

## SARSIA



### IS THE SCYPHOMEDUSA *CYANEA CAPILLATA* (L.) DEPENDENT ON GELATINOUS PREY FOR ITS EARLY DEVELOPMENT?

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Newly released ephyrae of the scyphomedusa *Cyanea capillata* did not grow on either *Artemia* nauplii or copepod dominated mixed zooplankton, but grew with an average rate of 16.5 % day<sup>-1</sup> (maximum of 30.6 % day<sup>-1</sup>) with a ctenophore as food. The two first food types did not generate medusae with normal development of tentacles and oral arms over a seven-week period, whereas the ctenophore food did. We suggest that availability of gelatinous prey for newly released ephyrae is a bottleneck in the development, making constraints on the population succession and at least partly explaining inter-annual variations in abundance of *C. capillata*.

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## INTRODUCTION

The scyphomedusa *Cyanea capillata* is common in most Scandinavian waters, but due to a salinity requirement of > 20 psu of the polyp stage (CARGO 1984) it is excluded from brackish waters. It co-occurs with other gelatinous zooplankton like ctenophores, other scyphozoans, and hydromedusae and laboratory experiments have shown a potential trophic link between *C. capillata* and such prey organisms (BÅMSTEDT & al. 1994). In contrast to the other common scyphozoa *Aurelia aurita*, the developed medusa of *C. capillata* has long tentacles, exceeding its bell diameter by ten times (COSTELLO & COLIN 1995) and its morphology is therefore better suited for taking large-sized gelatinous prey. Although field investigations give evidence for a variable diet for adult *C. capillata* (BREWER 1989; FANCETT 1988; FANCETT & JENKINS 1988; MARTINUSSEN & BÅMSTEDT 1995) mixed copepod zooplankton and *Artemia* nauplii seemed to be poor foods for ephyrae in our preliminary studies during 1994-95, despite the suitability of such food for the early development of *A. aurita*. In order to specifically study quantitative ef-

fects of the food type on growth and development we therefore carried out controlled growth experiments with *C. capillata* over a seven-week period and report the results here.

## MATERIAL AND METHODS

Newly released ephyra from scyphistoma polyps of *Cyanea capillata* were used in the two experiments. The polyps had been reared in the laboratory in darkness at 10 °C, with excess of *Artemia* nauplii as food. Strobilation was stimulated by increasing the temperature to 15 °C and changing to continuous dim light.

A preliminary growth experiment with three individual ephyrae in 2-litre beakers and a mixture of *Artemia* nauplii and copepod zooplankton as food was conducted in Bergen High-Technology Centre in February-April 1996. The main growth experiment was performed at the Marine Biological Station at the University of Bergen in April and May 1996. Newly released ephyrae were incubated in aerated glass aquaria of 30 litre volume at 10 °C. Three different types of food were supplied to the ephyrae: (1) *Artemia* nauplii, (2) mixed zooplankton, and (3) the lobate ctenophore, *Bolinopsis infundibulum*. *Artemia* eggs were hatched 2-4 days before feeding the experimental animals. The mixed zooplankton

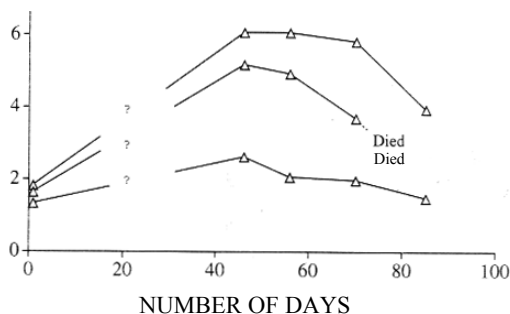


Fig. 1. *Cyanea capillata*. Development in medusa diameter of three separately held individuals given a mixture of *Artemia* nauplii and natural copepods.

was collected either with a plankton net (300  $\mu$ m mesh size) in Raunefjorden, near the laboratory, or from an automatic filtering system (200  $\mu$ m mesh size) at the dock. The material was strained through a 2 mm meshed screen in order to eliminate any medusae and ctenophores. It consisted mainly of copepods, with a strong numeric dominance of copepodids of *Calanus finmarchicus*, but also including *Temora longicornis*, *Oithona* sp. and *Acartia* sp. *Bolinopsis infundibulum* was collected from the surface water off the dock, either with short vertical tows of a conical net (45 cm mouth diameter, 500  $\mu$ m mesh) or with a bucket directly from the surface. A mixture of sizes, up to 50 mm height, were added to the experimental aquaria in order to eliminate prey size as a constraining factor for growth. The two natural food types were collected immediately prior to addition into the aquaria. All food types were supplied in excess, in order to saturate feeding. The aquaria were emptied and cleaned usually every third day, food and water renewed, and the experimental animals analysed. Each treatment (food type) consisted of two aquaria, each holding ten ephyrae. The animals in the two parallel aquaria were statistically treated as one group in all three treatments, due to the lack of differences. The bell diameter (between lappets in ephyra

Table 1. *Cyanea capillata*. Minimum and maximum diameter (mm) of medusae with a given number of tentacles developed, shown for three different types of food. The + sign indicates presence of tentacle buds. Only *Bolinopsis* supported development of more than four tentacles.

