GROWTH AND LIFE-SPAN OF SEPIA OFFICINALIS UNDER ARTIFICIAL CONDITIONS (MOLLUSCA, CEPHALOPODA)

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RESUME. L'auteur décrit les résultats d'une série d'élevages effectués pour la plupart dans des conditions très artificielles. Des animaux soumis à une sous-nutrition continue qui ne permet qu'une faible croissance, peuvent atteindre le stade adulte plus ou moins tardivement. La durée de vie maximale a en effet été observée, dans ces élevages, chez des animaux à très faible taux de croissance. Ces conditions très artificielles de croissance ne correspondent pas aux conditions naturelles, du moins en ce qui concerne les Seiches de la Méditerranée. Cependant la remarquable "souplesse" physiologique des animaux pourrait prendre son importance dans le milieu naturel lors de profonds changements des conditions écologiques.

INTRODUCTION

Sepia officinalis L. is one of the few cephalopod species that have been studied in detail over their entire life cycle. In addition to the embryological investigations (NAEF, 1928; RANZI, 1931; LEMAIRE, 1970) and the anatomical and biological studies on young and adult animals (DENTON and GILPIN-BROWN, 1961; MANGOLD-WIRZ, 1963; SCHIPP and SCHAEFER, 1969; BOUCAUD-CAMOU, 1976; CHICHERY and CHANELET, 1978), the entire life cycle has been studied in the context of an analysis of growth and sexual maturation (RICHARD, 1971).

The results presented here give a few complementary indications on the consequences of artificially reduced growth rates (BOLETZKY, 1974). Despite the comparatively high mortality ensuing from continuous underfeeding (either by food deprivation or by inappropriate diets), an animal surviving under these conditions demonstrates that the organism can cope with them. Certain "adaptations" are observed in such individuals (SCHIPP and BOLETZKY, 1976; BOLETZKY and WIEDMANN, in prep.).

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The capacity to survive under extremely unfavourable feeding conditions, rarely encountered in the natural environment, opens interesting perspectives, for experimentation as well as for interpretations concerning obscure events in the history of the cephalopods.

MATERIAL AND METHODS

Sepia officinalis were hatched from eggs that had been laid in the laboratory by animals captured in the area of Banyuls-sur-Mer (Western Mediterranean). The hatchlings generally have a dorsal mantle-length (ML) of 8 to 9 mm. In one experiment (E) smaller hatchlings (ML 6 - 8 mm) were included (the small size is due either to premature hatching and loss of the remaining outer yolk sac, or to smaller egg-size). Such animals may grow normally, but they lag behind the animals hatched at larger sizes.

If not stated otherwise, the rearing tanks were 45 - 50 liter aquaria, either round and made of PVC, 40 cm in diameter and height, or rectangular plexiglass tanks with covered walls, 40 X 60 cm, 20 cm deep. Batches of young animals were kept each together in one of these tanks. Larger sub-adult animals were distributed in individual tanks to avoid mutual interference and uncontrolled mating, which always causes considerable agitation among animals living in confinement.

The experiments under continuous light were made in a room entirely isolated from day-light. The tanks were illuminated from above by a fluorescent tube suspended 60 to 75 cm above the water surface (PHILIPS TLS 40 W/33 "blanc industrie").

The living prey offered were: mysids for hatchlings; small palaemonid and crangonid prawns and very small crabs as well as small fish (mainly gobiids, occasionally small soles) for larger juveniles; larger fish and prawn, but predominantly crabs of appropriate size (carapace width not more than 50 % of mantle-length of Sepia) for sub-adults and adults. The animals that were systematically underfed received only small quantities of these food items or small pieces of crab that are readily taken by hungry cuttlefish. It was also found that Artemia represents a very poor food for Sepia. Hatchlings presented with a choice of mysids and Artemia or amphipods always take the mysids. When presented with amphipods only, they attack the prey only occasionally when very hungry. Thus facultative underfeeding ensued despite super-abundance of prey, which was, however, inappropriate.

