

**Corrigendum Notice**

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Sea Anemone *Epiactis Epiactis prolifera*.

The title should read:

Dynamics of External Brooding in the Sea Anemone *Epiactis prolifera*.

# Dynamics of External Brooding in the Sea Anemone *Epiactis* *Epiactis prolifera*\*

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## Abstract

The sexually produced young of the externally brooding actinian *Epiactis prolifera* Verrill, 1869 are attached to the parent's column just above the base. A transitory "brood groove" may be formed around the limbus when the parent contracts. In the population studied on the coast of Sonoma County, California, USA, from 27 to 49% of the adult anemones were brooding at any time, the proportion being inversely related to seawater temperature and directly related to size of the anemones. A brood usually consisted of young of various sizes. Overall, number of young being brooded was directly related to parent size and inversely related to size of the brooded juveniles. The growth rate of juvenile anemones was inferred to average about a millimeter in pedal disc diameter per month. Juveniles dislodged from the parent when smaller than 4 mm in basal diameter apparently cannot survive in the intertidal zone. Juveniles which successfully make the transition to adulthood have, therefore, been brooded for at least 3 months. Fewer than 50% of the smallest juveniles survived to a size at which they could live independently. The transition to adulthood was accompanied by a mortality of 80%. The survival rate, from egg to adult, was calculated to be about 1% per season.

## Introduction

A.E. Verrill described the sea anemone *Epiactis prolifera* in 1869 as the type of a new genus, noting, "The young borne upon the sides give this Actinian a very singular appearance, and are very remarkable, since nothing of the kind has, apparently, been previously observed" (p. 493). Actually, he had encountered the trait before without recognizing what it was, for in his (1868) description of *Phellia arctica* [later determined by Carlgren (1921) to be *Epiactis arctica*], Verrill noted "... ova-like bodies embedded in circular cavities formed in the epidermis and true wall. ... Possibly they are the eggs of some parasite" (p. 329).

*Epiactis prolifera* occurs in the lower intertidal zone of rocky shores on the Pacific coast of North America from Puget Sound to La Jolla (Ricketts and

Calvin, 1968). The presence of juvenile sea anemones on the column of the parent (see Fig. 1 in Dunn, 1975b) gives the anemone its specific designation and common name of "brooding" (Braun and Brown, 1966) or "proliferating" (Buchsbaum and Milne, 1960; Hedgpeth, 1962) anemone. (I term individuals attached to a parent "young" or "juveniles" while those that are independent are considered adults.) The young, which have the appearance of being buds, are used as a criterion for field identification (MacGinitie and MacGinitie, 1968; Ricketts and Calvin, 1968; Hand, 1975) since no other externally brooding species of actinian is known to occur on the west coast of North America, and because in other respects these anemones may vary considerably, even within a tide pool.

Since the sexually produced young are easily accessible and can be studied repeatedly *in situ*, *Epiactis prolifera* provides an unusually favorable opportunity to examine the dynamics of juvenile recruitment and mortality. Prior to the present study, none of the approximately 16 species of externally brooding ac-

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Table 1. *Epiactis prolifera*. Adult size classes (ranges of measured basal diameters). Values in parentheses are measurements on single individuals which fell considerably outside range

Size class	Range (mm)
Very small	4.4 - 4.9
Small	5.7 - 7.2 (8.5)
Small-medium	7.5 - 11.2
Medium	10.8 - 14.4 (15.5)
Medium-large	(13.3) 14.0 - 16.9
Large	(15.6) 16.2 - 20.1
Very large	19.0 - 27.8
Very, very large	30 and more (maximum diameter about 35 mm)

Table 2. *Epiactis prolifera*. Juvenile size classes (ranges of measured basal diameters)

Size class	Range (mm)
Tiny	0.5 - 1.0
Small	1.2 - 1.7
Medium	2.3 - 3.2
Large	3.1 - 3.9
Very large	4.8 - 6.7

tinians (Carlgren, 1949) had been studied in this way.