Tentacles	<i>Artemia</i> nauplii		Mixed zooplankton		<i>Bolinopsis</i>	
	Min.	Max.	Min.	Max.	Min.	Max.
None	1.2	2.6	1.8	2.2	2.0	2.6
+	1.7	2.0	2.0	3.0	2.6	3.5
2	1.6	2.8	2.8	3.8	2.8	4.1
2+	1.8	3.4	2.2	4.7	3.8	5.5
4	1.6	4.4	2.8	5.2	4.3	7.1
4+	3.0	5.4	2.5	6.3	4.3	10.9
8					8.5	14.1
>8					11.9	35.0

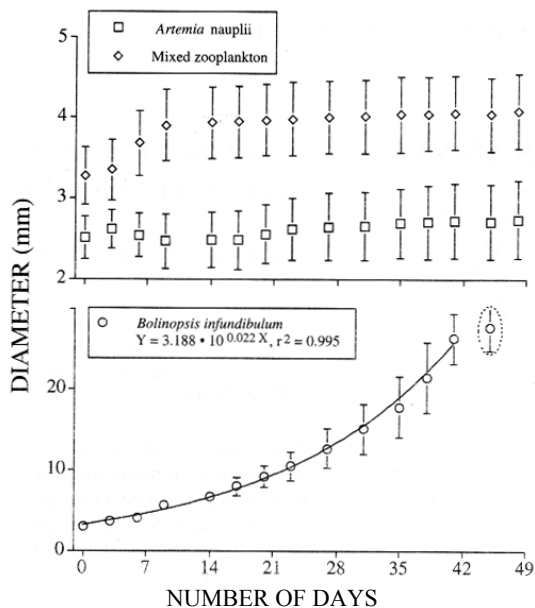


Fig. 2. *Cyanea capillata*. Succession in average medusa diameter (vertical bars = 95 % confidence intervals,  $n = 20$ ) of animals held in three different food environments. The last value in the lower panel was not included in the regression analysis, due to a high frequency of injured animals.

stage) was used as the size measure and the number of tentacle buds and fully developed tentacles was used as a comparative index of development. Both measurements were done under a dissection microscope with the medusae kept in a petri dish with a low level of sea water, in order to get the bell flattened out without injuring the medusa. These measurements were finished within one minute. The tentacle development was defined into eight categories by their numbers; None, +, 2, 2+, 4, 4+, 8, and >8, where + indicates the presence of tentacle buds. It was impossible to count the tentacles precisely when the number exceeded eight, without injuring the animals. The experiment was finished after 48 days, when the biggest medusae began to be injured due to entangling of oral arms and tentacles in the circulation device and entrapment of air bubbles.

The growth rate (% day<sup>-1</sup>) was calculated on the basis of increments in diameter:

$$\% \text{ growth day}^{-1} = \ln[(D_2/D_1)^3]/(t_2 - t_1) * 100 \%$$

where  $D_1$ ,  $D_2$  is the individual diameter (mm) at two consecutive analyses,  $t_1$  and  $t_2$  (days), respectively. We decided to use this arbitrary equation in preference to one based on an empirical relationship between body mass and diameter, because the only empirical one available for *C. capillata* was defined for the size range 45-300 mm diameter, i.e. not including the gradual development from ephyra to medusa. The effect of using the arbitrary one as compared to the empirical one was a slight increase in growth rate (average for ctenophore food rose from 15 to 16.5 % day<sup>-1</sup>).

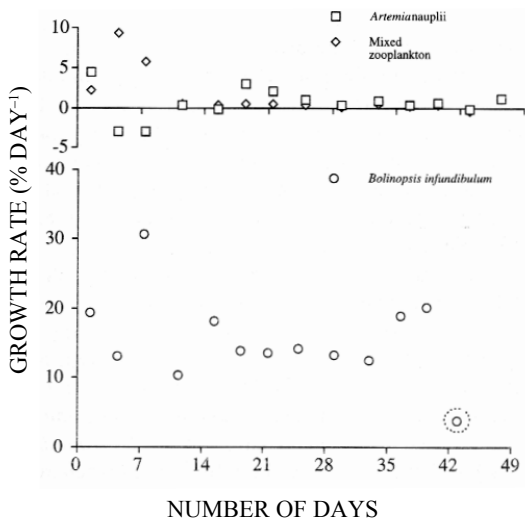


Fig. 3. *Cyanea capillata*. Growth rate ( $\% \text{ day}^{-1}$ ) for three different types of food, based on changes in diameter. Encircled value too low, due to high occurrence of injured animals (see text).

