻¹, which is highly artificial. It just shows the ingestive capacity of an adult copepod, which is feeding on nauplii.

Nauplius IV and the older stages often managed to escape from the water current. Our observations support the idea that the more rapid swimming of older naupliar stages, rather than their size, made them less vulnerable to cannibalistic predation.

Also eggs have been fed, but, during a 2 h period of observation, these were never seen to be taken by adults. On the contrary, eggs that came near to the mouthparts were, without exception, thrown aside by the adult copepod as unsuitable food.

Laboratory experiments

Under both experimental conditions, in the presence and in the absence of alternative food, predation rates increased with increasing prey density (Fig. 5), even at prey densities higher than found under natural circumstances (maximally 100 l^{-1}). In the experiments with N I and N II it seems that even the highest experimental prey densities were not enough to meet the feeding capacity of the adults, which is consistent with the high rates observed under the microscope for individual copepods. For all naupliar stages the relation between predation rate and prey density is presumably linear at natural prey concentrations.

Fig. 5 illustrates that cannibalism is considerably enhanced, when alternative food is not available. Analysis of covariance (Sokal & Rohlf 1981), applied to predation rates on N I through N III, revealed significant ($p < 0.05$) differences in slope (N I and N II) or elevation (N III) of the regression lines, due to the presence or absence of alternative food. Volumes cleared by adult females in the absence of alternative food were on average 3 times higher than in the presence of alternative food (Table 2).

Table 2. *Temora longicornis*. Clearance rates of adult females feeding on different naupliar stages in the absence of alternative food (F_0) in relation to clearance rates in the presence of alternative food (F_a)

Nauplius stage	$F_0 : F_a$
N I	3.2
N II	2.4
N III	3.3
Mean:	3.0

The rate of capture declined when older developmental stages of nauplii were offered (Fig. 6). Nauplius V appeared the oldest stage to be ingested by adults. N VI was never captured, even not at the highest experimental concentrations.

Total naupliar mortality and significance of in-situ cannibalism

Mortality was calculated from mean densities observed within each week, resulting in an estimate of mortality characteristic of the water mass sampled that week. Instantaneous naupliar mortality coefficients – representing relative mortality rates – showed a marked peak in Week IV of the field work period (Table 3a), when the lowest naupliar densities were found. In that week adult densities culminated (Fig. 1),

