

Partitioning of a Brackish Water Habitat by Copepod Species

by

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ABSTRACT

1. The successful species of copepods in a brackish water habitat show a separation in time with regard to the date of maximum occurrence and the date of maximum reproductive activity. The succession of the five species examined is: *Mesochra lilljeborgi*, *Paronychocamptus nanus*, *Tachidius discipes*, *Halicyclops magniceps* and *Canuella perplexa*.
2. These species and others show moreover a separation in space: *C. perplexa* is an endopsammic, *P. nanus* a mesopsammic and *T. discipes* an epipsammic species. Three cyclopoid species are planktonic. Two other species (*Nilocra typica* and *Mesochra lilljeborgi*) are more numerous in the periphyton than in the benthos.
3. It seems that redundancy exists in the ways these species avoid competition, and the habitat could probably support more species.

INTRODUCTION

The existence of more than one species in a given habitat poses problems with regard to the separation of niches between species. The aim of this study was to establish some of the ways in which copepods attain this separation. Special emphasis was laid on the separation in time and in space between the different species. The locality chosen being a brackish water habitat, the number of species is low compared with marine or freshwater habitats (REMANE, 1958). As only a few species occur it was possible to identify all individuals and the analysis was greatly simplified.

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MATERIAL AND METHODS

The locality studied is shallow brackish water pond, called Dievengat, in northern Belgium. Depth at the place of sampling is about 15 cm, salinity as measured by MOHR's method fluctuates greatly (8—24% S) during the year. Temperature was measured fortnightly with 0.1° C precision and continuously recorded with a thermograph allowing estimations at 0.5° C.

The sediment is a fine sand covered with a layer of detritus. There is always an oxidized layer, varying from a few mm to 2 cm deep. The underlying sediment is black and reducing. Three samples were taken fortnightly with a glass tube covering a surface area of 6.06 cm². The tube was pushed 5 cm into the sediment, closed with a cork and removed. The water column above the sampled area was also taken. Samples were fixed with 70% alcohol.

In the laboratory, the fixed samples were placed in a shallow trough as described by BARNETT (1968) and washed with a current of tapwater; the material washed away was caught in a sieve with a mesh size of 50 mu. With this method, BARNETT (1968) recovered 18 adults and 489 nauplii of the harpacticoid copepod *Platychelipus littoralis* from a residue previously freed from copepods. In another test, repeated five times, 70 nauplii were recovered. We tested the method ten times with known numbers (50) of adults and copepodites of *Paronychocamptus nanus* and *Canuella perplexa*; recovery was complete in all tests but one, when two were missing.

A major inconvenience of this method is that all the detritus is removed from the sand as well, so a very careful and time-consuming extraction of the animals from the detritus under the dissecting microscope was necessary. This extraction, however carefully performed, remained the major source of possible errors; in the case of the smallest nauplii, hardly visible under the dissecting microscope, I was not convinced of the reliability of my figures and omitted them from calculations.

Copepods in the benthos are restricted to the uppermost few centimeters of the sediment; our samples therefore contained probably all individuals in the vertical dimension and those present in the water column above. To examine the horizontal distribution one square meter was sampled every 10 cm; the results for *Canuella perplexa* show a variance/mean ratio of 2.71, differing significantly from the expected 1.00 for the Poisson-distribution. This species shows a pattern fitted by the negative binomial distribution.

All copepods were determined to species; a further distinction was made between females carrying or not carrying eggs, males and copepodites. Egg sacs of *Canuella perplexa* were sometimes found

loose; as they could have become detached during treatment of the sample, they were attributed to some female. Non-quantitative, living samples were taken to the laboratory to permit observation of living animals.

We made a comparison with an investigation by CORIJN (not published) who studied the copepods on immersed glass slides of the same locality during 1968—1969. My investigation started in august 1968 and is still being continued; it was discontinued from august 1969 till november 1969.