Food intake was not quantified. *Ad libitum* conditions were maintained by offering some (not excessive!) surplus food. With the underfed animals, care was taken that they were always able to regulate their buoyancy (DENTON and GILPIN-BROWN, 1961) and would stay on the bottom when they were inactive. Starving animals floating up must be fed immediately, if necessary in a vessel containing little water, so that living prey can not escape from the attacking cuttlefish. Severely underfed animals often present a dark strip on the dorsal midline of the mantle (persistent contraction of the pigmented integument). This sign of malnutrition can remain distinct even after the animal has been fed abundantly.

Living animals were measured in water, either in their rearing tank or in a smaller dish. For checking the state of maturation, the animals were anaesthetized in 2 % ethanol in sea water; the funnel-locking was carefully disconnected, and the mantle cavity was viewed under bright light. With a pipette of appropriate diameter, the oviducal opening of females and the penal opening of males was sucked; fully mature, free ovarian eggs and spermatophores can thus be extracted without causing any lesion in the animal.

RESULTS

Representative periods of growth and the maximal life-span in different batches of *Sepia* reared in the laboratory are presented in Figures 1 and 2. Details concerning numbers of animals, rearing conditions and circumstances of the accidental or intentional close of an experiment are given in the following short records.

A. Batch of originally 10 animals, hatched 23 June 1976, reared in natural day light in a 500 liter tank, fed *ad lib*. Of the 5 animals remaining 150 days after hatching, the smallest specimen ceased growing; it died aged 280 days. This was a mature male, with a dorsal ML of 55 mm, spermatophores 5 mm long (this specimen is not represented in the graph). The 4 larger animals were 3 females and one male; one female was much larger (ML 124) than the other 3 animals (ML 80 - 87) at the last check, 312 days after hatching. At that time, the females approached sexual maturity, the accessory nidamental glands were orange (RICHARD, 1971). These females died one month later after a stoppage of the water supply. The male survived for another week and was fully mature when it died aged 345 days (spermatophores 6 - 7 mm long).

B. Batch of originally 10 animals, hatched 19 June 1976, reared at constant light in a rectangular 50 liter tank, fed ad lib. Of the 6 animals alive 130 days after hatching, one was much smaller than the rest; it was transferred to a separate tank. This male specimen grew to a size of 73 mm (ML) and was fully mature at the age of 400 days (not represented in the graph). Of the 5 animals of the batch, two (ML 53, 84) were killed at the age of 170 days. Both were immature. The larger animal, a female, had an ovary at stage 3 of vitellogenesis (staging of RICHARD). When 200 days old, the remaining 3 animals were separated in individual 50 liter tanks. They were checked 310 days after hatching, and the two males only were fully mature (ML 115, 120), with spermatophores ca 8 mm long. One died one month later. When 385 days old, the female was in bad condition (degenerating skin, no buoyancy control) and was killed. It had large nidamental glands and orange accessory glands. The ovary was small, the largest ovarian eggs measured 4 mm and still showed the network of follicular folds. The remaining male continued to grow and died aged 440 days.

C. Batch of originally 10 animals, hatched 20 June 1976, reared in continuous light in a rectangular 10 liter tank during the first month, afterwards in a rectangular 50 liter tank. Food was offered regularly, but not in super-abundance. The 7 animals remaining 175 days after hatching were killed for an analysis of individual variations in the cuttlebone structure. There were 6 females (ML 40 - 54) and 1 male (ML 62), all were immature.

D. Batch of originally 10 animals, hatched 25 and 26 August 1976, reared in constant light under conditions similar to C, but at different water temperatures. Of the 5 animals surviving beyond the sixth month, 3 reached the age of 1 year. They were killed aged 350 days. One (ML 72) was a female, with orange accessory glands and an ovary about 10 mm in diameter. The largest ovarian eggs measured slightly over 3 mm and showed the typical network of follicular folds. The 2 larger animals (ML 85, 87) were males, fully mature, both with a testis about 13 mm in diameter and with spermatophores measuring 7 mm.

E. Batch of originally 15 animals, hatched between 6 and 10 September 1976, at different sizes (ML 6 - 9), reared in continuous light and conditions similar to D, except for food supply. The animals were systematically underfed; 8 animals died during the first two months. After 10 months, only 2 animals survived and were from then on fed more abundantly. Of these, one died aged 405 days (immature female, ML 35), whereas the remaining male specimen reached the age of 2 years, growing continually until 2 months before dying.

