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Temporal variation in the morphology of the rotifer *Keratella quadrata* (Müller, 1786)

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Keywords : Temporal variation, *Keratella quadrata*, morphology, taxonomy.

Changes in body shape of the rotifer *Keratella quadrata* in a pond were recorded over the course of half a year (end of November 1981 to beginning of June 1982). Body and caudal spine lengths increased from November until the end of February, and then decreased until June. Such changes were not significantly correlated consistently positively or negatively to water temperature, pH, hardness, food levels or copepod numbers. The individuals present during the first half of the study period corresponded most closely to the literature descriptions of the group or subspecies *quadrata*, while those present during the second half resembled the form, group or variety *dispersa*. The first half of the study period was characterized by water of relatively low temperature, low pH and high hardness, while, for the second half, temperature and pH increased and hardness decreased.

Variation temporelle de la morphologie du rotifère *Keratella quadrata* (Müller, 1786)

Mots clés : Variation temporelle, *Keratella quadrata*, morphologie, taxonomie.

Des changements dans la morphologie du corps du rotifère *Keratella quadrata* dans un étang au cours d'une demi-année (fin novembre 1981 à début juin 1982) ont été notés. Les longueurs du corps et de l'épine caudale ont augmenté de novembre à fin février, et ensuite diminué jusqu'en juin. Ces changements ne sont pas correlés significativement à la température de l'eau, au pH, à la dureté, aux états nutritionnels ni à l'abondance des copépodes. Les individus présents pendant la première moitié de l'étude correspondent le plus aux descriptions dans la littérature du groupe ou de la sous-espèce *quadrata*, tandis que les individus présents pendant la deuxième moitié de l'étude ressemblent à la forme du groupe ou de la variété *dispersa*. La première période de l'étude est caractérisée par une température et un pH de l'eau relativement bas et une dureté élevée tandis qu'au cours de la deuxième période, la température et le pH ont augmenté et la dureté a diminué.

1. Introduction

Temporal variation in body from, often termed cyclomorphosis, occurs in several zooplankton groups, including rotifers. Such variation is common within the genus *Keratella*, chiefly involving changes in body and spine lengths. The type and degree of variation differs between water bodies, while the causative factors and adaptive significances of the changes are uncertain (Hutchinson 1967, Pejler 1980).

Keratella quadrata (Müller, 1786) shows a high degree of morphological variation both in time and between populations. This species has been classified into a number of forms, varieties, groups and subspecies (Carlin 1943, Ahlstrom 1943, Ruttner-Kolisko 1974, Koste 1978). The taxonomic relationships between these are uncertain. In *K. cochlearis*, different morphs have been recorded in the same water body without transitional forms being present (Pejler 1962 ; Hofmann 1980, 1983 ; Galkovskaya and Mityanina 1989). Whether this occurs in *K. quadrata* between the types recognized seems to be unrecorded. Also, the correlation of the occurrence of different morphs with differences in the environment is as yet unclear in this species, in contrast to *K. cochlearis*, for which several morphs have been found to occur largely at certain temperature ranges or levels of food availability, salinity or turbulence (Ruttner-Kolisko 1974). Some such morphs of *K. cochlearis* are now regarded as distinct species (Koste & Shiel 1989); whether this could be the case for morphs of *K. quadrata* requires to be investigated.

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In this study, I analysed the temporal variation in the morphology of *K. quadrata* in a pond over the course of half a year. Of particular interest was to determine which morphs (forms, varieties, groups) were present, and under what environmental conditions.

2. Materials and methods

The study area was a small pond located near the south coast of Ireland (National Grid Reference W 570 702).

Sampling was conducted near the shore, at approximately two to four week intervals, during the morning hours, from the end of November 1981 to the beginning of June 1982. Water depth in the sampling area was approximately 50-70 cm. Water temperature was measured *in situ*. On return to the laboratory, the water samples were stored at 4° C. pH was measured by means of a digital meter, while total hardness was determined by EDTA titration (APHA 1976).

For faunal sampling, a.*c*. 1.5 l volume tube was used. The animals were preserved with formaldehyde. Faunal samples were concentrated by filtration through nylon monofilament of mesh size 30 μm, and counted in their entirety by means of a compound microscope; two to seven samples were counted per sampling date. Individuals of *Keratella* and copepod copepodites and adults were counted. The percentage of *Keratella* individuals carrying eggs on each date was calculated.

