Morphological variation of *Keratella cochlearis* (Gosse) in a backwater of the River Thames

Jim Green
17 King Edwards Grove, TW11 9LY, Teddington, Middx
E-mail: jimgreen17keg@btinternet.com

Abstract

The morphological variation of *Keratella cochlearis* in a Thames backwater has been studied over 4 years. There was a general inverse relationship between lorica length and temperature, but the annual cycle of change depended upon the rate of change of the temperature, and there was considerable variation between years. There was a similar inverse relationship between posterior spine length and temperature, and a shift in both relationships depending on whether the temperature was increasing or decreasing. As the water temperature increased from winter to summer the lorica and posterior spine were longer than at the same temperature as the water cooled from summer to winter. This shift can be modified by anomalous temperatures, such as a late spring or a cool summer. The form lacking a posterior spine usually, but not consistently, had a longer lorica than the typical spined forms. It usually disappeared from the samples at the end of November and did not reappear until March, although with a mild autumn and winter it persisted until January before disappearing. Forms without posterior spines did not all have the same origins.

Introduction

Any consideration of morphological variation in *Keratella cochlearis* must begin with the work of Lauterborn (1900, 1903). He established the basic aspects of variation in this species by arranging the forms in three main series: *tecta, hispida* and *irregularis*. The name he gave to the first series was unfortunate because it is also the name of the form without a posterior spine that occurs in warm, eutrophic conditions. This series, which I shall call the *typica* series, is characterised by large, long spined forms (*macracantha*) in winter, followed by progressively smaller forms with shorter posterior spines (*typica, micracantha, tuberculata*) until the unspined *tecta* form is reached in summer. Lauterborn found all possible intermediates in this series so that the names are useful descriptors but lack any precise taxonomic

significance. The *hispida* series shows a thinning and shortening of the posterior spine, and characteristic development of pustules and spinules over the surface of the lorica. The *irregularis* series starts with long spined forms, with a kink in the median line of the dorsal sculpture, and proceeds through forms showing the progressive development of a median pentagon in the dorsal sculpture (*connectens, angulifera, irregularis*). A form lacking a posterior spine (*ecaudata*) also occurs. Lauterborn had thus shown two separate routes to unspined forms, so the use of the name *tecta* without careful examination of the dorsal sculpture is not valid.

Many aspects of Lauterborn's findings have been confirmed and extended by more recent work (Pejler, 1957, 1962, 1980; Hillbricht-Ilkowska, 1972; Ruttner-Kolisko, 1974; Koste, 1978; Hofmann, 1980, 1983; Eloranta, 1982). These

authors also made emendments to Lauterborn's interpretations. For instance Hofmann (1980) found that in many Holstein lakes the typical *cochlearis, hispida* and *tecta* forms were clearly separated. He found no intermediates between typical *cochlearis* and *tecta*, and the lorica length of the latter was consistently greater, so could not be the end of a reduction series. The *tecta* forms were also abundant in autumn, when the spine length of *cochlearis* was increasing. This implies a third type without a posterior spine, not derived from the *typica* series. Some authors have also raised *irregularis* and *hispida* to separate species (e.g. Ahlstrom, 1943; Eloranta, 1982).

My observations on *K. cochlearis* in Broom Water began in August 1997, when Athene Jones drew my attention to an outburst of the freshwater medusa *Craspedacusta sowerbyi* (Lankester) (Green, 1998), but regular sampling did not begin until the end of 1998. The aim was to see how far the population in this part of the Thames conformed to the findings of Lauterborn and the other authors mentioned above.

The habitat

Broom Water is an artificial cut extending about 250 m from the main channel of the Thames above the weir at Teddington (Fig. 1). It is about 8 m wide and serves as a mooring area for numerous small boats of householders with gardens extending down to the water. The water is fresh, with conductivities ranging between 400 and 500 μS cm^{-1}. The water is open to fish movement from the main Thames, and serves as a spawning area for large carp (*Cyprinus carpio* Linn.) and as a nursery for young roach (*Rutilus rutilus* (Linn.)).

Methods

Samples were taken from the bank using a 55 μm meshed net. They were preserved in 4% formaldehyde, and subsamples were examined on a slide under a long coverslip. The slide was moved by a mechanical stage, so the sequence in which rotifers were encountered was essentially random. Measurements were made at a magnification of 400$\times$ using a calibrated eyepiece micrometer, using the limits shown in Green (1998). The normal sample size was 30, but this was sometimes increased to 50, and more rarely to 100. For most samples the standard errors of the means were <1 μm.