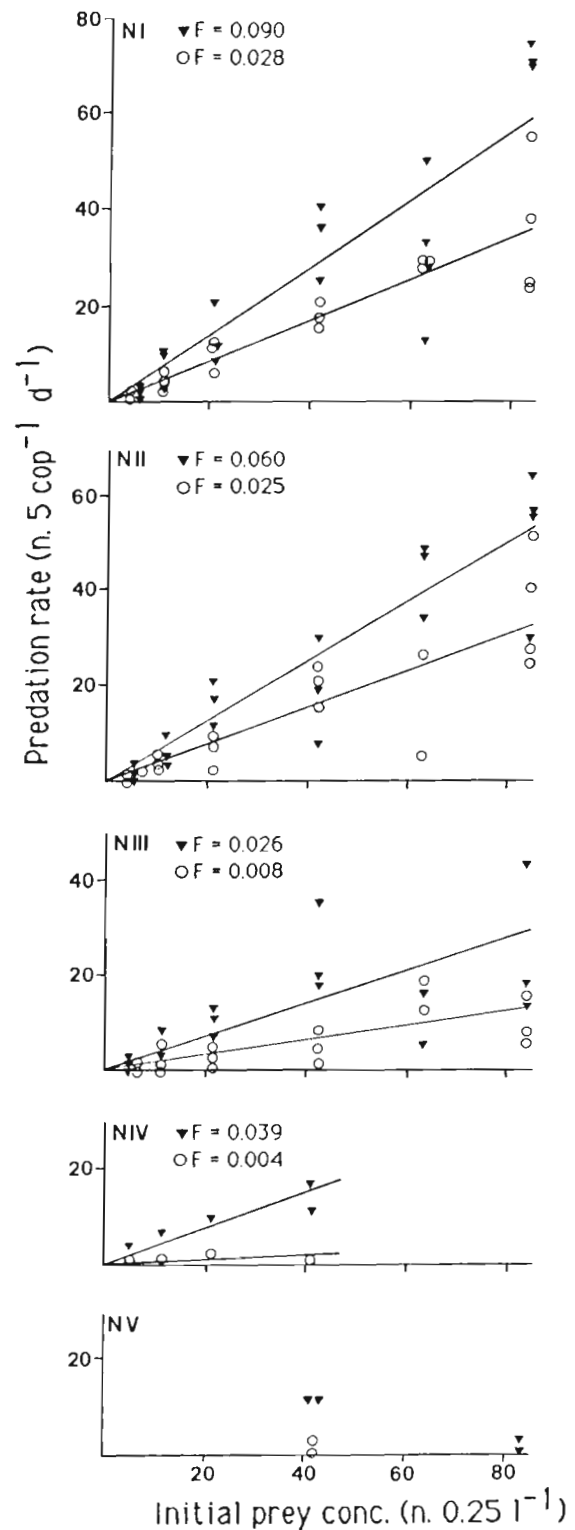


Fig. 5. *Temora longicornis*. Daily predation rates by adult females on different naupliar stages over a range of prey concentrations. (○) With algae; (▼) without algae. F: clearance rate (see text)

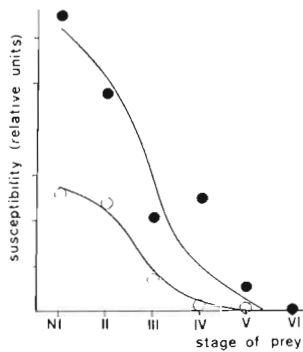


Fig. 6. *Temora longicornis* nauplii. Stage-dependent susceptibility for cannibalistic predation in presence (○) and absence (●) of alternative food

and chlorophyll *a* concentrations were low (Fig. 3). However, because of the low actual naupliar abundance, absolute mortality was low (Table 3b).

The results of the laboratory experiments on *Temora longicornis* have been used to estimate the contribution of cannibalism to total naupliar mortality in the field. Extrapolation of experimental data to in-situ cannibalism was done on the basis of a mean age distribution of the naupliar stock in the area and season, since actual field data on stage-specific densities are not available. A mean age distribution (N I: 14 %, N II: 27 %, N III: 19 %, N IV: 15 %, N V + N VI: 25 %) was derived from data collected by van den Ende (pers. comm.) at the same station and in the same season in 1984, when a similar copepod assemblage as in July 1985 was observed (Daan unpubl.). Thus mortality by cannibalism in each naupliar stage can be estimated from:

$$K_i = D_i \cdot F_i \cdot P \quad (7)$$

(see Conover 1978)

where K_i = mortality of stage N(i) by cannibalism ($n \text{ l}^{-1} \text{ d}^{-1}$); D_i = density of stage N(i); F_i = clearance rate of adult *T. longicornis* feeding on stage N(i); P = density of adult copepods. The sum of mortalities by cannibal-

ism among Stage N I through N IV was assumed to represent all naupliar mortality by cannibalism. Such estimates are made for both situations that theoretically could have occurred, i.e. optimal algal food conditions and the absence of any alternative food (Table 3c).

When comparing the estimates of total mortality in situ (Table 3b) with estimates of cannibalism (Table 3c), it seems that, during Weeks II through IV, cannibalism accounted for an important part of total naupliar mortality: in the presence of alternative food 17 to 90 % of mortality may be explained by cannibalism; without alternative food, 52 to over 100 %. In Week V naupliar mortality due to cannibalism was 7 to 43 %; in Week VI, 5 to 21 %.

DISCUSSION

Concerning susceptibility to intraspecific predation, *Temora longicornis* nauplii of subsequent developmental stages show the same trend as found by Landry (1978a) and Lonsdale et al. (1979) for *Acartia* spp., i.e. a declining rate of capture with ascending developmental stage (Table 4). In accordance with Conley & Turner (1985) we conclude from our visual observations that swimming speed rather than size of the nauplii is crucial in avoiding predation. This idea is also consistent with the observation of Lonsdale et al. (1979), reporting on the predatory behaviour of *Acartia tonsa*: the rapid swimming of the younger nauplius stages of *Oithona colcarva* resulted in lower predation rates compared to the older stages of this prey species.