Specimens of *Keratella* from both qualitative and quantitative samples were removed, mounted in 40 % glycerol on microscope slides under coverslips, and measured at a magnification of 1,000, with oil immersion, using an ocular micrometer with a graduation interval of 1.33 μm. The features measured are shown in Fig. 1. All measurements were made to the nearest graduation, with the exception of the caudal spine base width, which was measured to an accuracy of half this graduation. In many specimens, the left caudal spine was shorter than the right. Because both spines varied with time and body size in a similar manner, and the average difference in length was less than 3 μm, only the right spine length data are presented here. The anterior spines also showed changes, but were not measured in detail because of the difficulty due to their curvature; these spines showed length change trends similar to the caudal spines.

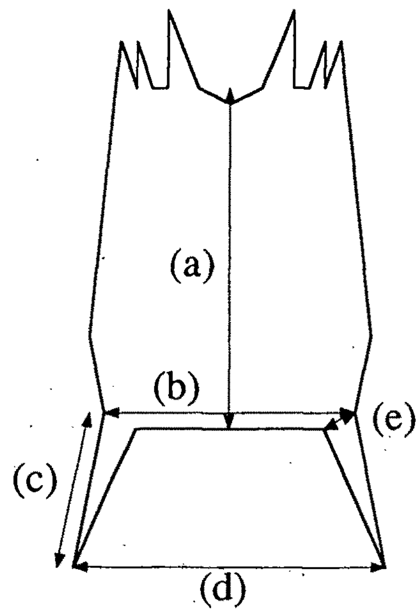

Fig. 1. Diagram showing the morphological measurements made.

Fig. 1. Diagramme montrant les mesures morphologiques effectuées.

Simple regression was carried out between the log transformed values of the caudal spine length (dependent variable) and body length (independent variable) for each date, and the mean caudal spine and body lengths between dates. The slope of the regression line (k) is the allometric growth factor. When it is equal to 1, growth is isometric, i.e. there is no relative change in the particular part when the overall body size changes. When k is not equal to 1, growth may be described as allometric or exhibiting heterauxesis; the particular structure becomes relatively smaller as body size increases when k is less than 1 (bradyauxesis) and larger when k is greater than 1 (tachyauxesis) (Hutchinson 1967).

The relationships between body and caudal spine lengths and water temperature, pH and hardness, the percentage of ovigerous *K. quadrata* (considered to be a measure of food availability), and copepod abundance, for the periods 30 November or 21 December to 24 February, and 16 April to 9 June, were examined by means of Spearman's Rank Correlation.

3. Results

3.1. Physical and chemical features (Fig. 2).

For the first half of the sampling period, water temperature remained below 10 ° C, approaching 0 ° C on the third sampling date. During the second half of the sampling period, temperature increased,

