

Variability of *Epiactis prolifera* (Coelenterata : Actiniaria) in the intertidal zone near Bodega Bay, California*

DAPHNE FAUTIN DUNN†

Department of Zoology, University of California,
Berkeley, California and University of California,
Bodega Marine Laboratory, Bodega Bay, California, U.S.A.

Introduction

As part of a larger study of the sea anemone *Epiactis prolifera* Verrill, 1869 (Dunn, 1972, 1975 a, b), data were gathered on morphological, ecological and behavioural variability of the species. *E. prolifera* is a distinctive actinian, since it broods its sexually produced young externally, but in other respects it may vary considerably, the extent of which is still not fully appreciated. This paper summarizes the variability of this species in three different intertidal habitats within a 2 km radius of the University of California Bodega Marine Laboratory, Bodega Head, Sonoma County, California, U.S.A.

Colour

The ground colour of the column and tentacles of *Epiactis prolifera* may be green, brown, red, orange, blue, lavender or grey, sometimes with a mottling of a second colour (Hand, 1955). Variable coloration is not unusual among actinians (Stephenson, 1928). Colour was noted in the course of 23 approximately monthly censuses made of *Epiactis* in one tide-pool in the rocky intertidal zone along the exposed coast west of the Bodega Marine Laboratory, from June 1970 until June 1972. The census began at the same point each time and followed an identical search pattern, ending when 100 (occasionally 50) adult *E. prolifera* above the water had been noted. ('Adult' means individuals that are not attached to a larger *E. prolifera*, while 'juvenile' or 'young' refers to individuals still adherent to a parent.) Each animal was tapped gently and a light was shone on it to provide uniform conditions for colour evaluation.

The proportion of individuals described as 'red', a shade corresponding to brick red in Ridgway's (1912) classification, varied from 33% to 80% of the total for each census, with a mean of 59%. If 'light red', 'dark red' and 'bright red' animals are added to this, the range was from 42% to 92%, with a mean of 76%. The next most common colour in the census population was reddish-green. Tan, brown, green and intermediates among these basic colours accounted for the balance of the animals. There were no trends in proportions of various colours through the study. The author consistently found groups of unusually coloured animals in certain places and learned to distinguish a few individuals among them. The author interprets this as evidence of stability in coloration of each organism. Thus, much of the variability in the prevalence of red animals was probably due to my subjective impression.

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† Present address: Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Colour was also recorded for 268 *E. prolifera* collected for histological study during the same time-span, and taken from a larger area of the same rocky intertidal. Since an effort was made to examine *Epiactis* of a variety of colours, and animals of unusual colours such as orange and grey were taken regardless of size, brooding condition or vertical level, the range of variation was greater than that recorded for the census area, and the proportion of red animals was only 49%.

Each anemone examined was entirely one colour, aside from white markings on pedal and oral discs of some, the occasional deepening of the ground colour around the rim of the pedal and oral discs, and the not infrequent mottling around the limbus ["The border along which the column joins the base" (Stephenson, 1928)]. (Mottling was absent from individuals below brooding size. When a juvenile was removed from the parent column, a pale discoloured spot the precise size and shape of the basal disc of the young animal was left on the adult. This indication that a juvenile had been present persisted for at least two weeks under laboratory conditions.) In the rocky intertidal, a juvenile *Epiactis* was usually nearly identical in colour to the adult brooding it. Most of the young which differed did so not in basic colour but only in colour value, commonly being paler than their parent, but the author never saw a juvenile of a strikingly different colour being brooded in the rocky intertidal. Small adults occurring beside large, brooding ones were nearly always identical in colour to the larger ones. *E. prolifera* of unusual colours were generally near others of the same colour.

There was no correlation between colour and size of the anemones in the census area, but of those collected the proportion of red animals among anemones smaller than 5.5 mm and larger than 25.6 mm in basal diameter ($N = 9$ and 14 , respectively) was significantly greater than for the population as a whole, whereas among those 5.6 to 10.5 mm in basal diameter ($N = 51$), the proportion was lower and the variety of colours was greatest. A higher prevalence of light red individuals among smaller animals was probably due partly to their translucence, which may also explain the paleness of some juveniles relative to the adults brooding them. Similarly, at least part of the higher proportion of dark red animals among the larger ones may be due to their greater bulk of tissue, hence opacity.

Evidence suggests that when juvenile *Epiactis* attain some minimum size, they move off their parent and on to the surrounding substrate (Dunn, 1972). This could account for groupings of animals of unusual colours. It may also explain why the prevalence of red coloration was so similar in very large and very small anemones, for the largest animals should theoretically contribute a disproportionately large share of the recruits to the population (Dunn, 1972).

