Reference: *Biol. Bull.* **188**: 32–45. (February/March, 1995)

Prespawning Behavior, Spawning, and Development of the Brooding Starfish *Leptasterias polaris*

JEAN-FRANÇOIS HAMEL AND ANNIE MERCIER

Département d'Océanographie, Université du Québec à Rimouski, Centre Océanographique de Rimouski, 310 allée des Ursulines, Rimouski (Québec), Canada G5L 3A1

Abstract. Our study focused on the precise reproductive behavior of the starfish *Leptasterias polaris* (Müller and Troschel) before and during spawning—a subject of much speculation and evident ecological importance. Between the third week of December 1992 and mid-January 1993, we observed spawning in the laboratory that roughly corresponded to field observations in the Lower St. Lawrence Estuary. In experimental tanks provided with natural environmental conditions, the spawning was preceded by 7 to 8 weeks of complex aggregative interactions among the starfish. The individuals, which usually avoid each other, began to make discreet arm contact, which intensified with time and eventually led to the superposition of two or more starfish, independently of sex. The interactions seem to be associated with decreasing temperature, because aggregative and spawning behaviors were not observed under stable temperature conditions. Male spawning is first initiated when the temperature falls to about 2°C during minimum daylength (<9 h $\cdot$ d^{-1}). In seawater, the spermatozoa are negatively buoyant and tend to deposit as a sticky film on the substrate, where they enter a state of low activity. Stimulated by male spawning, females spawn on the layer of sperm, which is reactivated by contact with the oocytes, ensuring fertilization. In the laboratory, the fertilized eggs undergo first cleavage in 45 h, become brachiolaria in 40 days, and form fully developed young starfish within 5.5 to 6 months, synchronously with populations in the field. The embryos develop at the same rate even when not brooded, suggesting that the brooding behavior in *L. polaris* serves mainly to keep the eggs clean, healthy, and protected against predation.

Introduction

Successful fertilization constitutes a critical stage in marine invertebrate reproduction, and many organisms develop strategies to maximize this important step (Himmelman, 1981; Giese and Kanatani, 1987). Starfish show diversified reproductive behaviors. In many species, gametes are broadcasted by both sexes, with fertilization in the water being enhanced by synchronization of spawning (Hyman, 1955; Strathmann, 1987; Chia and Walker, 1991). In other starfish, males broadcast spawn in the usual fashion, and females emit fewer gametes but brood their embryos to fully developed young starfish (McClary and Mladenov, 1990; Chia and Walker, 1991). *Leptasterias polaris,* which protects its embryos for 5 to 6 months, is among the few species that brood by overlaying the eggs deposited on the substrate (Emerson, 1977; Himmelman *et al.,* 1982; Boivin *et al.,* 1986). Although brooding starfish are generally small-sized, with lecithotrophic development (Chia and Walker, 1991), *L. polaris* can reach diameters up to 50 cm (Boivin *et al.,* 1986) and are probably among the largest brooders.

Prespawning and spawning behaviors are very important to reproductive success in marine invertebrates. Breeding aggregations have been observed in a number of asteroids (Chia, 1968; Komatsu, 1983; Minchin, 1987; Young *et al.,* 1992; Slattery and Bosch, 1993). Many authors suggest that such aggregations could minimize sperm dilution and increase fertilization success (Ormond *et al.,* 1973; Levitan, 1991; Levitan *et al.,* 1992), as exemplified by the pairing strategies in *Archaster typicus* (Run *et al.,* 1988) and *Neosmilaster georgianus* (Slattery and Bosch, 1993). In those species, the male, after finding a female, mounts her before spawning (Ohshima and Ikeda, 1934; Komatsu, 1983; Run *et al.,* 1988; Slattery and Bosch, 1993). There is also evidence that the spatial distribution of broadcast spawners has a major influence on the probability of fertilization due to gamete viability (Pennington, 1985; Yund, 1990; Levitan *et al.,* 1992; Young *et al.,* 1992). Young *et al.* (1992) suggested that aggregations

Received 7 December 1993; accepted 4 November 1994.