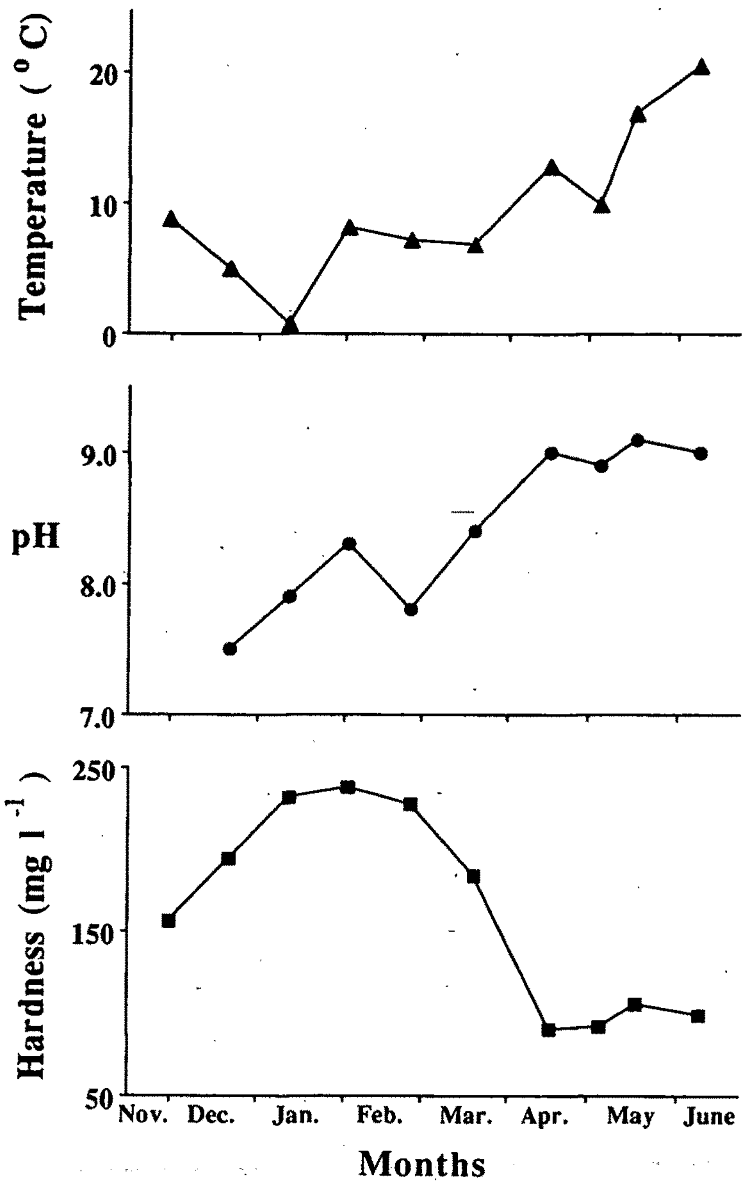

Fig. 2. Changes in physical and chemical features of the pond water with time.

Fig. 2. Modifications dans le temps des variables physiques et chimiques de l'eau de l'étang.

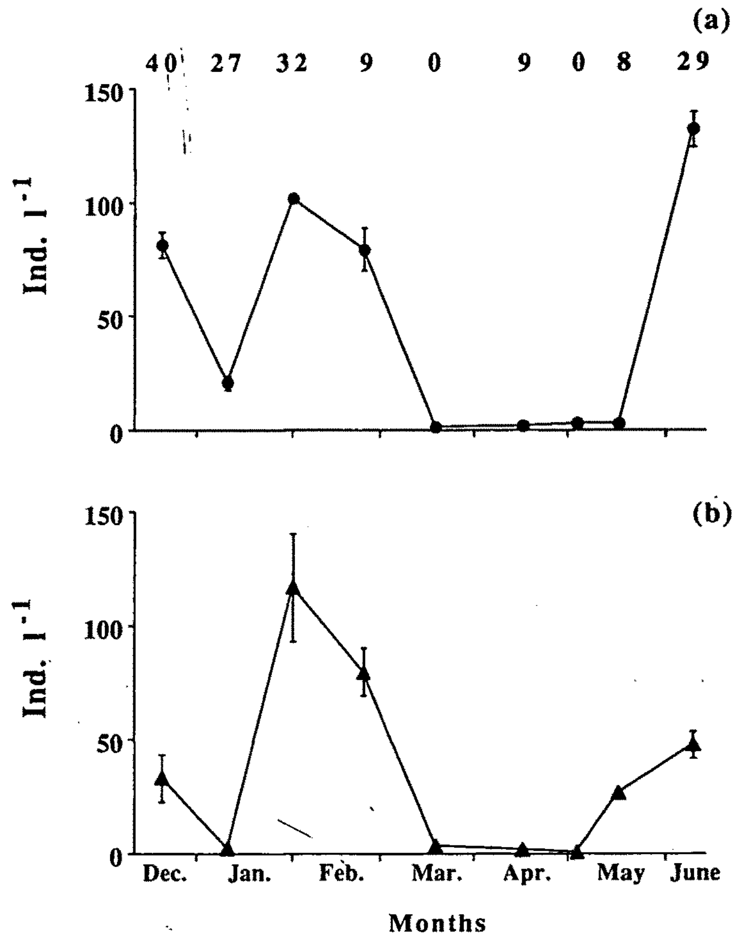

Fig. 3 a, b. Changes in abundance of (a) *Keratella* and (b) copepod copepodites and adults with time. Standard errors are shown. The percentages of ovigerous *Keratella* individuals (excluding specimens with body lengths < 120 μm) per date are given.

Fig. 3 a, b. Modifications de l'abondance (a) de *Keratella* et (b) des copépodites et adultes de copépodes, dans le temps. Les erreurs standards sont incluses. Les pourcentages des individus ovigères de *Keratella* (spécimens avec une longueur du corps < 120 μm exclus) sont indiqués à chaque date.

to reach *c.* 20 ° C on the last sampling date. pH increased during the course of the sampling period. Total hardness increased during the first three months, before decreasing markedly in the last part of the sampling period.

3.2. Changes in population densities (Fig. 3 a, b).

All *Keratella* specimens possessed two caudal spines. Individuals with body lengths of 100-118 μm occurred in low numbers from March to May. The latter were not identified to species, as the facets of the lorica could not be distinguished; all larger specimens were identified as *K. quadrata*.

The population size of *K. quadrata* decreased from December to January, before increasing again to reach a peak in February. During March, April and May, densities remained very low, and increased again in June. The percentage of ovigerous females was relatively high on the first three sampling dates and the last.

The pattern of change in copepod copepodite and adult densities was similar to that of *K. quadrata*.

