VISCO-ELASTIC PROPERTIES OF THE MESOGLOEA OF JELLYFISH

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INTRODUCTION

The creep of the body-wall of sea anemones (Anthozoa) under constant tensile stress has recently been investigated (Alexander, 1962). It seemed to be controlled by the mesogloea. Similar experiments have now been carried out on the mesogloea of jellyfish (Scyphozoa).

The sea anemone Metridium is capable of spectacular changes of size, which are achieved in periods of the order of one hour (Batham & Pantin, 1950). The creep properties of the mesogloea to large strains and over long times are of considerable importance to the life of this animal. These properties are not, however, of any functional importance in jellyfish, as the distortions of the bell in swimming are completed in periods of the order of 1 sec. They are interesting, however, in relation to the structure of the mesogloea.

The strain which occurs when a polymer is subjected to a constant stress can conveniently be regarded as the sum of three components: instantaneous purely elastic strain, slow elastic strain which occurs at a gradually decreasing rate, and (in non-cross-linked polymers) purely viscous strain which occurs at a constant rate. The gradient of a graph of the slow elastic component against the logarithm of time has a broad maximum; commonly the gradient is more or less constant over a period of several factors of 10 of time (Tobolsky, Dunnell & Andrews, 1951). The slow elastic component can conveniently be described in terms of a distribution of retardation times, \( L(\log \tau) \), which is given approximately by this distribution of gradients (Alfrey & Doty, 1945). \( L(\log \tau) \) thus has a broad maximum. This is true of gels as well as pure polymers (Bisschops, 1954; Hastewell & Roscoe, 1956). The experiments of Fukada & Date (1963) on solutions of collagen in dilute hydrochloric acid are particularly relevant to this paper since the mesogloea proteins of both sea anemones and jelly fish are regarded as collagens (see Chapman, 1953a, 1959; Grimstone, Horne, Pantin & Robson, 1958, and Gross, Dumsha & Glazer, 1958). Fukada & Date carried out dynamic experiments from which they calculated a distribution of relaxation times. This was found to be broad, and implies a broad distribution of retardation times.

The body-wall of sea anemones is remarkable for having a very narrow distribution of retardation times; indeed, the course of creep can be described rather closely in terms of a single retardation time (Alexander, 1962). In this it contrasts so sharply with all pure polymers and solutions of polymers that have been investigated that it
seems probable that it is due to two polymeric systems, one cross-linked and the other not, acting in parallel. It was suggested that these might be the fibres and the matrix of the mesogloea (Alexander, 1962). It will be shown in this paper that the mesogloea of jellyfish does not behave in this way, but has a wide distribution of retardation times.

MATERIALS AND METHOD

The same apparatus was used as for the experiments on sea anemones (Alexander, 1962). This apparatus is designed to apply a constant tensile stress to a portion, of unstressed length 1 cm., of a strip of tissue. The load at zero strain is 5 g. The course of strain is recorded on a smoked drum. The apparatus gives a reliable record of the course of slow elastic creep (for times greater than about 1 sec.) and pure viscous creep, but values for instantaneous strain are unreliable owing to strain in the apparatus and errors in the initial tautening of the specimen. Creep recovery as well as creep can be investigated.

Three experiments were carried out on strips of mesogloea cut from a specimen of *Cyanea capillata* (L.) whose diameter was 25 cm. They were taken from the umbrella peripheral to the gastric cavity, and were stretched in the radial direction. Each had a cross-sectional area of about 4 cm.². The ligatures, 1 cm. apart, which were required for attaching the specimens to the apparatus were of Pearsall's plaited silk no. 12. This material is thick enough to be tied quite tightly round pieces of mesogloea without cutting them. As the specimens consisted of mesogloea alone, narcosis was considered unnecessary. They were stretched in sea water.

Experiments were also carried out on strips of *Chysaora hysoscella* (L.). The edges of these strips were the edge of the umbrella and the edge of the gastric cavity, and they were stretched in the circumferential direction. They included muscle and epithelium as well as mesogloea. The ligatures were of Pearsall's Chinese twist silk no. 3. As the strips were much broader than they were thick, they had to be rolled about the axis of stretching before they were tied. Circumferential stretching was preferred for convenience of rolling. One of the *Chrysaora* had a diameter of 14 cm., and the strips cut from it were estimated to have cross-sectional areas of about 2 cm.². The others had diameters of about 10 cm. and the areas were about 1 cm². The *Chrysaora* were narcotized with magnesium chloride and stretched in the narcotic solution, as in the experiments with sea anemones (Alexander, 1962).

RESULTS

The results of the experiments with *Cyanea* are shown in Figs. 1 and 2. After an apparent instantaneous strain of about 0.5 (it should be remembered that the method does not give reliable values for instantaneous strain) the specimens stretched at a continuously decreasing rate, until after 10 hr. they had reached a strain of about 2 which was increasing extremely slowly (at about 0.015/hr.). If there was any pure viscous strain, the rates of pure viscous strain cannot have been greater than these very low final rates of strain. Most of the difference between the instantaneous strain and the total strain must thus be slow elastic strain, and the distributions of gradients on the graphs of strain against the logarithm of time can be taken as giving approximately the distribution of retardation times, \( L (\log t) \). From examination of Fig. 2 it appears
that $L(\log r)$ is low at small times, and higher and, within a factor of 2, constant from 200 sec. to the ends of the experiments at about 100,000 sec.