#### Methods

The *Epiactis prolifera* Verrill, 1869 along two sides of a large tide pool on the rocky open coast northwest of the University of California Bodega Marine Laboratory, Sonoma County, California, were censused during low tide at approximately monthly intervals from June, 1970 through June, 1972. The census area, extending from about 0.5 m above to 0.5 m below mean lower low water, contained a variety of situations in which *E. prolifera* is normally found, including vertical, horizontal, exposed and algae-covered surfaces oriented north, south, toward and away from direct surf action. In this area the anemones are attached to rock or, more commonly, to encrusting coralline algae (species of *Lithophyllum* and/or *Lithothamnion*) dotted with burrow openings of the cirratulid polychaete *Dodecaceria* sp./spp.

A census was always begun in the same place and an identical search pattern was followed around the pool, usually until 100 adult anemones above the water line had been recorded. On 6 occasions, high tides and stormy weather permitted

enumeration of only 50. Thus, specimens at the lowest levels were not counted at the higher tides and those at the extreme end of the pool were not reached at the lowest tides. After the first 5 censuses, I could recognize smaller areas within the larger one and could thereby interpret the data both in terms of a constant number of anemones in a somewhat variable area, and in terms of a variable number of anemones in each of several constant areas. The size class (since time did not permit actual measurement), color, and number of young (also categorized by size) were recorded for each anemone, in addition to incidental information such as spawning or predation. Each anemone was tapped gently with a pencil, and a diving light was shone on it to standardize conditions for color determination and to reveal young. The edge of the brood groove was depressed when necessary to expose hidden juveniles.

After familiarization with the population under study, I subjectively defined 8 size categories of adult anemones. To determine the range of basal diameters to which these categories corresponded, and the consistency of this method of estimation, 100 different adult *Epiactis prolifera* were measured *in situ* to the nearest 0.1 mm. The diameter of the pedal disc was chosen as the least variable and most easily accessible dimension. A similar series of measurements to define juvenile size categories was made on 20 specimens. Results of these procedures are shown in Tables 1 and 2. Overlap of categories, where it occurred, was slight, and the classification was quite consistent, making this a useful method for the rapid evaluation of a large number of anemones. Gaps between both adult and juvenile size classes occurred in a few cases because I did not happen to measure an individual of intermediate size.

#### Results and Interpretation

##### *The Brood Groove*

It is often stated that the young of this anemone are carried in "brood pits" (e.g. Buchsbaum and Milne, 1960; Braun and Brown, 1966; Ricketts and Calvin, 1968), possibly because Verrill (1899) used the term in his expansion on the description of *Epiactis prolifera*. As Verrill himself noted, however, invaginations of the ectoderm, such as he described in the same paper for three spe-

cies of deep-water and Arctic anemones, are not macroscopically evident in *E. prolifera*, and the young appear simply to be attached to the column of an expanded parent. When fully contracted, non-brooding individuals are usually smoothly convex. Contracted brooding anemones, on the other hand, may have a conspicuous indentation around the limbus ["The border along which the column joins the base" (Stephenson, 1928, p. 6)]. In the population that I studied, the young were localized at and just above the limbus. When the parent contracts, the edges of this fold, or "brood groove", completely cover small juveniles; larger ones may be at least partly enveloped.

#### Population Density

The area covered during a census of 100 anemones was approximately 4.75 m<sup>2</sup>, although this varied by as much as 10 to 12%, depending on the time of year and height of the tide. Thus, the average density of adult anemones in the census area was about 21/m<sup>2</sup>. The average number of juveniles per adult, considering adults and juveniles of all sizes, was 4.3, so the total mean density of *Epiactis prolifera* was approximately 111 anemones/m<sup>2</sup>. However, distribution was spotty, with apparently suitable sites often unoccupied.

This adult density is considerably greater than the 7/yard<sup>2</sup> (=8.3/m<sup>2</sup>) found at Monterey by Hewatt (1937), apparently the only published value for density of *Epiactis prolifera*. My census area, however, was chosen in part for its relatively dense population of this actinian.

#### Periodicity and Prevalence of Brooding

*Epiactis prolifera* is a gynodioecious hermaphrodite, virtually all medium-size and larger individuals being egg-producers and therefore potential brooders (Dunn, 1975a, b). At no time of year was less than 27% (in July, 1970) nor more than 49% (in April, 1971) of the census population brooding. Thus, some brooding occurs at all times, its prevalence roughly inversely correlated with seawater temperature (Fig. 1). This is the same pattern as is exhibited by the internally brooding sea anemone *Actinia equina* in Britain (Chia and Rostron, 1970).

