LABORATORY OBSERVATIONS OF LARVAL BEHAVIOR AND METAMORPHOSIS IN THE MEDITERRANEAN SOLITARY CORAL *BALANOPHYLLIA EUROPAEA* (SCLERACTINIA, DENDROPHYLLIIDAE)

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ABSTRACT

In sessile marine organisms, the potential for larval dispersal affects the degree of genetic differentiation among populations as well as the spatial distribution of adults. We describe larval behavior and metamorphosis in a laboratory population of *Balanophyllia europaea* (Risso, 1826), a zooxanthellate solitary coral common to rocky coasts in the Mediterranean Sea. When released by adult polyps, the planulae are zooxanthellate and large; their major diameter is about 2 mm. Planulae have neutral buoyancy, with a swimming and pelagic behavior. Larval longevity averages 10 d, with a maximum of 53 d. The average period between the time of release and metamorphosis is 7 d, with a maximum of 42 d. These two periods differ because some larvae died before metamorphosis. Almost half of the larvae that metamorphosed settled as far away from the parental polyp as possible. Thus, the dispersal potential of *B. europaea* larvae appears greater than that of its congener, *Balanophyllia elegans* Verrill, 1864, which is azooxanthellate. We suggest that the relatively high dispersal potential of larvae of *B. europaea* is enabled through symbiosis with zooxanthellae.

Recruitment is essential for the maintenance of populations. In sessile marine organisms, recruitment usually takes place after larval dispersal, which in most cases occurs in a pelagic environment. Larval dispersal in most scleractinian corals occurs in the water column, but the extent of dispersal is not well known (Harrison and Wallace, 1990). Some authors suggest that planulae can cover considerable distances via planktonic dispersal, crossing barrier reefs or geographic regions (Veron, 1995). Other authors describe a limited dispersal capacity and propose that corals often are passively transported (i.e., attaching themselves to boats or other floating objects as a means of dispersal; Jokiel, 1990).

Dispersal capabilities are also determined by reproductive mode. Planulae generated by brooding species are released at an advanced developmental stage and are therefore capable of adhering to the substrate and metamorphosing as soon as they are released by parental polyps. Broadcast spawners produce planulae that must pass through a planktonic stage before they are able to settle to the bottom and metamorphose (Jackson, 1986; Benayahu, 1989; Harrison and Wallace, 1990; Richmond and Hunter, 1990).

Dispersal capability is an essential characteristic of species life histories. The capacity to reach and colonize new geographic areas may add to the chances of survival of species in the event of localized extinctions (Pechenik and Cerulli, 1991). Larval dispersal affects the genetic differentiation of populations, and may also affect the spatial distribution of adults. Theoretically, high larval dispersal should result in genetic homogenization of populations, and the dispersed distribution of adults. In contrast, limited larval dispersal should lead to genetic fragmentation of populations, and an aggregated distribution of adults (Carlon and Olson, 1993; Hellberg, 1996, Goffredo and Chadwick-Furman, 2000).

Balanophyllia europaea is a zooxanthellate solitary coral of the family Dendrophylliidae. It occurs along the rocky coasts of the Mediterranean Sea and the Atlantic Ocean in Spain (Zibrowius, 1983). This species reaches its maximum population density of about 100 ind m^{-2} in shallow waters, at 5–10 m depth (Goffredo, 1999), but occurs to about 50 m depth (Zibrowius, 1980). This solitary coral is a brooding simultaneous hermaphrodite with a yearly reproductive cycle. Fertilization takes place between April and May. The embryos go through a 4–5 mo incubation period and planulae are released towards the end of summer during August–September (Goffredo and Telò, 1998; Goffredo et al., 2000, 2002). We describe the behavior of larvae and the dynamics of metamorphosis in a laboratory population of *B. europaea*.