There was no correlation between colour and intertidal level, brooding condition, or degree of exposure to wave shock and to light. Animals of the predominant shade could always be found on all sides of unusually coloured individuals or groups of individuals. However, substrate was clearly correlated with colour so that *E. prolifera* generally matched its surroundings. *Epiactis* attached to *Cystoseira osmundacea* in gravelly clefts of the lower rocky intertidal zone were almost invariably a brown similar to that of the algae. All of the adult *E. prolifera* living on the eel-grass *Zostera* and the green alga *Ulva* in Bodega Harbour were green with darker green vertical stripes (their

coloration and patterning being very similar to those of the tectibranch *Phyllaplysia taylori* which also occurs on *Zostera* blades). In the habitat examined in greatest detail—dark rocks usually encrusted with pink coralline algae—*E. prolifera* often occurred among red algae very similar in colour to the most prevalent shade of anemone pigmentation. Occasionally individuals were found on or surrounded by grey tunicates or sponge, in which cases the *Epiactis* were greyish.

The marine isopod *Pentidotea montereyensis* can alter its coloration over time to match its substrate (Lee, 1966). If such a species were a major component of the diet of *Epiactis* [which does feed on crustaceans, at least in part (Dunn, 1972; Fox & Moe, 1938)], the anemones might match their substrate simply because their prey does so. However, it is unlikely that the diets of anemones of different colours living side by side would diverge sufficiently through time to produce such variability, and experiments on other actinian species have shown that colour cannot be altered by diet manipulation (Abeloos-Parize & Abeloos-Parize, 1926; Fox & Pantin, 1941). For these reasons and because actinians are carnivores, it is impossible that this polymorphism is due to direct ingestion by *E. prolifera* of its substrate. Thus, while colour value or even shade might vary with diet, size or physiological condition, the basic colour of each *Epiactis* is probably fixed.

This evidence, derived from a study of natural history, implies that colour in *Epiactis prolifera* is genetically controlled, the same conclusion as was reached from pigment studies (Fox & Moe, 1938; Fox & Pantin, 1944). Uchida (1934) likewise postulates a genetic basis for the wide variety of colour in Japanese '*Epiactis prolifera*', now believed to be *E. japonica* (Uchida, pers. comm.). Whether hermaphrodites of *E. prolifera* are facultatively self-fertile remains to be determined (Dunn, 1975 a), but even if crossing is obligatory, the chances are that crosses would be between individuals of similar colours within each habitat. Marshalling evidence similar to that presented here on similarity of parent and offspring coloration, Cain (1974) concludes that in the internally brooding sea anemone *Actinia equina*, colour is genetically controlled and self-fertilization probably occurs.

All of the *Epiactis* of unusual colours collected from the rocky intertidal were 5.6–10.5 mm in basal diameter. The explanation for this restricted size range may involve selective predation on conspicuously coloured individuals following passive or active immigration from other habitats where they were cryptically coloured. Immigrants would most likely be smaller adults which move about more than do large, brooding ones, often appearing at sites where there had been none before (Dunn, 1972, personal observation), and conspicuous individuals would be eliminated before they had grown very large. Maintenance of the colour polymorphism by such a mechanism implies the existence of at least one species of predator that locates its prey by visual means. The situation appears similar to that in the sea star *Leptasterias hexactis* (Menge, 1972).

Size

Size also varies considerably in *Epiactis prolifera*. Ricketts & Calvin (1968) state that generally individuals from Puget Sound are larger than those from California, and southern Californian specimens appear to be smaller still

(Fox & Moe, 1938), so it seems that there might be a latitudinal gradient along the coast. Carlgren's (1952) finding that nematocysts of Oregon specimens are larger than those from California anemones is consistent with this hypothesis. However, Torrey (1902) found specimens in San Pedro that were twice the size of those from Pacific Grove. A parameter not specified in any of these reports is the environment from which the *Epiactis* were taken.

Relative to the animals attached to coralline algae encrusted rock near the Bodega Marine Laboratory, many of the *E. prolifera* living on *Zostera* and *Ulva* in Bodega Harbour were exceptionally large, and even the largest of those epiphytic on *Cystoseira osmundacea* in the rocky intertidal were small. Thus in the vicinity of Bodega Bay, *Epiactis* is larger in calm water than in areas of high surf, and is smallest of all where surge could be expected to be greatest. The large size attributed to Puget Sound specimens may simply reflect their situation on eel-grass (Bovard & Osterud, 1918) and/or in quiet water (Ricketts & Calvin, 1968). The southern California specimens collected by Fox and Moe (1938) were from *Macrocytis pyrifera*, and their small size may be related to their substrate, by analogy with the animals from *Cystoseira*.

Other characters

Other characteristics may also be related to environment.

Juveniles occurred much farther up the parent column of the harbour form than of those in the rocky intertidal. It is likely that ova adhere to the parent ectoderm along the entire length of the column in all populations. However, along the open coast all except those protected from wave action by their location in the brood groove (see Dunn, 1972) are washed away. In the harbour, those settling high on the column are able to survive there and develop. For a somewhat similar reason, females of the externally brooding sea star *Leptasterias hexactis* "... at protected areas produce more eggs than do comparably sized females at exposed areas" (Menge, 1974, page 89).