Fig. 2 graphs brooding prevalence in adults of three sizes (medium includes categories small-medium and medium, large includes categories medium-large and large, and very large includes all

larger specimens). No anemones smaller than small-medium were found brooding. These data show that brooding prevalence in *Epiactis prolifera* is directly related to the size of the brooding animals. Thus, it appears that both an exogenous factor (temperature) and an endogenous one (size) affect brooding prevalence in this anemone.

#### Brood Size

*Epiactis prolifera* adults may carry young of a variety of sizes, but very large broods comprise predominantly small juveniles. The largest brood I found, consisting of 10 small and 25 tiny juveniles, was on a very large adult. The greatest number of very large juveniles being brooded by a single adult was 10, also on a very large individual. Data in Table 3 confirm the direct relationship between size of the parent and brood size; data in Table 4 show the inverse relationship between size of juveniles and brood size. (The slight discrepancy in the total number of juveniles in the two tables is because in the first two censuses the size of the juveniles was not always recorded.)

Fig. 3 illustrates the variability of mean, median and maximum brood size during the 2 years of this study. Peaks in these statistics occurred slightly after temperature peaks, at times of intermediate brooding prevalence. Conversely, when brooding was most prevalent, brood size was intermediate, probably because most of the additional anemones brooding at those times were the smaller ones with fewer young.

Larger anemones brood more of the time and have larger broods, so they probably contribute a proportion of the recruits to the population greater than would be expected on the basis of their relative abundance. The direct relationship between size of an adult and number in its brood, and the inverse relationship between size of juveniles and number on a single parent suggest that brood size is limited by the amount of physical space in the brood area. Indeed, the region of the limbus was often packed with young. When there was unoccupied brood space it was frequently discolored, evidence that it had recently contained juvenile anemones (Dunn, 1972).

#### Duration of Brooding

Because the census population of *Epiactis prolifera* spawned synchronously at least some of the time (Dunn, 1975b), if the

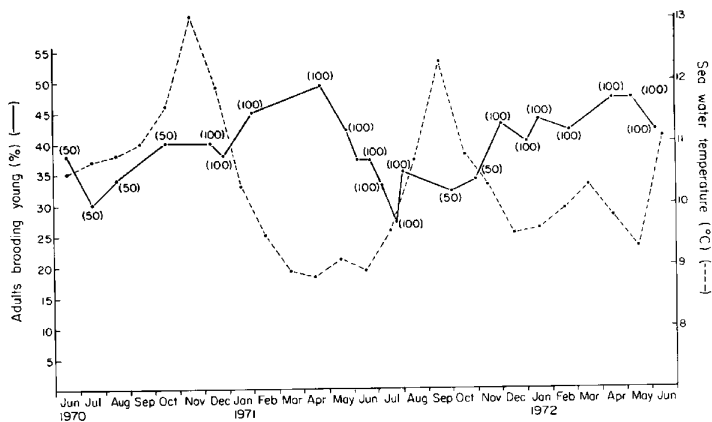


Fig. 1. *Epiactis prolifera*. Percentage of adults brooding young in the census population (solid line). Number censused is indicated in parentheses beside each point. Average in-shore seawater temperature at Bodega Marine Laboratory as measured at about 08.00 hrs each week-day by Bodega Marine Laboratory personnel is also shown (dashed line)

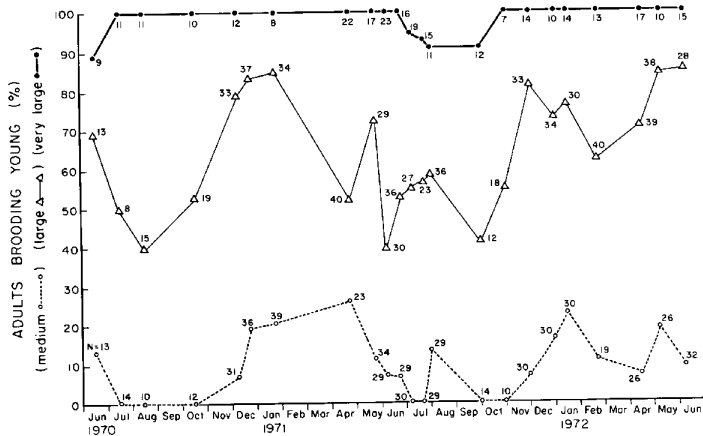


Fig. 2. *Epiactis prolifera*. Percentage of anemones brooding in 3 size classes of brooding adults. Number in each size class, considered as 100% for that census, is indicated beside each datum point