Materials and Methods

Twenty-one individuals of *B. europaea* were collected at Calafuria (Leghorn, Italy; 43° 28.4′ N, 10° 20′ E) during July 2001. Collections by scuba dives were performed at 4.5–10 m depth, where this population reaches maximum density (Goffredo, 1999). We chose July for collection because the adults were in mid-gestation period (Goffredo et al., 2002). Mature adults were recognized by their size (Goffredo and Telò 1998; Goffredo 1999; Chadwick-Furman et al., 2000; Goffredo and Chadwick-Furman, 2002; Goffredo et al., 2002). They were collected, transferred the same day to the University of Bologna, and placed in an aquarium set to the photoperiod cycle and temperature found in the Calafuria area (Goffredo et al., 2002). Within the aquarium, each individual polyp was placed in a separate glass beaker (volume = 958 cm^3; 10 cm diameter, 13 cm height). Glass appeared to be an appropriate substrate for the larvae to settle onto because polyps of this species were observed in the field growing on glass objects. Each polyp was attached to the bottom of its beaker using a non-toxic resin. The beaker opening was sealed with 400-µm nylon mesh; larvae were not allowed to pass through because they were up to 5× larger than the mesh size (Goffredo and Telò, 1998; Goffredo et al., 2002). A low flow rate in the aquarium reduced interference with the behavior and settlement of planula larvae. To identify planulation time, we performed daily observations up to the day of planulation. For the first 15 d after larval release, we conducted daily observations; thereafter, the mean interval between observations was 7 d (SE = 2, n = 7). Larvae were observed until all had either metamorphosed or died, for a total of 61 d after release. During each observation period, we recorded: (A) the number of larvae and their behavior (not moving, crawling on the bottom or wall, swimming), and (B) the number of newly metamorphosed polyps and their spatial distance from the parent. If the newly metamorphosed polyp was on the bottom of the beaker, we measured its spatial distance from the parent as the distance separating the two polyps. If the newly metamorphosed polyp was found on the beaker wall, the distance from its parent was measured as the sum of the radius of the beaker's base and the distance separating the bottom of the beaker from the newly-metamorphosed polyp. For the beaker wall settlers, we estimated settlement distance in this way because we observed some of these settlers to spend time exploring first a path along the bottom of the beaker, and then up the side of the glass wall. Morphological observations on larvae and newly metamorphosed polyps were carried out by means of a binocular microscope.

Results

The mean size of collected sexually mature adults (maximum diameter of the polyp oral disc) was 12.8 mm (SE = 0.5, n = 21). Approximately 2 mo after the polyps were first placed in the glass beakers (September 10, 2001), 57.1% of the collected individuals (12/21) planulated. Planulation was simultaneous in all individuals and was completed within 24 hrs. The individuals produced a mean of 6.8 (SE = 2.4, n = 12) planulae each, for a total of 82 larvae. The temperature of the water when planulation took place was

23°C and the photoperiod was 13:11 hrs (daylight:darkness). Both of these environmental conditions matched those found in the area of Calafuria when planulation takes place in natural populations (Goffredo et al., 2002).

Planulae (Fig. 1) were zooxanthellate and well-developed, with differentiated mouth, pharynx, and mesenterial septa in the gastrovascular cavity (Figs. 1D,E). Larvae were usually pear-shaped, but sometimes contracted into a more spherical shape or stretched out to become more cylindrical (Figs. 1A,B,C). Their color was brownish yellow, similar to adult polyp color. In their elongated shape, major diameter (oral-aboral axis) was 2.15 mm (SE = 0.06, n = 12), and minor diameter (transversal axis) was 0.59 mm (SE = 0.03, n = 12).

Larvae had neutral buoyancy, and swam by means of ciliar movement. They were very dynamic, and when swimming, the aboral pole was the anterior one (Figs. 1A,B,C). As soon as they were released, the larvae swam upward in an undulatory motion, rotating or spiraling around their oral-aboral axis. When they reached the top edge of the beaker, they swam against the nylon mesh, or settled against it for a brief span before detaching themselves and moving again to the bottom, and then moved back up to the upper edge once again. We observed larvae to repeat this cycle 3–5 times within each 10 min span.

Newly-metamorphosed polyps had a truncated cone shape; the oral disc was flat and circular with a mean diameter of 1.37 mm (SE = 0.02, n = 24; Fig. 1F).

Metamorphosis occurred mostly during the first 12 d following larval release; by the eighth day, 47% of larvae had metamorphosed, by the ninth, 57%, and by the twelfth, 76% (Fig. 2). Larval mortality was 22%, and occurred mostly between days 13–26. Length of the larval period averaged 10.3 d (SE = 1.0, n = 82) and ranged from 1–53 d. The average time from release to metamorphosis was 6.9 d (SE = 0.8, n = 64), with a maximum of 42 d. These two periods were different because some larvae died before they metamorphosed.

The spatial distribution of newly-metamorphosed polyps was not homogeneous (Fig. 3). There were two distinct groups, which were not significantly different in number of polyps (χ^2 test, P > 0.05). This spatial separation into two groups occurred when the planulae, upon release, chose two different locations in which to settle and metamorphose. Individuals in the first group (37/64 larvae = 58%) settled on the horizontal base of the beaker, at a mean distance from the parental polyp of 3.31 cm (SE = 0.22); while individuals in the other group (27/64 larvae = 42%) settled as far away from the parental polyp as possible, i.e., at the top edge of the beaker's vertical wall, at a mean distance from the parental polyp of 17.90 mm (SE = 0.04).