3.3. Body and caudal spine lengths (Fig. 4).

Body length increased irregularly from 30 November to 24 February, before undergoing a relatively large decrease between the latter date and 19 March, and decreasing further to the end of the sampling period. Caudal spine length increased from 30 November to 24 February, and then decreased till 9 June.

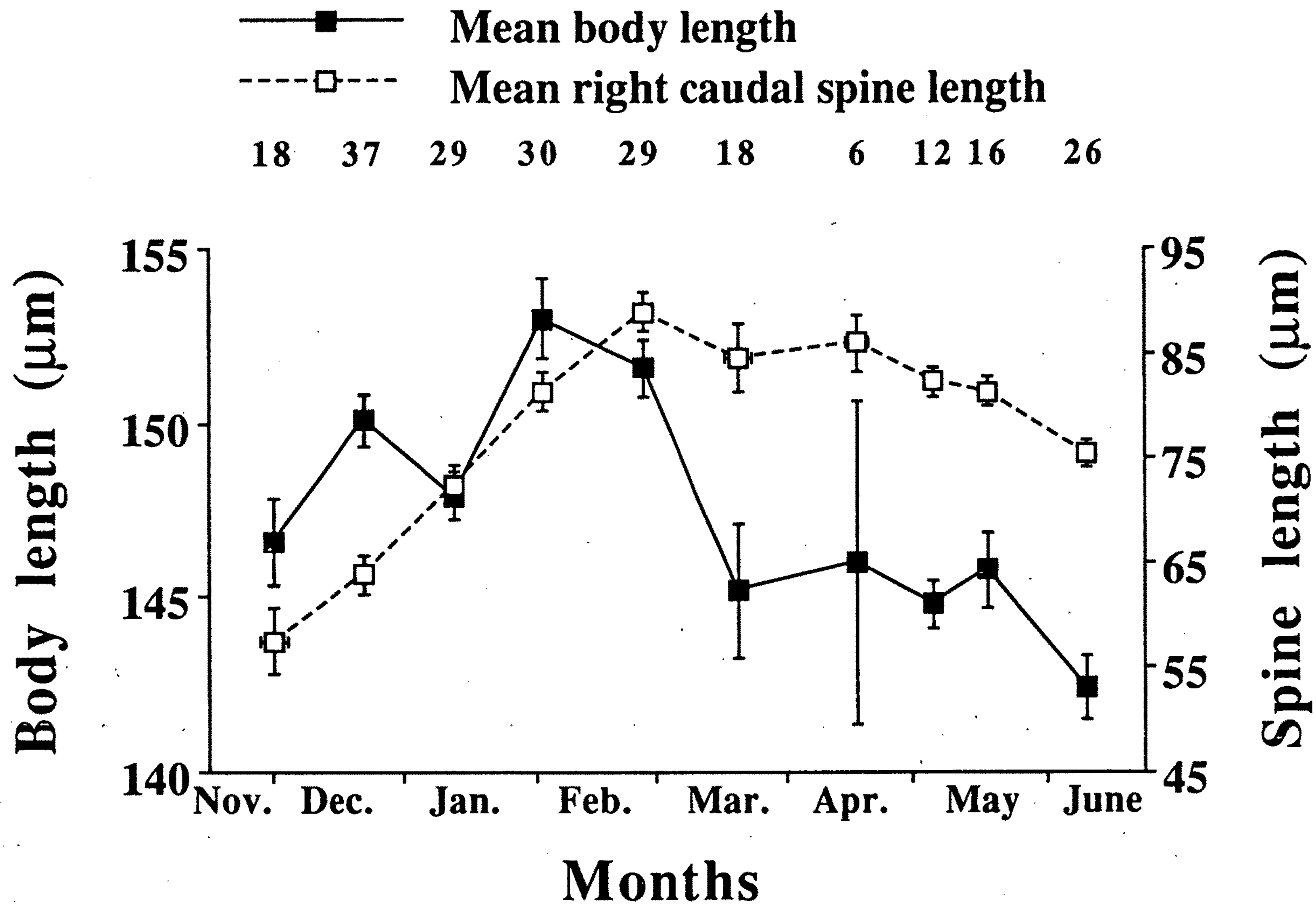

Fig. 4. Changes in mean body and right caudal spine lengths with time. Standard errors are shown. Specimens with body lengths < 120 μm are excluded. The numbers of specimens measured per date are given.

Fig. 4. Modifications des longueurs moyennes du corps et de l'épine caudale avec le temps. Les individus avec une longueur du corps < 120 μm sont exclus. Les nombres de spécimens mesurés à chaque date sont indiqués.