Table 3. *Epiactis prolifera*. Relationship between size of brooding adult and brood size. Values are totaled from all 23 censuses, and juveniles of all sizes are considered together

Size of adults	No. of juveniles	No. of adults	Juveniles/adult
Small-medium	7	1	7.0
Medium	474	64	7.4
Medium-large	398	49	8.1
Large	3772	376	10.0
Very large	3160	272	11.6
Very, very large	338	30	11.3
	Total	Total	Average
	8149	792	10.3

Table 4. *Epiactis prolifera*. Relationship between size of juveniles and brood size. Values are totaled from all 23 censuses. Adults of all sizes are considered together, and since an adult may brood young of various sizes, some were counted more than once

Size of juveniles	No. of juveniles	No. of adults	Juveniles/adult
Tiny	1401	202	6.9
Small	2814	517	5.4
Medium	2306	514	4.5
Large	1210	365	3.3
Very large	275	115	2.4

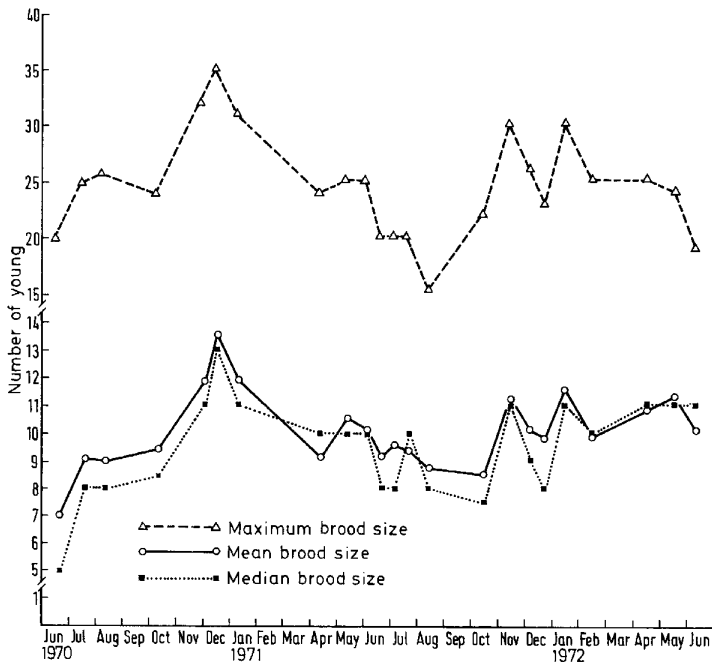


Fig. 3. *Epiactis prolifera*. Mean, median and maximum brood size

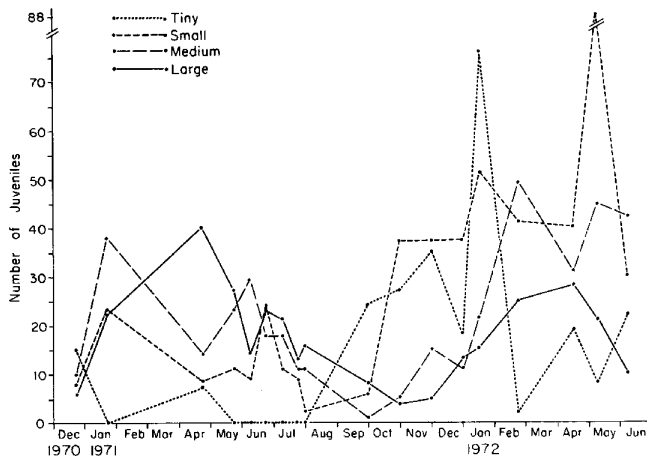


Fig. 4. *Epiactis prolifera*. Number of juveniles of various sizes in one subarea (the "gully")

juveniles produced by a single spawning (a "crop") grew at approximately the same rate, a plot of the number of juveniles of each size at each census would ideally reveal successive peaks of increasingly larger young. This was not evident in the data for the census area as a whole, but one portion of it, the "gully," a channel of area  $0.85 \text{ m}^2$  which was censused in its entirety each time and which contained from 12 to 31 adults, did exhibit a sequence suggestive of such a pattern (Fig. 4).