RESULTS

Eleven species of copepods were determined during the investigation:

Cyclopoida

Halicyclops magniceps (LILLJEBORG, 1953)

Diacyclops bisetosus (REHBERG, 1880)

Megacyclops viridis (JURINE, 1820)

Harpacticoida

Canuella perplexa T. & A. SCOTT, 1893

Tachidius discipes GIESBRECHT, 1882

Amphiascoides debilis (GIESBRECHT, 1881)

Schizopera compacta DE LINT, 1922

Nitocra typica BOECK, 1864

Nitocra spinipes BOECK, 1864

Mesochra lilljeborgi BOECK, 1864

Paronychocamptus nanus (SARS, 1908)

The space available in the habitat can be divided into a number of compartments: the principal of these are the open water, the surface of plants and other immersed objects, and the bottom. The communities living here are the plankton, the periphytal and benthic communities. Within the benthos, a further division can be made according to an existence on the surface of the sediment, a burrowing or an interstitial existence, respectively called the epipsammon, the endo- and mesopsammon. A first way of separation is possible here. The three cyclopoid species are planktonic; the harpacticoid *T. discipes* is a good swimmer but is often found on the sediment as well. As it probably feeds only in the benthos (MUUS, 1967 and own observations) it can be called epipsammic.

Three species are found both in the periphyton and in the benthos, but their importance is not the same in both biotopes (Table I).

TABLE I
Maximum number per m² in periphyton and benthos
(68—69)

	Periphyton	Benthos
<i>N. typica</i>	116000	13200
<i>M. lilljeborgi</i>	17800	1650
<i>P. nanus</i>	33200	599000

N. typica is the dominant species in the periphyton but its presence in the benthos is irregular and it occurs in small quantities.

A strange phenomenon was observed in aquaria in the laboratory where *N. typica* became the dominant species in the benthos, outnumbering *P. nanus*. A striking difference between these aquaria and natural conditions are the far more constant conditions in the first; another difference is the absence of a periphytal biotope. Which difference causes the phenomenon is an unsolved problem.

M. lilljeborgi is more abundant in the periphyton than in the benthos, while *P. nanus* is the dominant species in the benthos where it is joined by *C. perplexa*, a typical benthic species. *P. nanus* lives interstitially and can be called mesopsammic, while the larger *C. perplexa* is a burrowing, endopsammic species. We have no observations of the other species as they were too rare. With regard to the distribution in time, we shall not mention them either, as their presence is somewhat inconsequential. In Table II, the distribution

TABLE II
Distribution in time and date of maximum occurrence

<i>H. magniceps</i>	?—sep 68	?	
	may—sep 69	26 Jun 69	11550*
	may—sep 70	1 Jul 70	23000
	may—? 71	?	
<i>C. perplexa</i>	perennial	5 Aug 70	82500
<i>T. discipes</i>	?—sep 68	?	
	mar—jun 69	19 May 69	163300
	feb —jul 70	20 May 70	150000
	feb —may 71	15 Apr 71	70900
<i>N. typica</i>	probably perennial	21 Apr 69	13200
		5 May 70	21400
<i>M. lilljeborgi</i>	probably perennial	3 Dec 69	19800
<i>P. nanus</i>	perennial	12 Jun 69	599000
		3 Dec 69	570000
		5 May 70	261000
		9 Dec 70	931600
		29 Apr 71	448700

*Number/m² on date of maximum occurrence.

in time and the date of maximum occurrence are shown. *C. perplexa* was much more abundant in 1970 and 1971 than in 1968 and 1969. From August 68 till July 69 mean density over 24 samples was 3300 ind./m², while from December 69 till July 71 it was 31700 ind./m² over 41 samples. *M. lilljeborgi* was only common from December 69 till June 70. *N. typica* is a regular but rare species with a mean density of 1830 ind./m² over 65 samples. *H. magniceps* and *T. discipes* do not occur throughout the year but they are common when they do occur (mean density omitting zero samples 7550 ind./m² for *H. magniceps* and 32300 ind./m² for *T. discipes*). *P. nanus* is perennial with a mean density of 247600 ind./m² over 65 samples. When considering numbers and regular occurrence, four species must be considered the successful members of the community, with regard to the benthic and planktonic portions of the habitat. These are *H. magniceps*, *C. perplexa*, *T. discipes* and *P. nanus*; a fifth species, *M. lilljeborgi* has to be considered for the period December 69 till June 70. As already mentioned, *N. typica* is the most successful species in the periphyton, but as we did not investigate this portion ourselves it is left aside here.