Considering the mean body and spine lengths on each date for the periods 30 November to 24 February, and 16 April to 9 June, values of k (the allometric growth factor) were 7.9 and 4.4, respectively (when individuals less than 120 μm in body length are excluded; the latter had relatively short caudal spines) (Table 1). Thus, the rate of change in mean body length was less than in mean spine length, especially during the first half of the sampling period. For neither period was the relationship between mean caudal spine length and mean body length significant (at the level of $p < 0.05$) (when individuals less than 120 μm in body length are not considered). Similarly, spine length was not significantly (at the level of $p < 0.05$) related to body length on some dates. The value of k fluctuated between individual dates.

For the first half of the sampling period, the only significant correlation (at the level of $p < 0.10$) between rank order for body and spine lengths and rank order for the environmental features measured was a positive relationship between body length and copepod abundance (Table 2). For the second half of the sampling period, no significant correlations were found (Table 2).

3.4. Other morphological features (Fig. 5, 6).

From 30 November to 24 February, the posterior body width, the distance between the tips of the caudal spines (termed here the caudal spine spread), and the width of the base of the caudal spines (all three expressed as a percentage of the body length) tended to increase slightly. After the latter date, all three increased till 4 May, after which they decreased again.

Table 1. Results of the regressions of the log of the caudal spine length against the log of the body length of *Keratella*, for each sampling date, and for the means of the periods 30 November - 24 February, and 16 April - 9 June. The numbers of data points (individuals measured per date and sampling dates per period) are indicated (n). k (the allometric growth factor) is the slope of the line, p is the level of significance. For dates with two sets of figures, the second excludes individuals of body length < 120 μm.

Tableau 1. Résultats des régressions entre les logarithmes des longueurs de l'épine caudale et du corps de *Keratella*, pour chaque date d'échantillonnage, et pour les moyennes des périodes 30 novembre - 24 février, et 16 avril - 19 juin. Les nombres des pointes (individus mesurés à chaque date; et par date de chaque période) sont indiqués (n). k (facteur de croissance allométrique) est la pente de la droite. p est le niveau de signification. Pour les dates avec deux séries de valeurs, les secondes excluent les individus avec une longueur du corps < 120μm.

Date	n	k	p
30 November	18	4.6	0.001
21 December	37	2.5	0.009
11 January	29	1.0	0.428
1 February	30	1.1	0.035
24 February	29	1.2	0.114
19 March	21	2.7	< 0.001
	18	1.2	0.141
16 April	14	2.7	< 0.001
	6	0.2	0.698
4 May	15	2.9	< 0.001
	12	0.1	0.920
17 May	19	2.7	< 0.001
	16	1.0	0.108
9 June	26	1.2	0.023
30 Nov. - 24 Feb.	5	7.9	0.118
16 April - 9 June	4	2.2	0.010
	4	4.4	0.081

Table 2. Spearman's rank correlation coefficients for the relationships between the changes with time in body and caudal spine lengths of *K. quadrata*, and the following environmental features : water temperature, pH, total hardness, food levels (as measured by the percentage of ovigerous *K. quadrata*), and copepod abundances. Individuals of body length < 120 μm are excluded.

Tableau 2. Coefficients de correlation de rang de Spearman pour les relations entre les changements dans le temps des longueurs du corps et de l'épine caudale et les variables environementales suivantes : température, pH, dureté de l'eau, niveau de l'alimentation (mesuré par le pourcentage de *K. quadrata* ovigères), et abondances des copépodes. Les individus avec une longueur du corps < 120 μm.

	Temp.	pH	Hard.	Food	Cop.
Body lgth.					
Nov./Dec.-Feb.	0.00	0.40	0.70	0.00	1.00
Apr.-June.	−0.40	0.32	−0.40	−0.20	−0.40
Caudal spine lgth.					
Nov./Dec.-Feb	−0.20	0.40	0.70	−0.80	0.60
Apr.-June.	−0.80	0.32	−0.80	−0.40	−0.80

The specimens less than 120 μm in body length had relatively low values for these features.

The population found on 19 March was morphologically transitional between those occurring in February and in April to May (Fig. 6). The transitional nature of this population is shown especially by 8 individuals with caudal spine spreads between 80 and 100 % of the body length, and body lengths near or below the lower range of the preceding date. The larger individuals seemed to resemble typical individuals from 24 February.

