

# Locomotion by *Epiactis prolifera* (Coelenterata: Actiniaria)\*

D. F. Dunn

Department of Zoology, University of California; Berkeley, California, USA and  
University of California Bodega Marine Laboratory; Bodega Bay, California, USA

## Abstract

Overlay maps were used to study locomotion by the externally brooding actinian *Epiactis prolifera* Verrill, 1869, in the rocky intertidal zone near Bodega Bay, California, USA. A greater proportion of non-brooding individuals moved than did brooding ones. Although brooding anemones that moved traveled twice as rapidly as non-brooders that moved, brooders were generally larger, and the relative rate of travel of the two groups was identical. The net distance traveled by all the anemones was only 36.0% of the gross, and most of the movement appeared to be undirected.

## Introduction

Actinians are usually regarded as sedentary animals, but Hyman (1940) devotes nearly one page to their locomotion, recognizing that they are "...never immovably fixed" (p. 592). Most movement by sea anemones is said to be long-term and very slow (MacGinitie and MacGinitie, 1968). A dramatic exception is "swimming" by some anemones, which have been the objects of considerable study (Robson, 1966). However, few studies have been made on the more usual modes of actinian locomotion.

Overlay maps were used to follow 40 individuals of the externally brooding sea anemone *Epiactis prolifera* Verrill, 1869, in the rocky intertidal zone near the University of California Bodega Marine Laboratory, Sonoma County, California, during the summer of 1971. *E. prolifera* is admirably suited to such a study because individuals in a small area can be identified quite accurately on the basis of color, size, and number of juveniles being brooded. Although actinians can be stained with vital dyes (Bellomy, 1960), it might disrupt their normal activity, and this technique is unsuitable for field studies since the anemones must be removed from the substrate to be dyed.

Tagging is also impractical (Ottaway and Thomas, 1971).

## Materials and Methods

Six sites, each about 25 cm square, were studied. Two initially contained 5 adult *Epiactis prolifera*, two had 4, one had 3, and one had 2 specimens. The areas differed in degree of exposure to light and to wave action, and were at different tidal heights. They were checked once a day when accessible, which was only when the tide was lower than -15 cm, from 23 or 24 May, 1971, when the maps were made, through 7 August, 1971, the last day of the fortnightly low tides of the summer. This provided 24 or 25 checks during 76 or 77 days.

A piece of heavy-duty transparent plastic sheeting about 30 by 40 cm was laid over the study area and each *Epiactis prolifera* was circled, using a waterproof felt-tip pen. The number of adherent young, if any, and color were noted for each anemone. The position of other organisms and of topographical features were sketched in to permit re-orientation of the map. Each day the same map was replaced over the study area and the position of each anemone was recorded. Since I had attempted to select sites containing anemones of different colors and sizes, I assumed that an anemone of similar color, size, and with a like number of juveniles in the

\* This work was done in partial fulfillment of the requirements for the Ph.D. degree in the Department of Zoology, University of California, Berkeley, and was supported by a U.S. National Science Foundation Traineeship.

Table 1. *Epiactis prolifera*. Absolute (mm/day) and relative (pedal disc diameters/day) rates of travel of mapped anemones

	Brooders	Non-brooders
All mapped anemones	1.57 mm/day 0.09 pdd/day	1.25 mm/day 0.17 pdd/day
Anemones that moved	3.06 mm/day 0.18 pdd/day	1.29 mm/day 0.18 pdd/day