Animals from the rocky intertidal of Bodega Head deteriorate quite rapidly in captivity, although those from nearby Bodega Harbour do well. This may be related to the fact that the former animals are constantly subjected to wave action while the latter are adapted to calmer water.

The table lists other differences between harbour and exposed-coast *Epiactis prolifera* (and between populations attached to a rocky substrate and to *Cystoseira* where differences occur).

Discussion

Divergent observations and discrepancies in the literature on this species are probably mainly attributable to its variability. For instance, Waters (1971) notes that *Epiactis* being preyed upon by *Aeolidia papillosa* reacted by detaching and eventually rolling away, whereas the animals studied by the author showed no such response (Dunn, 1972). This may have to do with the fact that she worked at Dillon Beach, California, on green animals (personal communication) while the author used brick red and brownish-red ones from Bodega Head. Lenhoff (1965), being acquainted with individuals from eel-grass at Friday Harbor, advocates using *Epiactis prolifera* as a laboratory animal because of its hardiness, but those from the rocky intertidal of Bodega Head would be most unsuitable. The

Differences in populations of *Epiactis prolifera* near the Bodega Marine Laboratory

Bodega Harbour	Exposed Coast
<p>On <i>Zostera</i> or <i>Ulva</i> Adults green; column may be vertically striped.</p> <p>Adults often exceed 30 mm basal diameter.</p> <p>Juveniles white or off-white in colour.</p> <p>Juveniles slender, 3-4 times as tall as broad when expanded.</p> <p>Juveniles may occur the length of the lower half of the parent column.</p> <p>Juveniles on a single parent usually of one or two discrete size classes.</p> <p>Juveniles never embedded in mucus.</p> <p>Contracted adult nearly as tall as broad.</p> <p>Tentacles sinuous, pointed, without basal white dot.</p> <p>White lines on oral disc radiate around mouth.</p> <p>When water drained from bowl in which attached, tentacles dangle so animal droops to one side.</p> <p>Hardy animals in aquaria—survive weeks with little attention.</p>	<p>On coralline algae-covered rocks Adults generally brick-red; no stripes.</p> <p>Adults rarely larger than 30 mm.</p> <p>Juveniles same colour as parent or slight variant (never white).</p> <p>Juveniles twice as tall as broad at most, usually broader than tall when expanded.</p> <p>Juveniles in the region of the limbus only.</p> <p>Juveniles of variable sizes on a single parent.</p> <p>Sheath of mucus may cover young if parent disturbed.</p> <p>Contracted adult a third to a half as tall as broad.</p> <p>Tentacles blunter, shorter, less sinuous, white dot at base.</p> <p>No white lines on oral disc.</p> <p>When water drained from bowl, tentacles quickly retracted.</p> <p>Delicate animals in aquaria—become unresponsive and usually die within a week.</p>
	<p>On <i>Cystoseira</i> Adults tan with strong white basal lines; no stripes.</p> <p>Adults never exceed 30 mm (juveniles carried by smaller adults than in other populations).</p>

variety in arrangement of complete and fertile mesenteries (Carlgren, 1949; Dunn, 1975 b; Hand, 1955; McMurrich, 1901; Verrill, 1899) is another manifestation of the species' variability. [It is possible that some studies reported to have been on *Epiactis prolifera* may have inadvertently used or included the similar-appearing species *Cnidopus ritteri* (Hand & Dunn, 1974).]

Even in the very small portion of the range of *E. prolifera* examined in this study, discrete populations exist, each associated with a particular substrate and/or set of physical parameters. Morphological variability is found in other species of marine invertebrates which also lack a planktonic larval stage. What had once been considered to comprise as many as 20 species of the gastropod *Littorina* is now known to constitute a single variable one, *L. saxatilis*, (James, 1968) and what had been thought to be two or three species of *Leptasterias* is now designated *L. hexactis* (Chia, 1966). However, detailed genetic analysis of the much studied North Atlantic isopod *Jaera marina* (or *J. albifrons*) revealed the existence of six specifically distinct forms (Bocquet, 1953). Panmixis is probably even more limited in *Epiactis* than in these species due to its more sedentary nature.

Processes which produced this variability continue, possibly leading eventually to speciation, or at least subspeciation, if it has not already occurred. To resolve this question, research should be conducted on interhabitat variation in morphology and behaviour at other sites along the range of *E. prolifera*, as well as within a particular habitat throughout its range. In future, it would be well for investigators using *Epiactis prolifera* as a subject to specify the colour, size, and precise site of collection or study of their animals.

Summary

The externally brooding actinian *Epiactis prolifera* Verrill, 1869, is morphologically and behaviourally variable near Bodega Bay, California. Colour of animals generally matches that of their substrate. Size is also correlated with substrate, but differences may ultimately be due to degree of exposure to surge and waves, a parameter which is associated with other variable characters. *E. prolifera* should be studied elsewhere in its range to elucidate critical factors in its variability, and genetic studies should be undertaken to evaluate the degree of isolation of populations in this sedentary, brooding organism.

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