Results

Seasonal variation in lorica and spine length

Figure 2 shows variation in lorica length and spine length in specimens bearing any form of posterior spine over a period of 4 years. There was a regular decline in both dimensions during the summer. The most notable feature was the anomaly during the winter of 2001/2 when the lengths of the lorica and spine did not increase to the extent that they had in the previous three years.
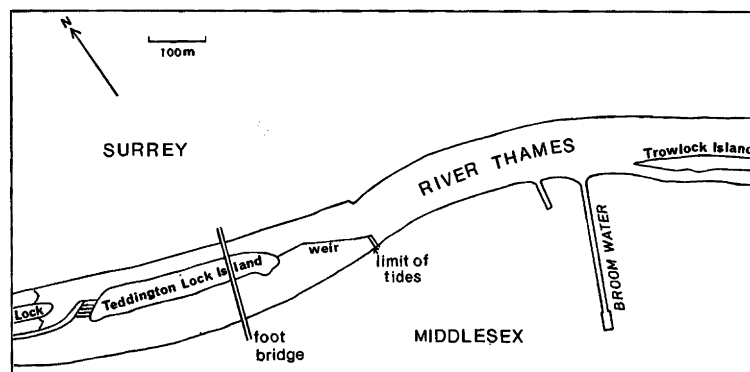

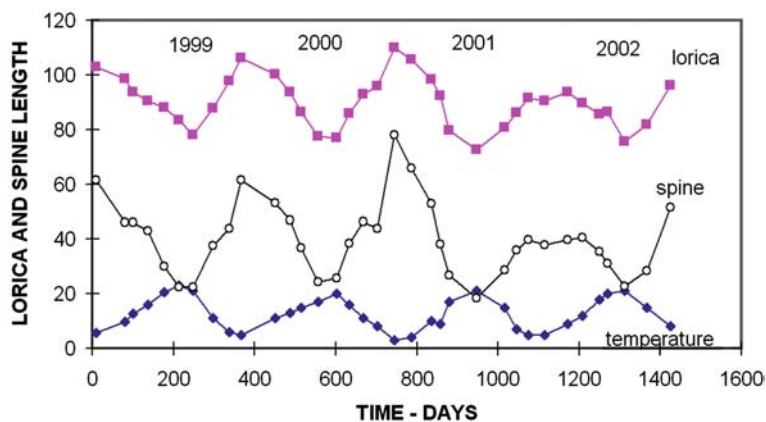*Figure 1.* Sketchmap to show the location of Broom Water.

Figure 2. Temporal variation in temperature, lorica length and spine length (μm) in *Keratella cochlearis* in Broom Water over 4 years. The standard errors for each point are small enough to be contained within the symbol.

Lorica length and temperature

Figure 3 shows the general relationship for all 4 years combined. Both the lorica and the posterior spine decreased with increasing temperature. Figure 4 shows the sequential changes in each of the 4 years. In 1999 there was a smooth progression, with the lorica length decreasing steadily as the temperature increased. From September to December the lorica length increased steadily, but along a line below that of the changes in springtime. The other years do not show such a smooth relationship, partly because the temperature changed at different rates. For instance the September 1999 sample was taken when the water temperature was 21 °C, while in September 2000 the water temperature was 16 °C. These differences in the temperatures in different years altered the slope of the relationship between temperature and lorica length. Figure 5 shows the regression lines calculated for the 4 years. In 2000 and 2001 the slopes were significantly steeper than in 1999 and 2002. The regression coefficients for 1999 and 2000 differed at the level $p <$ 0.005, >0.001, but there was no difference between 1999 and 2002.
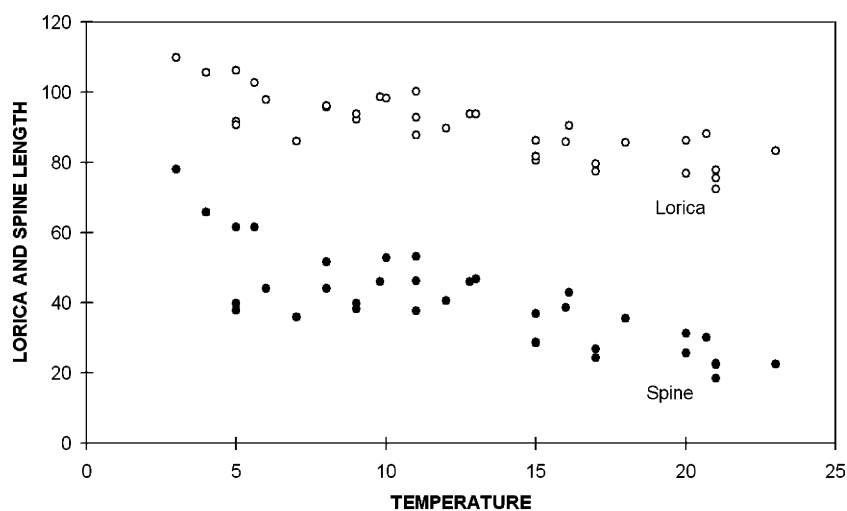

