Many early papers that considered some of these questions were based on laboratory findings. More recently a number of studies on field populations have added significantly to our understanding of fertilization kinetics in sea urchins. However there is an urgent need for further detailed studies on fertilization success on other invertebrate taxa, particularly brooding and oviparous forms. The assumption that the fertilization rate for species with internal fertilization is high may not be correct and evidence for this is needed.

Studies designed to model fertilization success should include distribution and size of adults and longevity, concentration, and post-spawning behaviour of gametes under natural conditions.

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## **Ecology of open populations**

Developmental mode determines the degree to which populations of benthic invertebrates are connected throughout their geographical ranges. Species with planktonic larvae are "open" in the sense that new individuals that are added to a population generally will have come from some other geographic location and spawning at a specific site contributes an unknown and generally unpredictable number of individuals locally or to any other geographic subdivision of the population.

In contrast, brooding or asexual reproduction contribute to the development of closed populations. However, marine organisms show a remarkable range of reproductive and developmental adjustments that modify the degree of population "openness" including combinations of sexual and asexual reproduction, apomixis and poecilogony. Dispersal during juvenile and adult stages (*e.g.* by rafting or ballooning) can also confer a measure of openness on a population of organisms with limited larval dispersal.

In studying meta- or spatially structured-populations of marine invertebrates, one goal is explicit to specify age, stage, or size transitions not only within a population but also among populations of the metapopulation. Transitions in a life-cycle graph are functions of biotic and abiotic factors that interact with morphological, behavioral and physical traits. These relationships define the role of plasticity in spatially-structured linkages which, together with gene flow, are determined by modes of reproduction and interactions with physical oceanographic processes.

Immigration and emigration often play a much larger role than local birth rates or mortality in open populations, making open populations notoriously difficult to study empirically or to model. Nevertheless, most marine invertebrates and many marine fishes produce pelagic larvae, so further development to further develop methods to study open populations is vital to our understanding of coastal and oceanic ecosystems.

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## **Parental retention and protection**

Some marine animals retain their offspring on the bottom or on their bodies. Others release them into the plankton. The consequences for survival and dispersal of offspring appear to be great. Benthic development of sedentary animals lead to further modifications of life histories, such as imbreeding, sibling cannibalism,