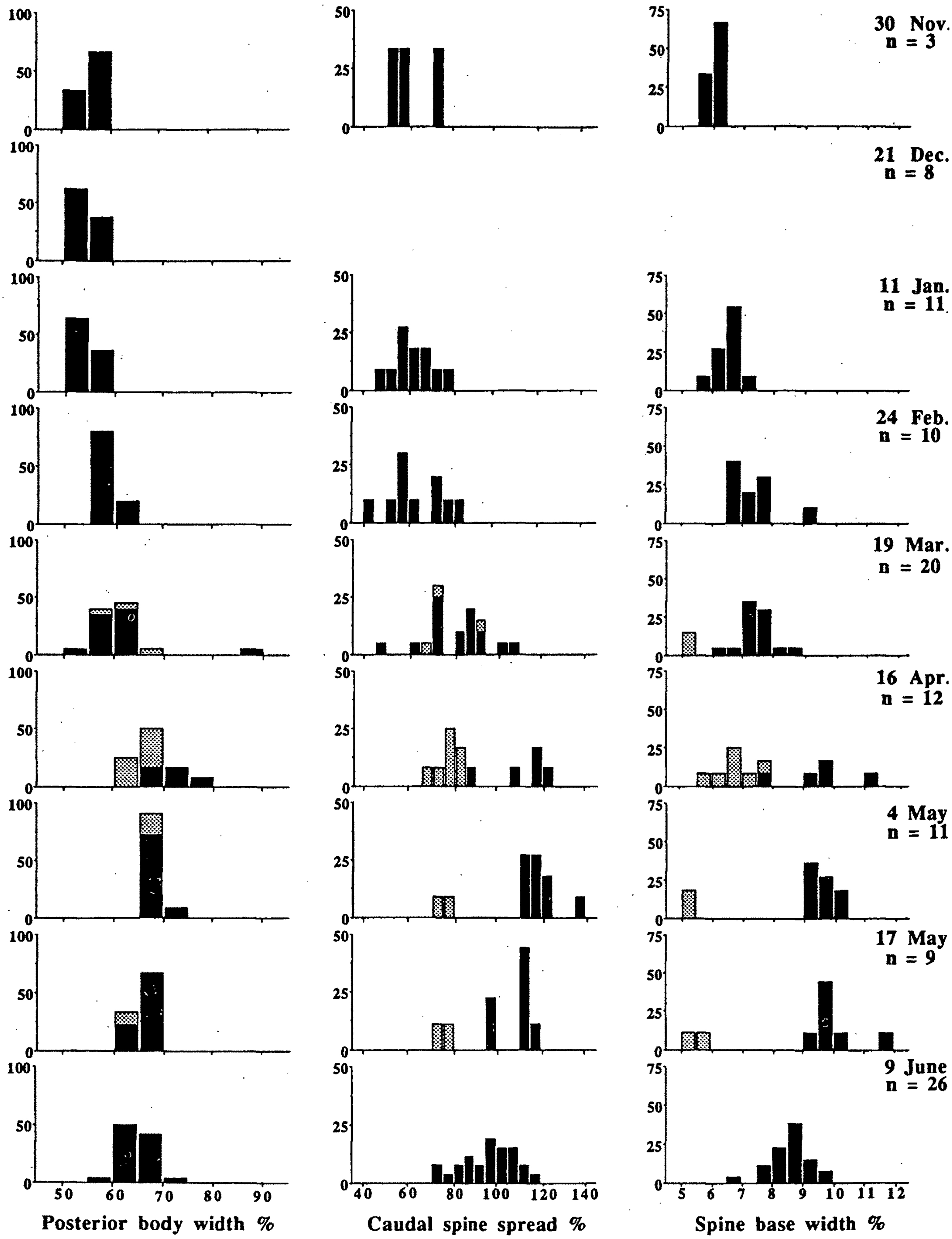

Fig. 5. Percentage frequency distributions of posterior body width, caudal spine spread, and caudal spine base width (all expressed as a percentage of body length) on the sampling dates. The numbers of specimens measured per date are given. Individuals with body lengths < 120 μm are represented by stippling.

Fig. 5. Distributions de la fréquence des pourcentages de la largeur postérieure du corps, de l'étendue de l'épine caudale, et de la largeur de la base de l'épine caudale (tous exprimés en pourcentage de la longueur du corps) aux dates d'échantillonnage. Les individus avec une longueur du corps < 120 μm sont indiqués en pointillés.