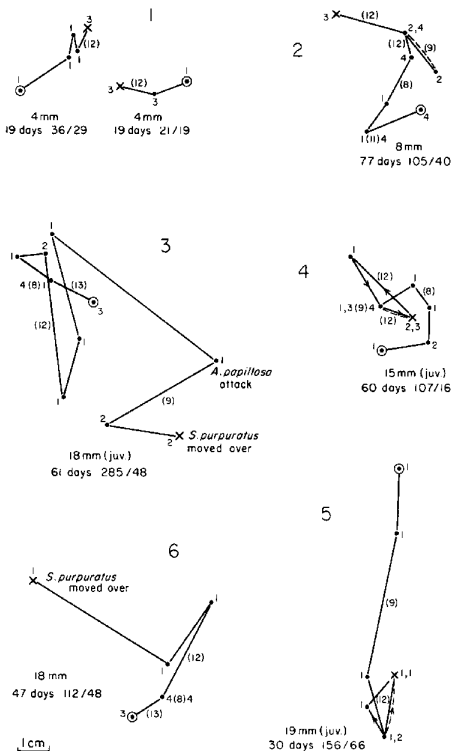


Fig. 1. *Epiactis prolifera*. Patterns of movement by 7 adult specimens. Each point represents position at which anemone was mapped. Distances between successive positions, connected by straight lines, are those from which calculations were made. Dashed lines indicate retracing of same path. Circled point is the first one at which anemone was located and crossed point is the last. Numbers beside points indicate number of days anemone was found in that spot, and a comma between two numbers signifies that anemones occupied site on separate occasions. Numbers in parentheses are number of days between observations when area was inaccessible. Beneath each map is indicated size of the anemone, whether it bore juveniles, number of days it was followed, and ratio of gross to net distance traveled in millimeters

same or nearby location to one previously recorded was the same individual. The straight-line distance between the center of the pedal disc at two successive observations was taken as the distance traveled during that interval.

## Results

Data were obtained in this way from 40 adult specimens of *Epiactis prolifera* (I define "adult" as a specimen which is not attached to a larger one, and "juvenile" or "young" as one which is still being brooded). The average length of time a single anemone was followed was 37.0 days, including 11 anemones that were observed on every occasion and 4 that were seen only once. Three of the latter were small specimens; the other, a brooding adult, was covered by a sea urchin the second day of the mapping study. Of the remaining actinians, 22 were not brooding and 14 were brooding. Twenty of the former and 9 of the latter moved during the study; the others did not.

The total distance traveled by all 29 anemones that moved was 2053 mm during the 77 days. The distance between the position of the center of the pedal disc at first and last sightings of each individual, however, totals (for the 29) only 739 mm.

Rate of travel was calculated both for all 36 anemones that were observed more than once, and for only those 29 individuals that moved during the study. These data were also figured separately for brooding and non-brooding anemones. Brooding anemones are generally larger than non-brooders (the average pedal disc diameter of the mapped non-brooders was 7.2 mm, and that of brooders was 16.8 mm). Therefore, Table 1 presents the locomotion data as both absolute and relative rates of travel.

Fig. 1 illustrates the movement patterns of 7 representative anemones from all 6 map areas. The greatest distance any anemone moved in one 24-h period was 66 mm (specimen illustrated in map 3).

I saw one individual *Epiactis prolifera* moving in the field. A large anemone brooding several young, it was submerged in a few centimeters of water. When I first came upon it, the lower part of its base partially overlapped a smaller conspecific. The leading edge of the base of the moving individual appeared inflated. The anemone wobbled, the lobular portion rising and falling, apparently effecting the detachment of the entire base except for the upper trailing portion. The inflated edge then abruptly deflated and adhered to the substrate. The top edge inflated, the base was lifted so that the anemone was very flat, and the turgid portion was pulled forward. It then deflated, attached, and the leading edge repeated the process. By this means, the anemone traveled 10 mm in 15 min as I watched.

#### Discussion

A greater proportion of the generally smaller non-brooding specimens of *Epiactis prolifera* moved than did larger, brooding ones. Brooding individuals that did move progressed considerably farther per unit time than did non-brooders that moved, but the average relative rate of travel is identical for the two groups. The sample size is too small to determine whether there are differences in amount of locomotion between individuals at different elevations and in areas with different degrees of exposure, but there are no obvious trends in the data.