Discussion

Studies on the reproductive biology of Mediterranean scleractinians are limited (Fadlallah, 1983b; Harrison and Wallace, 1990; Richmond, 1997; Goffredo and Telò, 1998; Goffredo, 1999; Goffredo et al., 2000, 2002). The only reported data on scleractinian larval behavior in this region come from observations on the corals *Caryophyllia smithi* Stokes and Broderip, 1828, *Balanophyllia regia* Gosse, 1860, and *Cladopsammia rolandi* made more than a century ago by Lacaze-Duthiers (1897). The present study, although limited to observations under laboratory conditions, contributes substantially to information on the larvae of a Mediterranean scleractinian coral. Observations of planula behavior and metamorphosis under field conditions are difficult to perform, but would be valuable for a better understanding of reproductive traits in *B. europaea*.
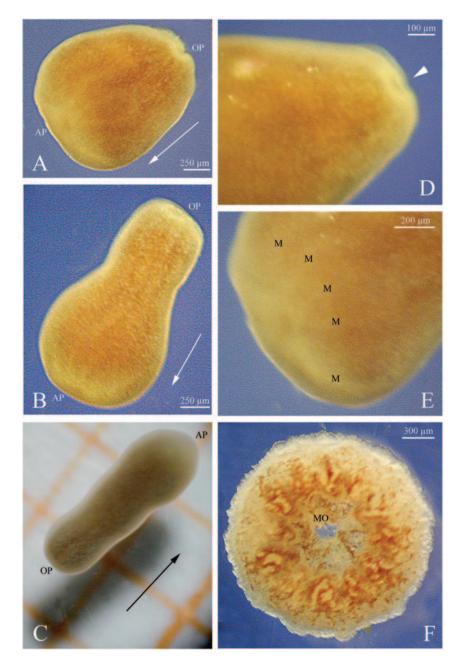
Figure 1. Aspects of larval morphology and metamorphosis in *Balanophyllia europaea*. (A) A swimming planula whose shape is contracted and somewhat spherical. The arrow indicates the direction in which the planula was moving. (B) A semi-contracted, pear-shaped swimming planula. The arrow indicates the direction in which the planula was moving. (C) A 'stretched-out', cylindrically-shaped swimming planula. The arrow indicates the direction in which the planula was moving. The squares on the graph paper that can be seen under the specimen are 1 mm per side. (D) The planula's oral pole. The arrowhead indicates the mouth. (E) The planula's aboral pole. The mesenteries are visible in transparency. (F) A young polyp, 23 d after metamorphosis. The brown dots visible in the polyp are the symbiont zooxanthella algae. AP aboral pole; MO mouth; M mesentery; OP oral pole.
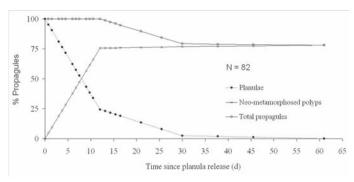
Figure 2. Dynamics of the metamorphosis process in *Balanophyllia europaea* under laboratory conditions.

The genus *Balanophyllia* includes about 50 species with a cosmopolitan distribution (Cairns, 1977). Studies on the reproductive biology and population dynamics of this genus have been carried out on only two species: *B. elegans* in Monterey Bay, California (Fadlallah and Pearse, 1982; Fadlallah 1983a; Beauchamp 1993) and *B. europaea* in Leghorn, Italy (Goffredo and Telò, 1998; Goffredo 1999; Goffredo et al., 2000, 2002). These species differ in one of their reproductive traits, the former being gonochoric and the latter hermaphroditic. On the other hand, they have the same reproductive strategy, both being brooders. As may be expected from brooding species (Harrison and Wallace, 1990; Richmond and Hunter 1990), larval ontogenesis in both species is completed at the time of planulation: the released larvae show a differentiated mouth and pharynx, and the coelenteric cavity is compartmentalized by mesenteries (Fadlallah and Pearse, 1982; Goffredo and Telò, 1998). Larvae of the two species differ substantially in their size, behavior, and competency period. Planulae of *B. europaea* are smaller (2.15 mm diameter) than those of *B. elegans* (3–5 mm diameter; Fadlallah and Pearse, 1982); the former tend to be swimmers and pelagic (see Results), while the latter are crawlers and benthic (Gerrodette, 1981). Furthermore, the time between release and metamorphosis is approximately three times greater in *B. europaea* than in *B. elegans*; an average of 7 d and a maximum of 42 d for the former versus an average of 2.7 d with a maximum of 14 d in the latter (Gerrodette, 1981). Thus, the potential dispersal capability is higher in
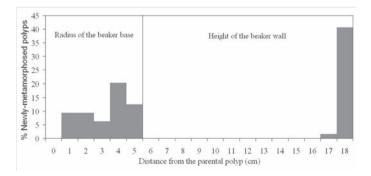

Figure 3. The spatial distribution of newly-metamorphosed polyps of *Balanophyllia europaea*. Parental polyps were located at zero, i.e. at the center of the beaker base, and 18 cm is the upper edge of the beaker; i.e., the greatest possible distance between parent and newly-metamorphosed polyps. Distances from 0–5 cm represent the radius of the beaker's horizontal base; distances from 5–18 cm represent the height of the beaker's vertical wall. The total number of newly-metamorphosed polyps was 64.