In its carnivorous behaviour *Temora longicornis* differs strongly from a typical raptorial feeder like *Tortanus discaudatus*, which purposively attacks its prey (Ambler & Frost 1974), while *T. longicornis* merely selects particles brought to the mouth by a self-generated water current. The passive predatory behaviour of a primarily herbivorous copepod like *T. longicornis*, resulting in highest predation rates on the youngest

Table 3. Estimates of naupliar mortality: (a) relative mortality ($m_N \text{ h}^{-1}$); (b) absolute mortality ($n \text{ l}^{-1} \text{ d}^{-1}$); (c) mortality by cannibalism ($n \text{ l}^{-1} \text{ d}^{-1}$) in situ in the presence and absence of alternative food. The real estimate (I) of mortality is based on naupliar recruitment calculated according to Eq. (3). The maximum estimate (II) of mortality is based on naupliar recruitment calculated according to Eq. (5)

Week	(a)		(b)		(c)	
	Instantaneous mortality coefficient (m_N)		Total mortality (M_N)		Mortality by cannibalism	
	Estimate I	Estimate II	Estimate I	Estimate II	+ alt. food	- alt. food
II	0.010	0.028	9.4	21.7	4.2	12.8
III	0.005	0.028	6.2	28.0	5.6	17.8
IV	0.075	0.125	2.5	2.9	0.5	1.5
V	0.015	0.035	4.2	8.1	0.6	1.8
VI	0.021	0.028	12.7	15.4	0.8	2.7

Table 4. Predation rates of omnivorous calanoid copepods at initial prey concentration of 50 nauplii l⁻¹. Values calculated by linear inter- or extrapolation of the data presented by the different authors. Data for *Acartia tonsa* in Lonsdale et al. (1979) are derived from their Figs. 6 and 7, since values given in their Table 1 probably apply to prey concentrations of 278 l⁻¹ and not to 50 l⁻¹ refer red to in their text

Predator species	Sex	Prey (genus)	Nauplius stage	Alt. food	Temp.	Prey ad. ⁻¹ d ⁻¹	Source	
<i>Acartia clausi</i>	♀	<i>Acartia</i>	I	+	10°C	0.21	Landry (1978)	
				-	and	0.23		
			II	+	20°C	0.13		
				-		0.19		
			III	+		0.08		
			-		0.14			
			IV	+		0.06		
				-		0.11		
<i>Acartia tonsa</i>	♀	<i>Acartia</i>	I–III	+/-	20°C	0.51	Lonsdale et al. 1979	
			IV–VI	+/-		0.25		
		<i>Scottolana</i>	I–III	+/-	1.42			
			IV–VI	+/-	1.03			
		<i>Oithona</i>	I–III	+/-	0.82			
			IV–VI	+/-	1.51			
<i>Centropages hamatus</i>	♂/♀	<i>Acartia</i>	I–IV	-	10–22°C	5.3	Conley & Turner (1985)	
<i>Centropages furcatus</i>	♀	<i>Pseudodiaptomus</i>	II–IV	+/-	20°C	10.5	Paffenhöfer & Knowles (1980)	
			<i>Temora</i>	II–IV		+/-		11.9
			<i>Centropages</i>	II–IV		+/-		4.6
<i>Temora stylifera</i>	♀	<i>Pseudodiaptomus</i>	II–IV	+/-		4.2–6.5		
			<i>Temora</i>	II–IV		+/-		7.7
			<i>Centropages</i>	II–IV		+/-		3.5
<i>Temora longicornis</i>	♀	<i>Temora</i>	I	+	15°C	1.4	This study	
				-		4.3		
			II	+		1.1		
				-		2.9		
			III	+		0.4		
			-	1.3				

nauplii, will probably influence stage dependent mortality in a way opposite to the predatory behaviour of typical carnivorous species, which, irrespective of the prey's ability to avoid capture, selectively feed on the largest prey they can handle (Landry 1978b, Mullin 1979, Yen 1985).

Our finding that predation rates on nauplii are significantly depressed in the presence of alternative food corresponds with the results of experiments on predation by *Sulcanus conflictus* on nauplii of *Gladioferens imparipes* (Hodgkin & Rippingale 1971) and with Landry's (1978a) observations on *Acartia clausi*. Landry found sub-adult, male adult as well as female adult cannibalism to be negatively affected by the presence of alternative food, although the influence was not significant in adult females. No significant effect of phytoplankton on predation rates was found by Lonsdale et al. (1979) and Paffenhöfer & Knowles (1980) in *A. tonsa* and in *Centropages furcatus* and *Temora stylifera* respectively. There is no reasonable explanation for these contrasting results. Possibly the latter

authors utilized suboptimal algal food concentrations.

It seems likely, that in water with low phytoplankton concentrations copepods will intensify their search for food or change their feeding strategy in order to meet their food requirements. On average we found that clearance rates of 'starving' copepods were 3 times higher than when alternative food was available. Enhanced filtering rates, resulting in a higher number of encounters with nauplii, might be responsible for this increased predation. This explanation is supported by Runge (1980) who experimented on feeding in *Calanus pacificus*. Runge also found clearance rates 3 times higher in starved than in well-fed copepods. Another possible explanation for increased cannibalism in starving copepods is a switch in feeding behaviour (between herbivory and carnivory) to the prey available in greatest relative abundance, as found in *C. pacificus* (Landry 1981).