Four intervals from peaks of tiny to peaks of small young (average length 7.8 weeks), 3 small to medium intervals (average length 3.7 weeks), and 5 medium to large ones (average length 5.6 weeks) are discernible. Thus, the average time required for a tiny juvenile to grow about 3 mm in basal diameter to a size at which it could survive independently (see below) appears to be slightly more than 17 weeks. One continuous sequence of tiny to large juveniles is apparent during the 18-week period from December, 1971 through April, 1972.

The number of tiny young counted in the gully is only 53.6% of the total of small ones, and in the census area as a whole it is slightly less than half the total of small young (Table 4). However, the average number of tiny juveniles per brooding adult is greater than that of small ones, consistent with the trend of fewer larger juveniles per brooding

adult. This implies that the low count is probably not due to missing a few tiny young hidden in the brood groove or among larger siblings on each of many adults. Assuming a relatively uniform growth rate among the juveniles of a crop, there are two possible explanations of this paradox: (1) new juveniles are added to the population over a period longer than the average interval between censuses (4.3 weeks for the 23 counts); or (2) the period of being tiny is shorter than the interval between censuses. Either way, only a portion of the ultimate total of tiny juveniles would be present at any time.

The first possibility seemingly contradicts the observation of simultaneous spawning, but several bursts of synchronous spawning might occur during a relatively short time as is known from the anthozoans *Tealia crassicornis* (Chia and Spaulding, 1972) and *Renilla* sp. (Wilson, 1884). The second hypothesis, contrary to the period of 7.8 weeks for development from the tiny to the small stage, clearly must be rejected, but could be accepted in combination with the first one. The former hypothesis can stand alone, but is strengthened by the second one. Rapid turn-over - that as some tiny young are entering the population, others are outgrowing that size category - is likely also because the tiny category spans a size range of only 0.5 mm, while each other category has a range of about

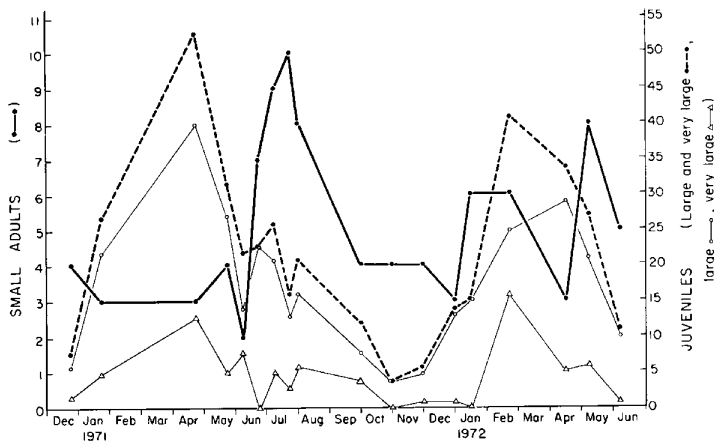


Fig. 5. *Epiactis prolifera*. Number of large and very large juveniles and of small adults in the "gully"

1 mm. Thus, 7.8 weeks probably represents the period during which one crop of new juveniles grows larger than 1 mm in basal diameter and accumulates in the small size class, producing the impression that there are about twice as many small as there had been tiny ones. If new juveniles continue to enter the population during about 5 weeks, but require only about 3 weeks to grow from tiny to small, the observations would be accounted for.

The small/medium interval and the medium/large one, each representing an increase in pedal disc diameter of about 1 mm, average 3.7 and 5.6 weeks, respectively. Decreased growth rate with increasing size is reasonable for geometric reasons, as is the increased attrition of juveniles from the column of an adult with increasing size of the young.

The inferred time required for a juvenile specimen of *Epiactis prolifera* to grow from tiny to large is therefore slightly more than 12 weeks. This value is influenced by censusing frequency, but a growth rate of about 3 mm in basal diameter in 3 months is roughly the same as that of *Actinia equina* at a similar size (Chia and Rostron, 1970), and as that of well-fed *Tealia crassicornis* during their first year (Chia and Spaulding, 1972), but faster than that of *Stomphia didemon* (Siebert, 1973).