Locomotion by *Epiactis prolifera* is unproductive in terms of progress, for the net distance traveled is only 36.0% of the gross. Even this value is probably an over-estimation, since it is calculated on the straight-line distance between successive observation points that were mapped as much as 13 days apart in one case (from the end of one low-tide period to the beginning of the next), and the distances between points marked even at daily intervals are likely to be underestimates of the actual distances traveled. In a quantitative study of actinian locomotion, Ottaway and Thomas (1971) showed that in aquaria, *Actinia tenebrosa* rarely moves in straight lines. Their maps indicating paths of movement and positions of individuals at 24-h intervals show that frequently the path followed covered at least twice the straight-line distance between points marked a day apart. Another such study (Osburn, 1914) indicated that in 82 days' travel, the net distance covered by a *Sagartia* (= *Diadumene*) *leucolena* was 13.5% of the gross, and that its movement, as well

as that of *Metridium marginatum* (= *M. senile*), is sporadic and apparently undirected.

Although much of the movement by *Epiactis prolifera* is apparently random, some of that by the individual of map 3 in Fig. 1 may have been provoked by a nudibranch attack, for at the end of the 24-h period during which the anemone traveled 66 mm, a nudibranch (*Aeolidia papillosa*) was feeding on it. Edmunds et al. (1976) found that other species of actinians are stimulated to move by *A. papillosa* predation, and that the nudibranch will follow a moving anemone, feeding as the two progress. A similar stimulus might have been responsible for activity shown by the individual of map 6, which had remained in one spot for some time before moving away and becoming quite active. Some anemones appear to circle one spot (e.g. maps 4 and 5) as if that might be a particularly favorable location. *Actinia tenebrosa* moves less when it is within its preferred intertidal zone than when it is not, although it moves to some extent at all levels (Ottaway and Thomas, 1971).

Locomotion by *Epiactis prolifera* is, at least sometimes, not so slow as to be imperceptible, as Osburn (1914) and MacGinitie and MacGinitie (1968) state to be the case for actinians. Rather, there may be short periods of relatively rapid movement. Being covered with water may be necessary for progression, either due to the need for a wet substrate, as is the case for *Actinia tenebrosa* (Ottaway and Thomas, 1971), or to enable the hydrostatic skeleton to function. Illumination inhibits locomotion in *Metridium senile* (Batham and Pantin, 1950) and in *Diadumene* sp. (MacGinitie and MacGinitie, 1968), and *Haliplanella* (= *Sagartia*) *luciae* will move away from light (Parker, 1917). I observed *E. prolifera* moving at 08.15 hrs on a bright day.

Ottaway and Thomas (1971) do not discuss how *Actinia tenebrosa* accomplishes the movements they quantify so well, beyond mentioning that some of the anemones detach from vertical surfaces, fall, and reattach at the bottom. Similarly, Francis (1973) and Pearse (1974) discuss some causes of locomotion by *Anthopleura elegantissima*, but not how it is accomplished. The extension of a turgid lobe from the pedal disc of an advancing anemone is mentioned by Parker (1917), but movement is usually attributed to waves of muscular contraction across the pedal disc (e.g. Batham and Pantin, 1950). McClendon (1906) and Parker (1917) describe a wave of detachment traveling from the rear of the pedal disc, but the mode of locomotion I saw used by *Epiactis prolifera* requires that a considerably

greater portion of the base be lifted off the substrate at one time. Edmunds et al. (1976) report that in *Actinia equina* being preyed on by *Aeolidia papillosa*, large areas of the pedal disc are lifted from the substrate as the anemone prepares to detach.

I had hoped through the mapping study to substantiate the circumstantial evidence that juvenile *Epiactis prolifera* move directly from their parents onto the surrounding substrate (Dunn, 1972). This was not accomplished, mainly because counts of juveniles were somewhat variable, and although small adults were found beside large brooding ones on several occasions, I could never be positive that the presumed parent had one fewer large juvenile than it had had the previous day.

