Fertilization in *Fucus*

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Summary. Methods are described for the collection, treatment and uniform discharge of large quantities of gametes, and a measure of fertilization control in the monoecious brown alga, *Fucus distichus*. Fertilization was examined using the techniques of blister formation, gamete separation experiments, and electron microscopy. Sperm enter the freshly-discharged egg packets through a mesochite pore and juxtaposition with the eggs early. However, experimental and thin-section data indicate that fertilization does not occur until the eggs dissociate from the mesochite and round up. Hence, the egg surface appears to undergo three functional changes following its release from the thallus: (1) a pre-dissociation state which inhibits fertilization within the mesochite; (2) a dissociation state when fusion of gametes is possible; and (3) a post-fertilization state characterized by the formation of extraneous coats. As the egg is activated by the sperm a non-membranous layer appears to detach from the egg surface to form an activation layer. This is augmented by fibrous units to function as a fertilization barrier which ultimately thickens to form the cell wall. The area between the eggs within the egg packet is characterized by the presence of fibrous and particulate substances which are continuously given off through the egg surface. These apparently play a functional role in the sequential stages of fertilization in *Fucus*. These observations are discussed in terms of analogies with fertilization in the sea urchin.

Introduction

While polarity in *Fucus* has been studied quite extensively, fertilization has been studied much less (for reviews see Jaffe, 1958, 1968). Thuret (1854) was the first to describe fertilization in *Fucus*. However, the most notable work on this subject is that of Farmer and Williams (1898) and Levring (1952). Though Farmer and Williams did not actually describe fusion of egg and sperm, they did account for some characteristic changes during the process. They concluded that fertilization was quick, completed within 10 min, and that fertilized eggs formed a "membrane" at once. Levring concluded that there are structural similarities between eggs of the sea urchin and eggs of *F. spiralis* and

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F. vesiculosus. Based on blister formation and centrifuge microscopy he described the unfertilized egg as having a peripheral layer of cortical granules beneath the plasma membrane, which in turn is covered by an external egg membrane. He concluded that at fertilization the cortical granules combined with the egg membrane to form a fertilization membrane external to the plasma membrane. Our current understanding of fertilization in Fucus is based primarily upon these interpretations. Presently, no biochemical data are available and fertilization events have not been examined ultrastructurally, perhaps because of the difficulties encountered in the fixation of such a large and complex cell (Torrey, 1967). This problem has been overcome and it is now possible to combine ultrastructural analysis with physiological work in order to study the problems of fertilization in Fucus.

However, in order to approach these problems it was first necessary to develop methods for obtaining immediate, massive release of gametes from the thallus in monoecious species, and a precise control over fertilization. This paper reports on the methods for best achieving these conditions and describes some of the fine-structural and physiological characteristics of the gametes following their discharge from the thallus and subsequent fusion.

Materials and Methods

Materials. The monoecious F. distichus L. Powell, which predominates along the western coast of North America, was used for these studies. This species has a special advantage in that fertile plants are available all year round as contrasted with F. vesiculosus, which is seasonal. On the other hand, gametes are extruded together from F. distichus; but this proved to have hidden advantages for fertilization studies. Collections were made both from the Monterey Coast of California and from the San Juan Archipelago, Washington.

Collecting. All collecting and handling of Fucus plants was carried out with the objective of achieving the following conditions: (1) massive, uniform discharge of gametes to yield large quantities of eggs for growth analysis; (2) a uniformity in egg and sperm fusion to within 1 min over the entire population of a given discharge; and (3) the highest percentage of viability possible. These requirements were met most successfully by adhering to the following procedure.

(1) Plants were selected for their maturity based on well-developed conceptacles, with mucous slightly discharging from the protruding ostioles, dark-brown coloration, and well-developed gas bladders. Plants completely free of mucous offered little potential for a healthy discharge of gametes. Conversely, plants that discharged gametes profusely in the field continued to do so while being transported and stored, and when needed they usually had spent their yield.

(2) Collection sites were chosen on the basis of consistent low temperature (under 17°C) between layered thalli. This was found to be especially significant when the intertidal region suffered long-term exposure during low tides on warm, sunny days in summer.

(3) Collections of homogeneous plants were made within the intertidal zone (Pollock, 1968). Plants high up on the edge of the intertidal region were never used.