Figure 3. The general relationship between temperature and the lengths (μm) of the loricas and posterior spines of *Keratella cochlearis* in Broom Water.
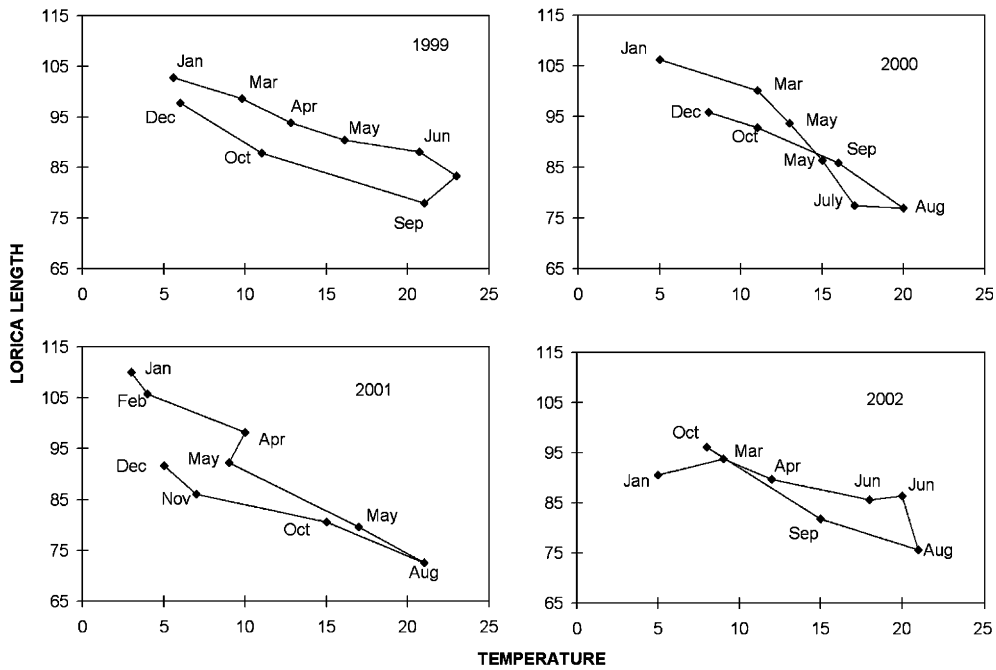
Figure 4. Sequential variation in the relationship between temperature and lorica length (μm) of *Keratella cochlearis* in Broom Water in 4 years.
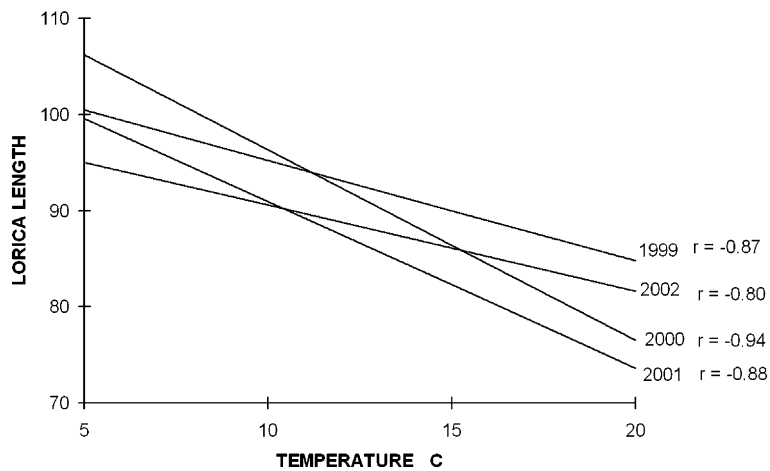

Figure 5. Regression lines for the 4 years shown in Fig. 4.

Lorica and posterior spine length

Figure 6 shows the relationship between lorica and posterior spine length for all 4 years combined. The correlation is high ($r = +0.956$).