## RESULTS

In the preliminary experiment the size of three individually held ephyrae supplied with *Artemia* nauplii and mixed zooplankton all showed the same type of growth dynamics (Fig. 1). There was an initial gain in size, especially in two of the three individuals, although the long interval between measurements made it impossible to determine the extension or peak value of this. The period from 46 to 85 days was characterised by decreasing size and one of the individuals did not survive over the final interval.

In the main growth experiment individual ephyrae could not be separately recorded, because ten were held together in each aquarium. Ephyrae supplied with *Artemia* nauplii as food did not increase their size significantly over the whole experimental period, as indicated by overlapping confidence intervals, and there was occasionally even a reduction in diameter (Fig. 2). Ephyrae supplied with mixed zooplankton showed an initial increase in diameter for the first week, but growth stopped also in these animals, although the initial increase caused a larger mean diameter than in the first group. The ephyrae supplied with *Bolinopsis infundibulum* as food showed an exponential growth in diameter throughout the experiment, but growth declined somewhat after five weeks, although this must be considered as a potential effect of experimental constraints (see Material and methods). Excluding the final value after 45 days, a logarithmic function described the size development very well (Fig. 2).

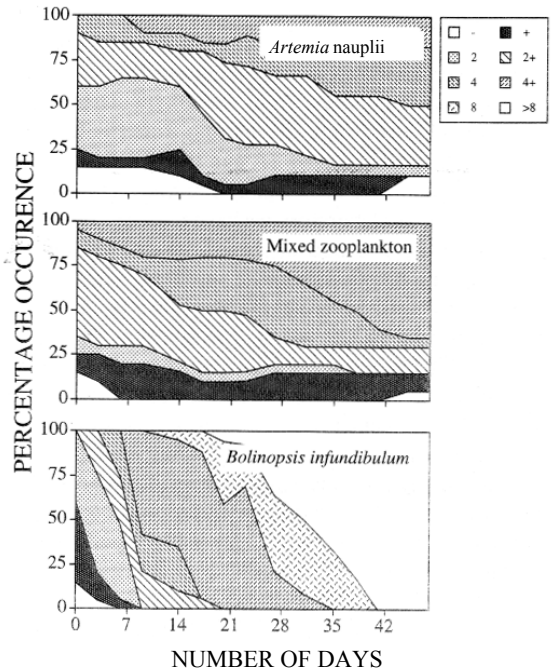


Fig. 4. *Cyanea capillata*. Succession in tentacle development over time for animals held with three different food types.

In the main experiment the daily growth rate showed initial values up to 4.4 % for *Artemia* nauplii and 9.4 % for mixed zooplankton, but close to zero most of the time (Fig. 3). In contrast, ephyrae supplied with *B. infundibulum* showed a high growth rate throughout the experiment, with a peak value in the beginning. The rather low final value must again be considered an artifact due to the experimental constraints (see above).

The development of tentacles differed between the three groups, with the third group (*B. infundibulum*) being outstanding (Fig. 4). The first group (*Artemia* nauplii) showed little development, with animals without tentacles being present even after seven weeks. The second group (mixed copepods) showed a clear increase in animals with 4(+) tentacles, although almost the same proportion as in the start were without tentacles. In none of the two first groups did development pass the four-tentacle level. In contrast, the third group showed a logical development with a gradual dominance of tentacle states, and with the whole population being passed the eight-tentacle level by the end of the study.

Table 1 shows that for a given tentacle state (number) the size ranges in the three different groups usually overlapped, although the first group usually had the smallest individuals and the third group the biggest. Thus, the two first groups were restricted both in growth and development of tentacles.

## DISCUSSION

The only previous report in the literature describing culture of *Cyanea capillata* from the ephyra stage is that of CARGO (1984), where *C. capillata* from Chesapeake Bay, USA, was raised to 18 mm diameter on 'small plankton organisms or *Artemia* or strained ctenophore material'. In our laboratory we have reared *C. capillata* polyps since 1994 and produced several batches of ephyrae. The two first years we supplied both *Artemia* nauplii and mixed zooplankton (mainly calanoid copepods) as food, got initial growth and development of a few thin tentacles, but thereafter a cessation or even retardation in size. Because a mixture of ages of ephyrae were held together and no size measurements were performed we were unable to quantify these results. Considering all observations made, our results indicate that a mixed copepod diet but not a diet of *Artemia* nauplii can support some growth (cf. upper two panels in Fig. 2) and that this growth mainly occurs during the first week. The size of ~6 mm recorded in Fig. 1 is not contradictory to the results in Fig. 2, because the largest individual diameter was 6.4 mm in the group fed mixed zooplankton. Although development was not sustained with these two diets, survival throughout the whole experimental period of 85 and 48 days (Figs 1; 2) shows that the food can be used for maintenance.