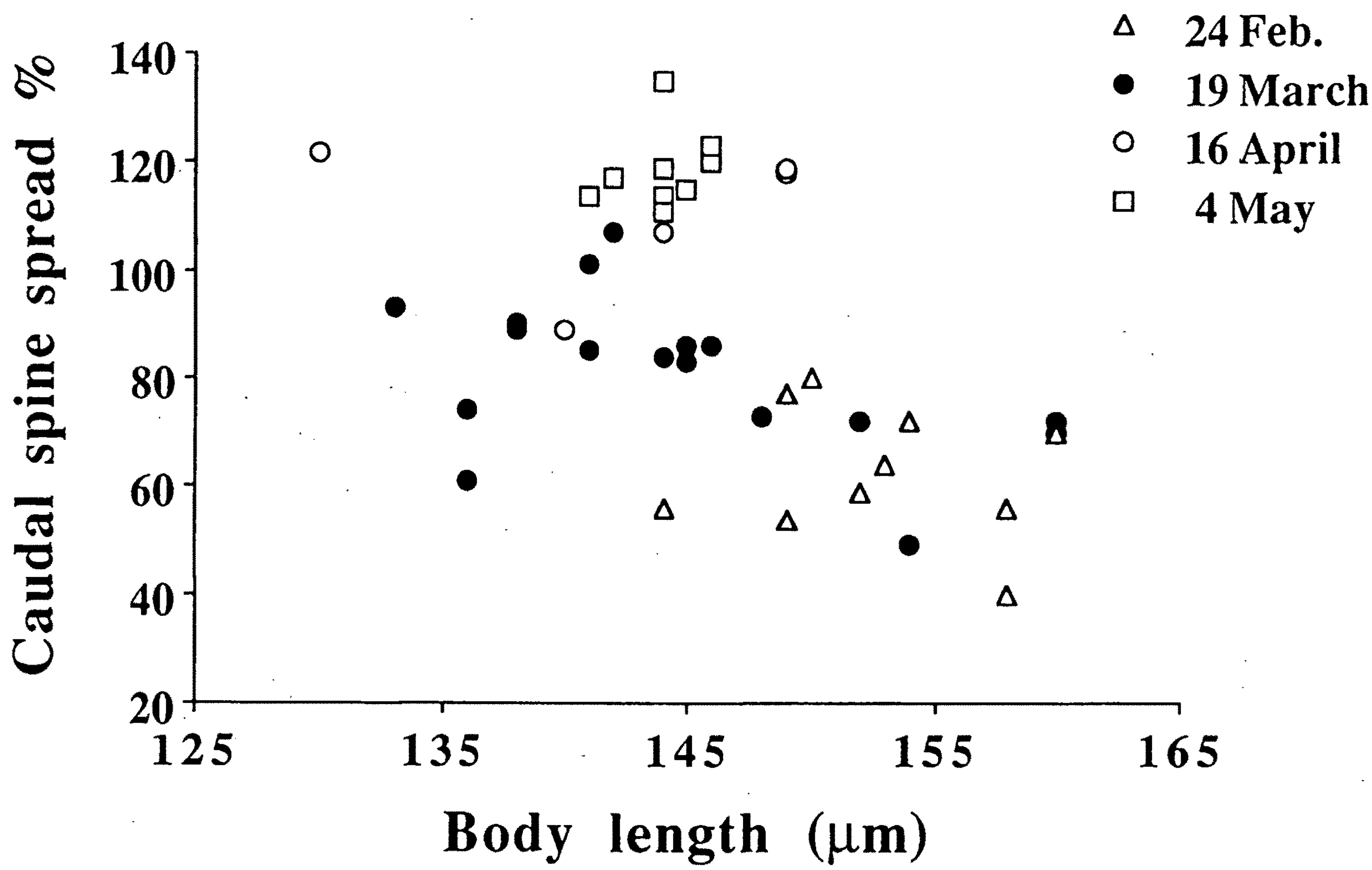

Fig. 6. Relationship between body length and caudal spine spread (expressed as a percentage of body length) on 24 February, 19 March, 16 April, and 4 May.

Fig. 6. Relation entre les longueurs du corps et de l'épine caudale (exprimée en pourcentage de la longueur du corps) les 24 février, 19 mars, 16 avril, et 4 mai.

4. Discussion

For the *Keratella quadrata* populations of the present study, the body and spine lengths increased from winter to spring after which they decreased as summer approached. This general pattern has also been recorded by Hartmann (1920), Carlin (1943) and Ruttner-Kolisko (1949).

It now seems generally accepted that changes in environmental factors are the main cause of the temporal variation in *Keratella*, with the possibility that internal factors may be involved to a small degree (Pejler 1980). The latter author (1962, loc. cit.) considered that, because spine length is strongly correlated to body length, in studies of temporal variation, it is the factors which change body length which are primary. However, Hillbricht-Ilkowska (1983) suggested that body length and caudal spine length may be controlled by separate factors (i.e. temperature and food availability, respectively). In the present study, there was some degree of variability in the body length - spine length relationship, as shown by the changes in the value of the allometric growth factor with time, and the lack of significance of some of the regressions between spine and body lengths. In addition, there was a relatively large decrease only in body length between 24 February and 19 March, so that the spine lengths for the second part of the study period were greater in proportion to the body than for the first part.