Although the average interval from peaks of tiny to peaks of large juveniles

during the warmer half of the year (July-December) was only 56.8% of what it was during the rest of the year, the average interval between censuses during the colder half of the year was 5.1 weeks, compared with only 3.2 weeks between July and December. Thus, although it is possible that development is more rapid when the seas are warmer, my data cannot provide conclusive evidence.

The existence of a pattern of successive peaks for juveniles of increasing size in the gully but not in the census area as a whole is probably due to the homogeneity of the gully relative to the larger area which was selected partly because of its wide range of conditions. It is likely that microenvironmental conditions affect the growth of juveniles, thus creating asynchrony among those of a crop, and that some members of the population are spawning most of the year (since young of all sizes are found at all times), further confounding the trends. Asynchrony in both processes is probably minimized in the smaller, less diverse area.

#### Recruitment of Small Adults

The smallest adults found in the study area were 4 mm in basal diameter, corresponding in size to a large or very large juvenile. This implies that smaller displaced juveniles do not manage to

survive independently along the open coast, and that those which attain adulthood are brooded for at least 3 months. Attached young are able to capture prey from an early stage (Dunn, 1975b), and detached juveniles 2 or 3 mm in diameter appeared to thrive in aquaria. Failure of individuals less than 4 mm in diameter to survive as adults is thus not due to inability to feed, nor to separation from the parent *per se*. The relatively small number of very large juveniles (Table 4) presumably means that most young leave the parent before attaining such a size. However, they may remain attached until they are nearly as large as a small-medium adult.

Both conspicuous peaks in numbers of larger juvenile *Epiactis prolifera* in Fig. 5 were followed by sharp increases in the number of small adults in the gully, circumstantial evidence that large and very large juveniles settle in the immediate vicinity of their parents. In addition, since juveniles are usually the same color as their parent, the fact that the colors of small adults and large brooders often found nearby are so frequently the same implies that the small adults had recently detached from the large anemone and settled on the substrate adjacent to it. Fig. 5 also illustrates that there were times when the increase in small adults must have been due to large juveniles gaining independence, for there had been few or no very large young during the preceding period.

I did not determine how juveniles gain independence, but they are said to "crawl" (MacGinitie and MacGinitie, 1968) or "glide" (Ricketts and Calvin, 1968) away from the parent. MacGinitie and MacGinitie (1968, p. 460) also state "...that a strong light would cause the young of *Epiactis* to drop loose from the parent and roll away." Although I used a bright light and photographed with flash bulbs, I never encountered such a phenomenon. I believe that when juveniles attain some critical size - at least 4 mm in basal diameter - they move off the adult brooding them and onto the surrounding substrate. This may be when the strength of the growing juvenile exceeds that of the adhesive force of the parent (Dunn, 1975b) so that the juvenile can detach itself, or when it has developed the ability to move, so that it can leave the parent. For several days after being ejected from the gastrovascular cavity of the parent anemone and adhering to the first solid substrate they encounter, small *Actinia tenebrosa* do not possess locomotor ability (Ottaway and Thomas, 1971).

Fig. 5 suggests that the mortality of juveniles making the transition to adulthood is about 80%. Although there appears to be a lag between the decline in number of juveniles and the increase in number of small adults in 1971, which could be construed as evidence for a brief dispersal stage, the facts that it did not appear in 1972, that the numbers involved are small, and that anemones at this stage of development appear ill-suited to a planktonic existence, make it likely that this was due to my having overlooked one or two small and sometimes inconspicuous adults.

A moderate-sized anemone contains about 350 yolky oocytes (Dunn, 1975b), and a maximum of 35 developing juveniles was found on one adult. The average number of young that attained large size was 43% of the number of small ones originally present. In the gully area, only 20% of the large and very large juveniles survived to become small adults. I therefore estimate that from 350 ova, up to about 35 small juveniles may develop on the parent; of these, about 15 grow into large juveniles, and, ultimately, perhaps only 3 anemones may become independent adults, resulting in a survival rate to adulthood of about 1% per season for the reproductive output of an average-sized individual of this species.

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