Preliminary semi-in-situ experiments (Table 1) indicate the possible impact of cannibalism in natural copepod populations. However, these experiments

were inadequate for calculating accurate rates of cannibalism. Therefore laboratory experiments were conducted resulting in statistically improved estimates of the rate of cannibalism. The good correspondence, particularly during Weeks II through IV, between our estimates of total naupliar mortality in the field and of mortality due to cannibalism, deduced from these experiments, shows that cannibalism may represent a substantial factor in naupliar mortality. This conclusion, however, might be biased by either underestimation of total mortality or overestimation of cannibalism. The most realistic estimate (I) of total mortality is based on a stable recruitment. This condition is not likely to be fulfilled in a natural situation. Any instantaneous naupliar assemblage is the result of about 10 d recruitment and mortality. Even in such a short period these variables will certainly not be constant. However, this will not a priori lead to an underestimate of mortality. On the other hand the developmental period of 240 h used seems a maximum approximation at ambient temperatures ($> 15^{\circ}\text{C}$) and chlorophyll *a* concentrations, and will thus result in a maximum estimate of mortality. Only in Week IV chlorophyll *a* concentrations were so low ($\approx 1 \mu\text{g l}^{-1}$), that naupliar development might be significantly delayed. Particularly in that week, however, mortality was so high that even a development time in excess of 300 h would hardly have affected the results of our mortality calculations. Estimate II of mortality, based on hatching of all eggs, is certainly an overestimate, since loss in eggs by predation has been shown to occur (Daan 1987) and since the possibility of diapausing copepod eggs was ignored (see Kasahara et al. 1975).

Extrapolation of our laboratory experiments, performed in a standing beaker, to the natural situation possibly involves various sources of error. In the small experimental volume used (250 ml) feeding rates of adult copepods may have been depressed by the edge effect (O'Brien 1988). Moreover it seems that clearance rates of *Temora longicornis* feeding on N I and N II were underestimated, since in many experiments the adults consumed more than 50 % of the prey and were, thus, limited in taking more prey by the strongly declining naupliar densities in the small experimental beakers. Indeed clearance rates of a congenerous species (*T. stylifera*), feeding on nauplii in much larger (31) experimental volumes (Paffenhöfer & Knowles 1980) appeared considerably higher than we measured. Furthermore, in nature turbulence may affect distribution and chance of encounter of predator and prey. In addition to specific differences in predation rate (Table 4) *T. longicornis* nauplii may be more susceptible to copepod predation than nauplii of other species. Finally the estimates are based on predation by adults only, assuming equal rates for males and

females. Although male predation may be lower, this bias might be largely compensated for by cannibalism exerted by subadult copepodites (see Landry 1978a) which were on average twice as abundant as adult copepods (Daan unpubl.).

The present study suggests that cannibalism is a substantial factor in naupliar mortality in the area of study. This could imply that other causes of naupliar mortality – macroplanktonic predation and physiological death – are relatively unimportant. Simultaneous observations on predator abundance during our field study tend to support this. Apart from larval fish, which were not adequately sampled, the most numerous predator of different copepod stages was the hydromedusa *Phialidium hemisphaericum* (Daan unpubl.). However, analysis of stomach contents revealed that this species fed selectively on older copepodite stages and on copepod eggs. Ingested nauplii were found only very seldom. On the other hand, significant physiological mortality, e.g. as a consequence of shortage of food, should have manifested itself also in the field experiments by the presence of dead or dying nauplii. These were not found and all nauplii counted seemed vital.

If indeed cannibalism is a key factor in naupliar mortality, the present estimates of total mortality in situ would indicate that after mid July (Week IV) algal food conditions became strongly limiting to the adults. There is direct evidence that such food limitation actually occurred. In Week IV chlorophyll *a* and diatom concentrations (Daan unpubl.) were at a minimum, as was individual egg production by adult copepods (Daan 1987). We conclude therefore that food limitation may affect the population dynamics of copepods in 2 ways: first, it seems probable that the recruitment of new generations will fail because of strong reduction in egg production; second, the actual naupliar generation is exposed to enhanced cannibalism. These effects, limited egg production and cannibalism, may be regarded as mechanisms with a definite survival value, since they prevent total food depletion for the whole copepod stock.

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