In comparing the creep-recovery curves with the creep curves it should be noted that the values for creep include the instantaneous strain, while those for recovery do
not, as the strain was re-imposed momentarily for the taking of each reading, as in the experiments on sea anemones (Alexander, 1962). Creep recovery was found to be much slower than creep, and was very far from complete when the experiments were ended. Since creep was allowed to continue until the rate of creep was extremely low, the recovery curve (after addition of the instantaneous strain) would coincide with the creep curve at short times if the mesogloea behaved in accordance with the Boltzmann superposition principle (the long duration test of Leaderman, 1943). It plainly does not so behave. The very slow recovery is probably due to crystallization of the strained mesogloea (for accounts of similar behaviour in rubber and polyethylene see Treloar, 1940, and Ferry, 1961, respectively).

![Graph](image)

Fig. 3. The time courses of creep (continuous lines) and recovery (broken line) in experiments on 14 cm. (○) and 10 cm. (●) Chrysaora.

The results of the experiments on Chrysaora were of two types. These are represented by the two examples shown in Figs. 3 and 4. In the two experiments in which strips from the 14 cm. Chrysaora were used, the results were closely similar to the results of the experiments with Cyanea. The compliances were rather lower (the Chrysaora strips were thinner than the Cyanea strips) but the Cyanea specimens lacked the surface layers of the mesogloea which in at least some jellyfish are particularly rich in fibres (Chapman, 1959). Few fibres can be seen in Cyanea. Some of the difference may have been due to the different directions of stretching.

In all the experiments with strips from 10 cm. Chrysaora the rates of strain at long times were very much higher. It seems probable that bonds which held in the experiments with the larger specimens broke under the higher strains in the experiments with smaller specimens, so that there was an important purely viscous component in the behaviour of these specimens. Some flow of the mesogloea through the ligatures
apparently occurred in these experiments, so that part of the recorded strain was outside the original 1 cm. specimen. In several cases one of the ligatures eventually slipped off the specimen.

An experiment with a strip from a 10 cm. Chrysaora from which the subumbrellar muscle had been removed gave a result indistinguishable from the results of the other experiments with 10 cm. Chrysaora.

DISCUSSION

The visco-elastic properties of the mesogloea of the jellyfish Cyanea and Chrysaora are rather different from those of the body-wall (believed to be due to the mesogloea) of the sea anemones Metridium and Calliactis (Alexander, 1962). The results of typical experiments with Cyanea and Metridium are compared in Fig. 5. The loads were the same, and (though it had not reached constant length at the end of the experiment) the Cyanea specimen, whose initial cross-sectional area was about 4 cm.², reached as high a strain as the Metridium specimen, with mesogloea of about 0.1 cm.² initial cross-sectional area, which did achieve constant length. Jellyfish mesogloea plainly has a much higher compliance than sea anemone mesogloea.

Chapman (1953a) found that Chrysaora mesogloea contained only 0.11% dry matter insoluble in boiling water (presumably mainly protein). A similar determination on a sample of mesogloea from the anemone Calliactis has given a value of 14%. This value is very probably much too high, as the cutting and scraping necessary to isolate Calliactis mesogloea causes considerable compaction (see Chapman, 1953b), and the fluid lost in compaction seems likely to have a lower protein content than the material that remains. Nevertheless, it seems plain that the protein content of Calli-
actis mesogloea is immensely higher than that of Chrysaora mesogloea. The great difference in compliance between anemone and jellyfish mesogloea must be mainly due to this difference in concentration.

The distribution of retardation times for sea anemone body-wall is remarkably narrow, suggesting, as has been noted, a two-phase system, while that for jellyfish mesogloea is broad, as for homogeneous polymers and gels (these distributions are indicated by the distributions of gradients in Fig. 5). Jellyfish and sea anemone mesogloea, however, both have the appearance of a jelly permeated by branching fibres which seem to be concentrations of the matrix, though the fibres are more densely packed in anemones than in jellyfish (Chapman 1953a, 1959).

Creep recovery experiments (equivalent to the long duration test of Leaderman, 1943) showed that sea anemone body-wall behaves approximately in accordance with the Boltzmann superposition principle, while jellyfish mesogloea does not, recovering much too slowly. Presumably stretching results in crystallization in jellyfish but not in anemone mesogloea.

SUMMARY

The mesogloea of Scyphozoa (Cyanea and Chrysaora) differs from that of Anthozoa in having higher elastic compliance, in having a broad distribution of retardation times, and in that creep recovery is very slow. In the second of these properties the scyphozoan mesogloea resembles simple polymeric gels.

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REFERENCES