F. Batch of originally 15 animals, hatched between 3 and 7 May 1977, reared in continuous light and conditions similar to C. After 4 $^1/_2$ months the 10 remaining animals were distributed into two batches, one (F) with 6 animals (ML 39 - 65), the other (F') with 4 small animals (36 - 45). The F individuals were sacrificed at the age of 170 days. The three smaller specimens (ML 49 - 57) were all females, the larger ones (ML 61 - 80) were males. All were immature. Of the 4 F' individuals, 2 females died, one aged ca. 230 days (ML 41), the other aged ca. 275 days (ML 48), both were immature. The remaining two, a male and a female, differed greatly in size. At the age of 1 year, they were checked under anaesthesia. The male (ML 110) was fully mature, the female (ML 70) had light orange accessory glands. During the following two months, the growth rate of this female increased, whereas the growth of the male came to an end. The female started spawning, one day after mating, at the age of nearly 15 months (ca 450 days). The envelopes of the ca 300 eggs laid in the first ten days were entirely unpigmented (in contrast to the greyish eggs often observed in normal egg masses, there was no trace of ink in these envelopes). The embryos were normal. The first pigmented eggs were laid after 17 days of spawning. The animal continued to eat readily several crabs or fish per day. However, it grew increasingly "skinny" and died aged ca 510 days, 2 months after the onset of spawning, 1 month after the male.

G. Batch of originally 50 animals, hatched 21 July 1977, reared in continuous light, for the first month in a rectangular glass tank 10 X 15 cm, 15 cm deep (ca 1 liter !). The ten largest animals were then transferred to a 50 liter tank. Feeding was maintained below optimum conditions. Despite regular growth at a rather low rate, 5 of the 10 animals died between days 125 and 145 of hatching. When the temperature descended below 15°C, the water was heated to 17°C, and after a few days to 20°C. However, four more animals died within the following days. Only one survived and continued to grow. The water heating was maintained until the environmental temperatures approached 20°C. By that time the animal, a male, was 1 year old. At the moment of this report, it is still alive, aged 16 months.

H. Batch of originally 25 animals, hatched 30 June 1977, reared in natural day-light (+ artificial room light during day-time) in a round 50 liter tank with regular, but scanty food supply. After 50 days, 10 of the remaining 20 animals were killed. Five died during the following month. Of the last 5, only 2 survived to the age of 1 year; both were males. One died aged nearly 400 days (ML 43) and was mature. The other one is still alive at the time of this report, aged nearly 500 days.