B. europaea than in *B. elegans*. This difference in dispersal potential could be linked to a fundamental difference in the biology of the two species, i.e., the presence or absence of symbiosis with zooxanthellae algae. In zooxanthellate corals, photosynthetic products are translocated from the symbiotic zooxanthellae to the host tissue and thereby contribute to a variety of nutritional requirements: these compounds are used by the coral for its basic metabolism (respiration), the synthesis of new cells and extracellular products, growth (Muscatine et al., 1984), and reproduction (Edmunds and Davies, 1986; Stimson, 1987; Rinkevich, 1989). *Balanophyllia europaea* is the only species in this genus that contains zooxanthellae and releases zooxanthellate planulae, while *B. elegans* is azooxanthellate (Veron, 2000). Rinkevich (1989) demonstrated that most of the energy required for planula development in some corals is supplied by the photosynthetic material produced by the zooxanthellae. After release and during dispersal, zooxanthellate planulae continue receiving carbon, fixed through photosynthesis, from their symbiotic algae. These planulae, therefore, are able to take advantage of energy that is not available to azooxanthellate larvae during dispersal (Richmond 1987, 1989; Ben-David-Zaslow and Benayahu, 1998). We hypothesize, therefore, that the potential longevity and dispersal capability of *B. europaea* planulae are greater than that of *B. elegans* planulae owing in part to their symbiosis with zooxanthellae, which allows a longer time until settlement and metamorphosis (Richmond, 1989). A direct link between the amount of energy stored by larvae and their dispersal potential has been reported in many invertebrates (Pechenick, 1990; Qian et al., 1990; Harms, 1992; Jaeckle and Manahan, 1992; Havenhand, 1993; Jaeckle 1994). Among Scleractinia, Richmond (1987, 1989) demonstrated this association and reported a competency period of 100 d for the zooxanthellate planulae of *Pocillopora damicornis* in comparison with 21 d for the azooxanthellate planulae of *Acropora tenuis*.

The potential dispersal of larvae is one factor that may explain differences in adult spatial patterns among closely related invertebrate taxa in the marine environment (Carlon and Olson, 1993). The distributional pattern of *B. europaea* is dispersed (random), with population densities averaging 16 (SE = 3) ind m^{-2} in the Mediterranean Sea (Goffredo, 1999). In contrast, distributional patterns in *B. elegans* are aggregated with population densities averaging 563 (SE = 102) ind m^{-2} along the Californian coast (Fadlallah, 1983a). Differences in adult spatial patterns may be linked to differences in the larval dispersal potential of these species (Gerrodette, 1981). A limited dispersal capability has been linked to an aggregated spatial pattern in adults in some taxa such as bryozoans (Keough and Chernoff, 1987) and ascidians (Davis and Butler, 1989; Stoner, 1990). In scleractinians, Carlon and Olson (1993) found a similar relationship in two Caribbean brooding species: *Favia fragum* (Esper, 1795) with limited larval dispersal had aggregated adult spatial distribution versus *Agaricia agaricites* (Linnaeus, 1758) with a high larval dispersal capability and more dispersed adult spatial patterns.

Differences in larval dispersal capability also have been linked to variation in the population genetic structure of organisms (Wright, 1943; Kimura and Weiss, 1964; Endler, 1973). Hellberg (1994, 1995, 1996) found that gene flow between pairs of populations of *B. elegans* declined as the geographic distance between those populations increased, as would be expected in species with short distance larvae dispersal, in which gene flow occurs exclusively across neighboring geographic areas (the "stepping stone" model; Kimura and Weiss 1964). The swimming-pelagic behavior observed here in *B. europaea* larvae suggests that the genetic structure of populations of this species would not follow the stepping stone model, and therefore, it would not be possible to use geo-

graphic distance to explain possible variations in gene flow between pairs of populations. We are currently conducting studies on the population genetics of *B. europaea*, to be compared with those of Hellberg (1994, 1995, 1996) on *B. elegans*. These comparative studies will contribute to the interpretation of how differences in larval dispersal capability between congeneric species may yield different models of genetic exchange among populations, and thus different evolutionary mechanisms.

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