Lorica lengths of spined and unspined forms

Figure 7 shows seasonal variation in the loricas over 4 years. Specimens without spines were absent in January–February and November–December 1999, January–February 2000, January–March 2001, and February–March 2002, but enough were found to measure in January 2002. The main point made by Figure 7 is that the unspined forms in Broom Water generally have longer loricas than the spined forms. This was particularly notable in December 2001 and January 2002.
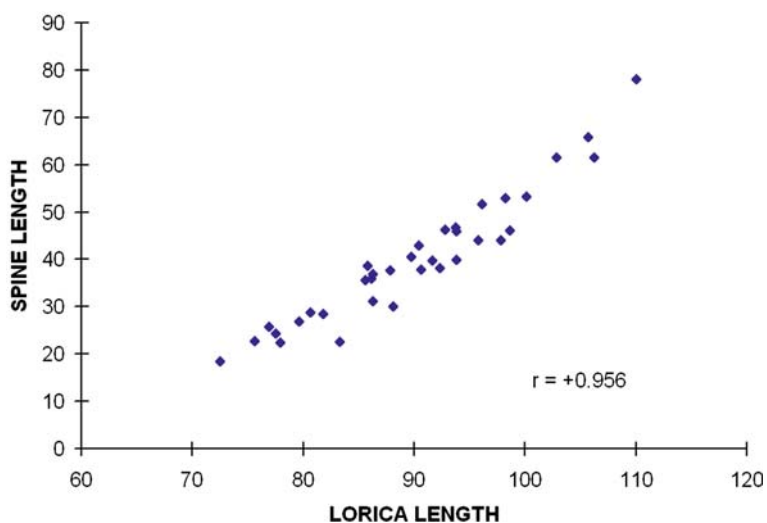
Figure 6. *Keratella cochlearis* in Broom Water, the relationship between lorica length and spine length (μm).
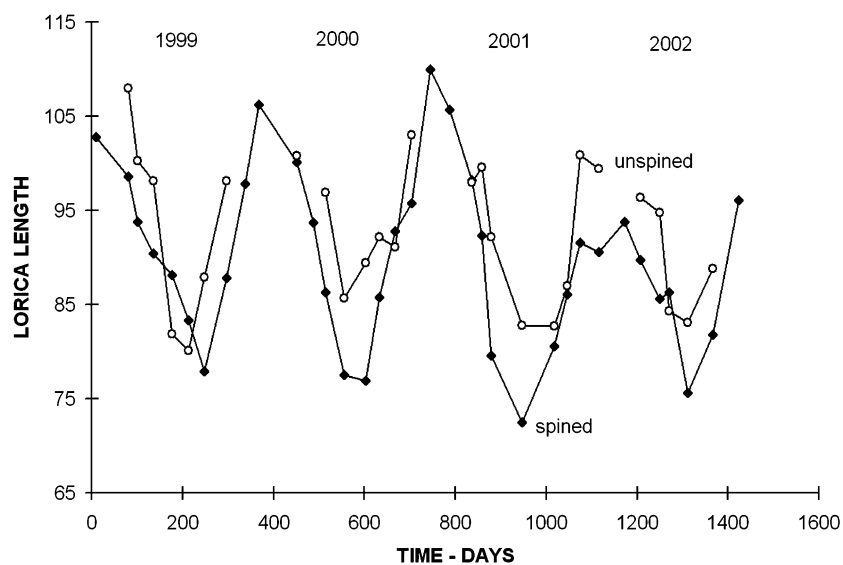

Figure 7. Temporal variation in lorica length (μm) of spined and unspined *Keratella cochlearis* in Broom Water. The standard errors of the means do not exceed one symbol width above and below each point.

Bimodality of unspined forms

Figure 8 shows the results from a sample taken on 29 September 2002. In this sample it was possible to distinguish forms with a somewhat more acuminate posterior end, like Lauterborn's figure 9. These had significantly shorter loricas than those with more rounded posterior ends.

Occurrence of irregularis *and* hispida *forms*

These forms were not usually common in Broom Water, but on 4 August 01 both were present: *irregularis* formed about 12% of the spined forms, and *hispida* about 0.5%. The *irregularis* were significantly larger (lorica length 83.3 ± 0.9 μm) than the typical form (lorica length 72.5 ± 0.3 μm).
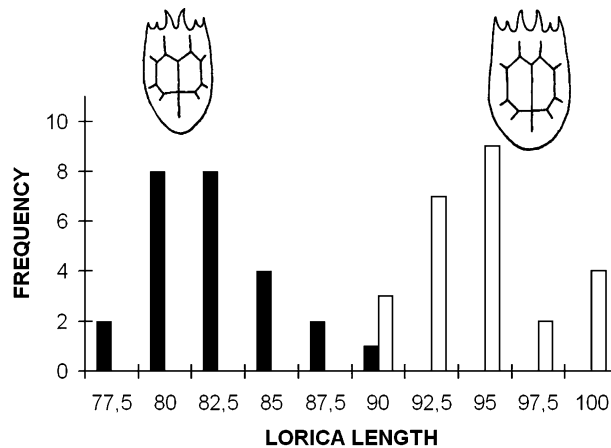
Figure 8. Bimodalism in lorica lengths (μm) of unspined *Keratella cochlearis* in Broom Water, 29 September 02.