The way in which they are separated in time was investigated by examining the moment of maximum reproductive activity and the moment of maximum occurrence. Accepting the percentage of females carrying eggs as a measure of the reproductive activity, it is found that there is a difference in the length of the period of reproductive activity and a difference in the moment when maximum activity occurs (Table III, Fig. 1) during the year investigated for this purpose (Dec. 69—Jan. 71). The first species to attain maximum reproductive activity is *M. lilljeborgi* at the end of March. It is followed by *P. nanus* which maintains a level of about 75% from the beginning of April till the beginning of May. In about the same period *T. discipes* reaches its maximum. *C. perplexa* starts much later and attains maximum reproductive activity in May. The last species *H. magniceps* begins in July.

The duration of reproductive activity is also different for these species. It lasts about 4 months for *M. lilljeborgi*, 5 months for *T. discipes*, two months for *H. magniceps*, about eight months for *C. perplexa* and nearly throughout the year for *P. nanus*.

As the moment of maximum reproductive activity is different for the different species, one should expect the moment of maximum occurrence to be different also. This is indeed the case. As numbers are not the same for the different species, an easier comparison is made by transferring the data to percentages of the maximal number during blooms. As can be seen (Table IV, Fig. 1a), the moment of maximum occurrence is the same for *P. nanus* and *T. discipes* in

TABLE III
Percentage of females carrying eggs

Date	<i>P. nanus</i>	<i>T. discipes</i>	<i>C. perplexa</i>	<i>M. lilljeborgi</i>	<i>H. magniceps</i>
17 Dec 69	3.7	0.0	11.8	0.0	—
31 Dec 69	1.9	0.0	0.0	0.0	—
16 Jan 70	3.2	—	0.0	0.0	—
11 Feb 70	7.3	23.8	0.0	5.7	—
25 Feb 70	16.6	40.9	0.0	33.3	—
11 Mar 70	34.1	43.7	0.0	60.0	—
25 Mar 70	48.2	44.5	1.7	65.2	—
8 Apr 70	75.5	61.1	33.4	59.2	—
22 Apr 70	74.9	67.5	54.8	44.8	—
5 May 70	77.0	64.4	85.0	21.4	0.0
19 May 70	57.5	52.3	80.0	0.0	0.0
3 Jun 70	56.5	26.8	68.2	—*	40.7
17 Jun 70	61.6	20.0	64.5	—	50.0
1 Jul 70	40.1	0.0	61.5	—	55.0
15 Jul 70	44.6	0.0	58.9	—	50.0
5 Aug 70	58.3	—	57.4	—	0.0
19 Aug 70	66.6	—	52.9	—	—
2 Sep 70	64.0	—	58.6	—	—
16 Sep 70	51.8	—	40.0	—	+**
30 Sep 70	56.1	—	17.2	—	+
14 Oct 70	56.8	+	10.0	—	+
29 Oct 70	39.7	+	5.7	—	+
12 Nov 70	25.0	+	0.0	—	—
25 Nov 70	6.9	+	0.0	—	—
9 Dec 70	1.9	0.0	0.0	—	—
23 Dec 70	0.7	0.0	0.0	—	—
6 Jan 71	0.4	0.0	0.0	—	—

*Not present.

**One individual present.

the beginning of May (numbers corresponding with 100% in Table IV are given in Table II). These two species are followed by *H. magniceps* in June and, still later, by *C. perplexa* in the beginning of August. There is a last peak of *P. nanus* in December: this peak, occurring when water temperatures are rather low (2—6° C) can be explained by the ability of this species to reproduce at low temperatures and the absence of predation (*Protohydra leuckarti*, the main predator, does not reproduce at temperatures below 10° C). The distinct peak in the reproductive activity of *M. lilljeborgi* did not result in any effect on the growth of the population of this species, which disappeared in July.

As can be seen (Table II) there is a fair amount of repetition of this events in different years. The moment of maximum occurrence is not always the same and numbers during bloom can also be different, but in general the sequence is maintained.