Our studies on the trophodynamics of adult medusae have shown that the scyphomedusa *Aurelia aurita* may be a key source of food supply for *C. capillata* (BÅMSTEDT & al. 1994) and experimental studies in the laboratory have shown a high predation potential also on hydromedusae, ctenophores and even the congener *Cyanea lamarcki* (own, unpubl. results). This contrasts the trophodynamics of *Aurelia aurita*, which grows and develops well on a diet of *Artemia* nauplii or mixed zooplankton and does not accept *B. infundibulum* or other scyphomedusae as prey (own unpubl. results from 1992-1996).

Our non-quantitative field observations from 1992 to 1996 reveal that the lobate ctenophore *Bolinopsis infundibulum* is abundant in the surface inshore waters along the Norwegian west coast from April till June, at the same time as *C. capillata* develops from the ephyra stage (cf. GRÖNDAL & HERNROTH 1987). The strong correlation we have shown here between growth success and availability of *B. infundibulum* prey therefore indicates that this trophic relationship is very important in the natural habitat. If we use our equation describing the size succession (see Fig. 2) and suggest a surplus of *B. infundibulum* to be available in the field, it would take 82 days for a newly released ephyra to reach a medusa size of 20 cm diameter. Thus, with the gelatinous diet available large medusae are to be expected in our waters

from June onwards, a prediction that is in agreement with field observations. The growth rate in nature has previously been recorded at 2-13 % day<sup>-1</sup> (BREWER 1989), i.e. somewhat lower than we recorded with only *B. infundibulum* as food. Thus, variable composition and variable proportion of gelatinous food will probably generate a variable growth rate and thereby variable size distribution at any given time.

Although we did not quantitatively investigate the effects of alternative gelatinous food, we have observed significant growth and development of *C. capillata* during short-term, uncontrolled tests with *A. aurita* as prey. It is also known from the literature that *C. capillata* readily takes hydromedusae (FANCETT 1988) and our unpublished results on predation on *Phialella quadrata* suggest that this prey can be fully utilised when available. Predator-prey interactions among gelatinous predators are not uncommon (PURCELL 1991) and recently OLESEN & al. (1996) recorded very high growth rates for ephyrae of the scyphomedusa *Chrysaora quinquecirrha* with small ctenophores (*Mnemiopsis leidyi*) as food during a four-day experiment. Thus, we suspect that *C. capillata* can use whatever gelatinous prey is available, except other *C. capillata*, for growth and development and that it has an obligatory dependence on this type of food in its early life.

With one exception, literature data do not indicate gelatinous prey to be a main diet for larger medusae in nature (cf. MARTINUSSEN & BÅMSTEDT 1995; FANCETT 1988; BREWER 1989), but this might be a somewhat biased picture due to the problem of identifying gelatinous remains in the gastric pouches of the predator. The recent report by HANSSON (1997) on high occurrence of *Aurelia aurita* remains (average 1.2 prey predator<sup>-1</sup>) in the stomachs of *C. capillata* from Gullmarsfjorden, Sweden, is the first one confirming the suggestion by BÅMSTEDT & al. (1994) of a close trophic connection between these two species. But it still remains that high predation rates on small fish and mesozooplankton, both from laboratory experiments (cf. BÅMSTEDT & al. 1994) and from field samples (FANCETT 1988; BREWER 1989; MARTINUSSEN & BÅMSTEDT 1995) are strong evidence of a more diverse food composition being adequate. Availability of gelatinous prey is therefore probably a bottleneck in the early development of *C. capillata* and variability in abundance of such prey organisms may then explain inter-annual variability in the population size of larger *C. capillata*.

This bottleneck effect is probably also double-sided. As long as the medusae are small and without the long, stinging tentacles and oral arms, they may be subject to predation themselves, whereas well developed medusae are larger and more resistant to predation. Reports from

Oslofjorden indicated an unusually dense bloom of *Bolinopsis infundibulum* in spring 1996 and extremely high abundance of *C. capillata* in the following summer (pers. commn, Stein Kaartvedt, University of Oslo). Although such a simple observational correlation does not need to be causal, it strengthens the supposition of gelatinous prey being a control mechanism for *C. capillata*. In fact, it is known among technical personnel at public aquariums in USA, where they have jellyfish exhibitions, that *C. capillata* needs gelatinous food to grow well, and at Baltimore National Aquarium, *C. capillata* is fed chopped pieces of *A. aurita* (Doug Allen, Baltimore Aquarium, pers. commn).

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