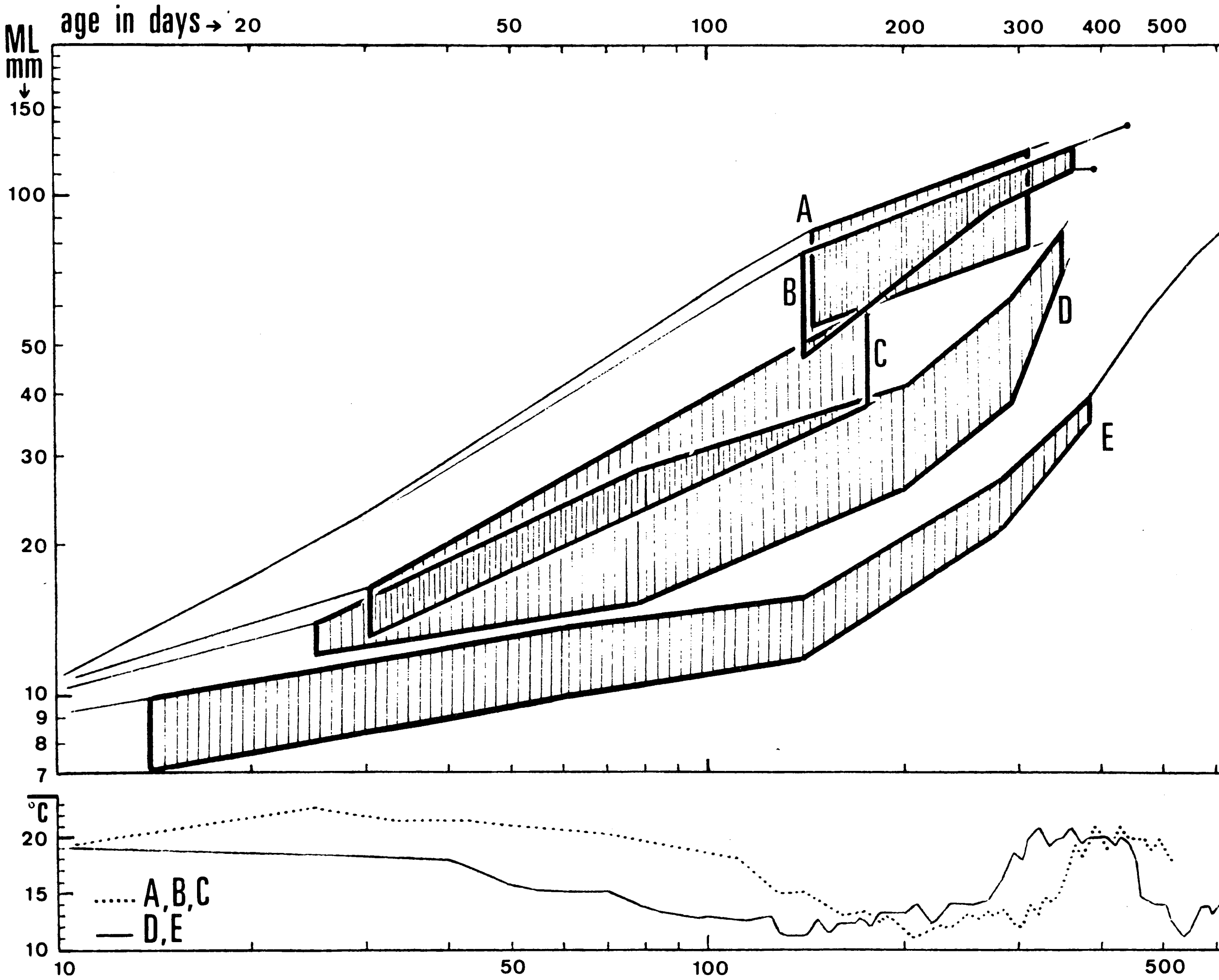

Fig. 1 - Growth in the five batches, A to E, of <u>Sepia officinalis</u>, hat
in the laboratory and reared under different conditions (see text). Th
water temperature (open system of running sea water) is indicated in th
lower part of the figure. ML = dorsal mantle-length.