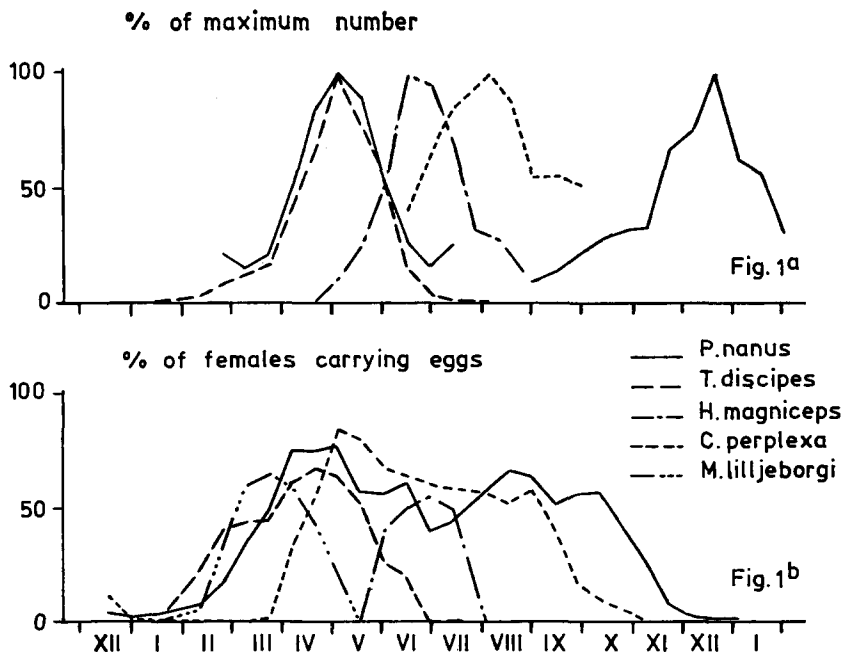


TABLE IV

Percentage of maximum number

Date	<i>P. nanus</i>	<i>T. discipes</i>	<i>C. perplexa</i>	<i>H. magniceps</i>
16 Jan 70		0.0		
11 Feb 70		2.4		
25 Feb 70	21.2	8.0		
11 Mar 70	14.1	12.4		
25 Mar 70	20.6	16.7		
8 Apr 70	48.8	42.2		
22 Apr 70	84.0	65.8		0.0
5 May 70	100.0	100.0	43.2	10.4
19 May 70	88.6	78.6	42.0	24.7
3 Jun 70	53.8	53.2	42.4	48.7
17 Jun 70	26.6	15.0	40.6	100.0
1 Jul 70	15.6	3.0	66.2	95.4
15 Jul 70	25.8	0.3	85.6	70.0
5 Aug 70		0.0	100.0	31.8
19 Aug 70			87.5	27.9
2 Sep 70	9.3		55.2	13.6
16 Sep 70	13.7		55.2	24.0
30 Sep 70	21.2		52.5	13.0
14 Oct 70	27.8		62.4	
29 Oct 70	31.5		54.6	
12 Nov 70	33.0		27.8	
25 Nov 70	67.5		24.9	
9 Dec 70	75.0		21.8	
23 Dec 70	100.0			
6 Jan 71	62.9			
20 Jan 71	56.5			
3 Feb	31.4			

The effect of temperature on reproduction is widely known; it was supposed that the differences in reproductive activity and maximum occurrence could be the consequence of different requirements with regard to temperature of the different species. To examine this, mean temperature was calculated for the period during which the percentage of females carrying eggs rose from less to more than 10% of the females present (Table V). This temper-

TABLE V
Mean temperature needed to start reproduction* ($^{\circ}\text{C}$) during different periods (2 till 14 days) before sampling datum

Number of days	2	<< 4	6	8	10	12	14
<i>P. nanus</i>							
1970	5.5	4.0	4.0	4.5	4.5	4.0	4.0
1971	5.5	5.5	5.0	5.5	5.5	6.0	5.5
<i>T. discipes</i>							
1970	6.5	6.0	6.0	5.0	4.5	4.5	4.0
1971	3.5	4.0	5.5	6.0	6.5	6.5	6.5
<i>C. perplexa</i>							
1970	11.0	12.0	12.0	11.5	11.0	10.5	10.0
1971	10.5	9.0	9.5	9.5	9.5	9.5	9.0
<i>H. magniceps</i>							
1970	18.0	19.0	19.5	20.5	20.0	19.5	18.0
1971	15.5	16.0	15.0	15.5	16.0	16.0	16.0

*See text for explanation.

ature needed to start reproduction is about the same for *P. nanus* and *T. discipes* (4–6 $^{\circ}\text{C}$); it is higher for *C. perplexa* (9–12 $^{\circ}\text{C}$) and still higher for *H. magniceps* (15–20 $^{\circ}\text{C}$).