Only one *hispida* was available for measurement. This had a lorica length of 85 μm, which was larger than any of the *typica* measured on the same day. In the same sample a single specimen without a posterior spine, but with an *irregularis* dorsal sculpture had a lorica length of 88 μm, which was larger than any of the *irregularis* with spines.

Discussion

The seasonal variations in lorica and posterior spine lengths of *K. cochlearis* in Broom Water are in general agreement with those observed by Lauterborn, and many other investigators, but Figure 2 shows an anomaly in the winter of 2001/2, when the spine lengths were only two thirds of those found in the previous 3 years. The water temperature had fallen to the same level as previous winters, so other factors must have been operating. The relationship between spine length and lorica length can be changed by variation in the food supply. Hillbricht-Ilkowska (1983) found an increase in lorica length from 89 to 94 μm between October and December, while the posterior spine decreased from 64 to 35 μm. This happened in the southern basin of Lake Biwa, Japan, during a period of nannoplankton abundance, and was accompanied by an increase in the fecundity of the rotifer.

The relationship between spine length and temperature can vary significantly from year to year. Predation pressure is a major factor contributing to this variation (Conde-Porcuna et al., 1993). At a given temperature when predation is high the spines are longer. Long spines give protection against predation by *Asplanchna*, but very short spines appear to offer less protection than being unspined. Conde-Porcuna et al. (1993) found positive selection by *Asplanchna* for individuals with spines less than 15 μm in length. This could be part of an explanation for the lack of intermediates between *micraspina* and *tecta* in some studies.

In Broom Water there was a strong correlation between lorica and spine length. Regression lines for each year show that spine length would reach zero at a lorica length between 60 and 65 μm. This was well below the actual lengths of the unspined forms in this locality. A precisely similar relationship was found by Bielanska-Grajner (1995) in Rybnik Reservoir, Poland. Figure 7 shows that the loricas of unspined forms in Broom Water were generally longer than those of the typical spined forms at any given time. But there were occasions when the unspined forms were as small, or even smaller than the typical forms. These could be produced from small (*micracantha* and *tuberculata*) parents at high temperatures. This was particularly well shown in June 1999, when the spineless loricas had a mean length of 82 (SE ± 0.7) μm while the typical forms were 88 (SE ± 1.04) μm. Very short spined forms (*micracantha* and *tuberculata*) were present at the time, and the water temperature was 20.7 °C. Evidence that unspined forms may have more than

one origin is provided by Figure 8. The morphological differences between the two forms are subtle, but the lorica lengths fell into two clear groups. Overall the samples from Broom Water indicate three possible origins for forms without posterior spines:

(1) As the end of a reduction series – the true *tecta*, occurring from June to September.
(2) An unspined form with a longer lorica than co-occurring typical forms, and absent from samples only in January and February. Most authors would call this *tecta* but it is not the end of a reduction series, and showed seasonal changes paralleling those of the typical form (Fig. 7). The name *aspina* is proposed for these, as a descriptor without taxonomic significance, to separate them from the true *tecta*.
(3) An unspined form with the same dorsal sculpture, but having a longer lorica than co-occurring *irregularis*, and occurring in summer (*ecaudata*).

The origins of the true *tecta* are supported by the experimental work of Stemberger & Gilbert (1984) showing that unspined forms could be induced to develop posterior spines by a water soluble factor released by cyclopoid copepods. From the true *tecta* they induced *tuberculata, micracantha* and *typica*, showing that they can all be derived from a single genotype. Their figure of *tecta* corresponds to the acuminate form from Broom Water. The recent work of Derry et al. (2003) appears at first sight to be incompatible with the results of Stemberger & Gilbert. They found 'a deep genetic divergence' between spined and unspined forms of *K. cochlearis*. Unfortunately they did not figure the forms they analysed, so it is not known what the dorsal sculpture or the shape of the posterior part of the lorica were like. If the form they analysed was the second of those described above (i.e. *aspina*) it is perfectly possible for it to show genetic divergence from the spined form. A similar result could possibly be obtained with the *ecaudata* form of *irregularis*. On morphological grounds one would expect these to show some genetic divergence from *typica* and the true *tecta*.

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