This study provided further evidence that *Epiactis prolifera* is preyed upon by *Aeolidia papillosa*, a fact previously discussed by Bertsch et al. (1972) and Waters (1973). Thrice, sea urchins (*Strongylocentrotus purpuratus*) moved onto *E. prolifera* (as with the anemones illustrated by maps 3 and 6 in Fig. 1), and when they were pried from the substrate a day or two later, the anemone was no longer there. Presumably the anemones were either eaten or dislodged by the urchins.

*Acknowledgements.* I wish to express thanks to Dr. C. Hand, Mr. C.H. Fautin, and Dr. F.L. Dunn for help and advice during this study.

#### Literature Cited

- Batham, E.J. and C.F.A. Pantin: Phases of activity in the sea-anemone, *Metridium senile* (L.), and their relation to external stimuli. *J. exp. Biol.* 27, 377-399 (1950)
- Bellomy, M.D.: Dyeing your anemones. *Aquar. J.* 31, 592-594, 596, 599, 633-634 (1960)
- Bertsch, H., T. Gosliner, R. Wharton and G. Williams: Natural history and occurrence of opisthobranch gastropods from the open coast of San Mateo County, California. *Veliger* 14, 302-314 (1972)
- Dunn, D.F.: Natural history of the sea anemone *Epiactis prolifera* Verrill, 1869, with special reference to its reproductive biology, Ph.D. thesis, University of California, Berkeley, California 1972
- Edmunds, M., G.W. Potts, R.C. Swinfen and V.L. Waters: Defensive behaviour of sea anemones in response to predation by the opisthobranch mollusc *Aeolidia papillosa* (L.). *J. mar. biol. Ass. U.K.* 56, 65-83 (1976)
- Francis, L.: Clone specific segregation in the sea anemone *Anthopleura elegantissima*. *Biol. Bull. mar. biol. Lab., Woods Hole* 144, 64-72 (1973)
- Hyman, L.H.: The invertebrates: Protozoa through Ctenophora, 726 pp. New York and London: McGraw-Hill Book Co. 1940
- MacGinitie, G.E. and N. MacGinitie: Natural history of marine animals, 2nd ed. 523 pp. New York: McGraw-Hill Book Co. 1968
- McClendon, J.F.: On the locomotion of a sea anemone (*Metridium marginatum*). *Biol. Bull. mar. biol. Lab., Woods Hole* 10, 66-67 (1906)
- Osburn, R.C.: Movements of sea anemones. *Bull. N.Y. zool. Soc.* 17, 1163-1166 (1914)
- Ottaway, J.R. and I.M. Thomas: Movement and zonation of the intertidal anemone *Actinia tenebrosa* Farqu. (Cnidaria: Anthozoa) under experimental conditions. *Aust. J. mar. Freshwat. Res.* 22, 63-78 (1971)
- Parker, G.H.: Pedal locomotion in actinians. *J. exp. Zool.* 22, 111-124 (1917)
- Pearse, V.B.: Modification of sea anemone behavior by symbiotic zooxanthellae: phototaxis. *Biol. Bull. mar. biol. Lab., Woods Hole* 147, 630-640 (1974)
- Robson, E.A.: Swimming in Actiniaria. *Symp. zool. Soc. Lond.* 16, 333-360 (1966)
- Waters, V.L.: Food-preference of the nudibranch *Aeolidia papillosa*, and the effect of the defenses of the prey on predation. *Veliger* 15, 174-192 (1973)

Dr. Daphne Fautin Dunn  
Department of Invertebrate  
Zoology  
California Academy of Sciences  
Golden Gate Park  
San Francisco, California 94118  
USA

Date of final manuscript acceptance: August 20, 1976. Communicated by J.S. Pearse, Santa Cruz