DISCUSSION

A partitioning of the habitat is made both in time and in space by the copepod species investigated. There is probably also some separation in the way energy is obtained but this was not investigated in detail. Muus (1967) showed that *T. discipes* feeds on diatoms fixed on sand grains, while *Nitocra* feeds mainly on detritus (bacteria). According to our own observations *P. nanus* is also a detritus feeder.

In the plankton only one successful species occurs (*H. magniceps*); the harpacticoid *T. discipes* is also found here but is separated from *H. magniceps* in time: it attains peak occurrence earlier (May) than the latter species (June). There might be a further separation in the way energy is obtained as *T. discipes* feeds in the benthos and *H. magniceps* in the plankton. *T. discipes*, when occurring in the benthos,

is epipsammic; I never observed it under the surface of the sediment, contrary to the two other benthic species. Separation between these two. *P. nanus* and *C. perplexa*, is again obtained through a separation in time. The peaks of *P. nanus* occur earlier (May) or later (December) than the peak of *C. perplexa* (August). Moreover, they occupy different habitats, *P. nanus* being an interstitially, living, mesopsammic species, *C. perplexa* being a burrowing, endopsammic species.

Two further species are more abundant in the periphyton than in the benthos: *N. typica* and *M. lilljeborgi*.

The reason for this separation could be the avoidance of competition between the species: food is probably never in short supply as there is a very thick layer of detritus throughout the year and high quantities of chlorophyll a (mean of 435 mg/m² of undegradated chl. a over 36 samples) in the benthos. But even when something would be in short supply, there should be no competition between these species either. The fact that the moment of maximum reproductive activity is different for the different species is important with regard to an eventual competition between the younger stages, nauplii and copepodites. These younger stages certainly do not occupy the same niches as the adults, but they avoid each other to a certain degree.

The mechanism which causes this separation might be the temperature needed to start reproduction, acting either directly or indirectly, as perhaps some other factor correlated with temperature is responsible. As has been shown (HEIP, 1972), the reproductive potential in nature for the four successful species does not differ much and lies in a range of $r = 0.04-0.06$ per day. The slight differences between species can not account for the large delay in time of maximum occurrence. It seems therefore that it is not the ability to reproduce slower or faster which governs the separation of the moment of maximum abundance, but rather the temperature needed to start reproduction (Table V).

There seems to be a certain redundancy in the possible ways to avoid an eventual competition: separation between species occurs both in time and in space and probably also in the way energy is obtained. It seems probable that the habitat could support more species than it actually does.

The fact that several species are found only occasionally is not always readily explained. *M. viridis* (24 Feb. 69) can only live in water with a salinity up to 18‰ and prefers zones with a rich vegetation (DUSSART, 1969), which are absent at the place of sampling. *D. bisetosus* was found in February—March 1969 and February 1970 and 1971; its scarcity cannot be a consequence of

salinity, as it can tolerate salinities as high as 58^{0/00}; it seems to prefer temporary ponds (LÖFFLER, from DUSSART 1969), perhaps an indication that it defends itself badly against competition. The fact that it occurs much earlier than the also planktonic *H. magniceps* might point in this direction.

A thorough investigation of the harpacticoid copepods of many localities in Germany by NOODT (1957) established that *P. nanus*, although nearly always present, was never a dominant species, even in very similar localities. The predominant species of mesohaline localities in Denmark are species of the genera *Nitocra*, *Ectinosoma* and *Tachidius*, which represented at least 80% of the harpacticoids observed (MUUS, 1967). In Niva Bay, a locality very similar to Dievengat, *Nitocra spinipes*, *Ectinosoma curticorne* and *Tachidius discipes* predominated at all seasons (MUUS, l.c.). It seems probable that the abundance of *P. nanus* in Dievengat might in some way be correlated with the absence of one of these species, and the species responsible could well be *N. spinipes*, which is also a mesopsammic detritus feeder. We found those species only once and its absence can be a matter of salinity tolerance: according to DE LINT (from LANG, 1948) this species is tolerant for salinities in the range 0—11^{0/00}; according to NOODT (1957) the range is 0—15^{0/00} but MUUS (1967) cultured the species at 16^{0/00}. As however salinities of 24^{0/00} occurred in Dievengat, this could explain the rarity of the species.

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