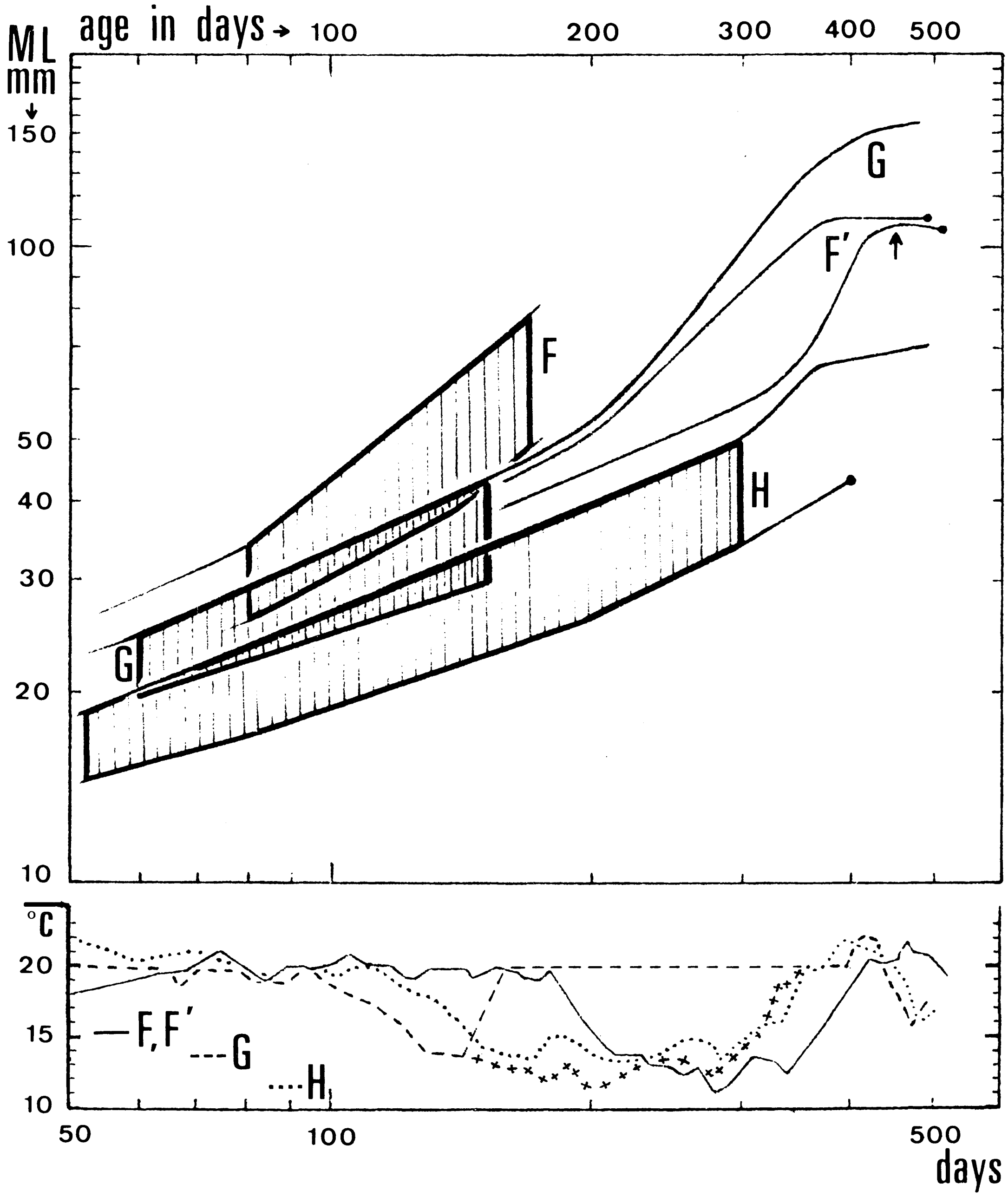

Fig. 2 - Growth in the four batches, F to H, of *Sepia officinalis*, hatched in the laboratory and reared under different conditions (cf. Fig. 1). Crosses in the temperature curve for G represent the temperature of the open system (see text).

DISCUSSION

It has been shown by RICHARD (1966, 1971) that the growth rate of *Sepia officinalis* depends on the water temperature, and that the animals growing slowly at low temperatures have a greater life-span than those attaining the adult stage early due to rapid growth. Thus large animals with mantle-lengths over 200 mm are at least 1 $^1/_2$ to 2 years old. In an unpublished report on rearing experiments made in 1961 and 1962, DENTON estimates that cuttlefish spawning in the Plymouth area are at least 22 months old.

In the laboratory, it is generally difficult to provide living conditions that allow the animals to grow to the largest sizes observed in wild adults. However, the observations described above show that a life-span of 2 years can be obtained under highly artificial conditions, in very limited aquarium space.

Maintaining growth at a low rate makes it possible even at comparatively high temperatures. Combination of constant low temperature and continuous underfeeding would probably yield even greater life-spans.

Although the longest survival in these experiments was observed in animals reared in continuous light, similar results can probably be obtained in a normal day/night cycle. The optimum growth conditions in our experiments (batches A and B) were practically identical in both situations.

For many long-term experiments it is necessary to keep living animals over many months in aquaria; underfed, small, but otherwise normal cuttlefish are an ideal material for many physiological and ethological experiments.

As underfed animals can finally reach the adult stage and reproduce at quite a small size, they can also provide egg-masses for embryological work at times when this material is not otherwise available. However, it appears that males develop better under these artificial conditions, so that a regular supply of eggs would only be guaranteed by a fairly large set-up of rearing equipment allowing parallel culture of numerous animals.

Certainly cuttlefish are a versatile material for many kinds of experimental work. Not the least interesting of the possibilities they offer is the experimental approach of certain palaeo-biological problems (cf. BANDEL and BOLETZKY, in press; BOLETZKY and WIEDMANN, in preparation).

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