Environmental factors implicated in affecting changes in body and spine lengths of rotifers include temperature, food availability, predators, and, perhaps, water hardness (Carlin 1943, Buchner et al. 1957, Gallagher 1957, Pourriot 1964, King 1967, Hutchinson 1967, Lindström & Pejler 1975, Green 1980, Hillbricht-Ilkowska 1983, Lindström 1983, Stemberger & Gilbert 1984, 1987).

In the present study, none of the environmental features measured were significantly correlated consistently positively or negatively with the changes in body and spine lengths recorded during the entire course of the study. However, with regard to the possible effects of predators, it should be noted that the copepodite stages and adults were not enumerated separately or even identified to group. Also, the percentage of ovigerous *K. quadrata* was used as a measure of food availability; more direct measurements (e.g. phytoplankton species abundances, bacterial abundances) would have been more desirable.

In rotifers, a large degree of seasonal and local variation in the morphology of species is known. Some of this has been discussed in the previous section. Some species are more variable than others. *K. quadrata* is extremely variable, having been classified into a number of groups, varieties, forms and subspecies (Carlin 1943, Ahlstrom 1943, Ruttner-Kolisko 1974, Koste 1978) on the basis of such features as body and spine lengths, degree of thickness and pustulation of the lorica, proportional width of the body, and degree of spread (divergence) and stoutness of the caudal spines. The terms form and variety (as for the term morph) should be considered as descriptive, without taxonomic significance, while, in the absence of geographical separation, subspecies classifications should not be applied (Pejler 1977, Koste & Shiel 1989).

In the present study, the specimens on 30 November to 24 February corresponded most closely to the descriptions of *K. quadrata quadrata* by Koste (1978), and the *quadrata* - group by Carlin (1943), approaching the descriptions of *frenzeli* (variety or group) in February. The animals on 16 April to 9 June seemed to resemble *K. quadrata* var. *dispersa* (Koste loc. cit.), corresponding to the *dispersa* - group of Carlin (loc. cit.).

The population found on 19 March seems to have been transitional between the two. One or a comination of two types of transition could have occurred. The first alternative is that both morphs were present. This alternative suggests that one morph was dying out on 19 March, being replaced by the second, hatching, most probably, from resting eggs. The decrease in population density of *Keratella* between this date and its predecessor could be interpreted as reflecting such a succession.

The second alternative is that the first morph underwent a morphological transition, over several asexual generations, to become the second. In support of this hypothesis is the fact that some specimens on 19 March were clearly transitional between 24 February and 16 April with regard to the degree of caudal spine spread. It should also be noted that towards the end of the study period, the morphology seemed to be returning to the general shape encountered in the initial part of the study.

Thus, the mechanism of the change in unclear. The first alternative described implies genetic discontinuity between the two populations at the time of transition. This type of adaptation to seasonal variation of the environment has been suggested by King (1972, 1977) whereby he envisaged a succession of clones replacing each other through time. If indeed two genetically distinct populations occurred during the present study, this could explain why the recorded cyclomorphotic changes in body and spine lengths were not consistently significantly related to any of the environmental features measured (see above); each genotype could have reacted differently to environmental stimuli.

The forms or varieties of this species may vary in their ecological requirements. For example, *K. quadrata* var. *frenzeli* is said to occur mainly in large deep lakes, at moderately low temperatures, whereas *K. quadrata* var. *dispersa* is found more commonly in ponds (Koste 1978). Radwan (1984) found that *K. quadrata frenzeli* avoided waters with pH values above 8, unlike the typical *K. quadrata*. In the present study, the change from one morph to another seems to have been related mainly to one or a combination of the following; increase in temperature and pH, and decrease in total hardness, copepod densities, food availability (probably), and wind-induced turbulence (possibly).

It is recognised that the sample sizes in the present study were often small. A more detailed study of the *Keratella* population in this pond would be desirable using shorter sampling intervals and measuring larger numbers of animals on each date, over the entire annual cycle. This would permit more rigorous statistical analysis than was possible here. Laboratory experiments need to be carried out to investigate the effects of varying environmental factors (including predators) on the morphological changes occuring during the growth of individual animals and from generation to generation. Use of such techniques as isoenzyme analysis would be most valuable in elucidating the nature of the transition between the morphs recorded here (King & Zhao 1987, Koste & Shiel 1989).

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