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Reproduction Cycles and Strategies of the Cold-Water Sponges *Halisarca dujardini* (Demospongiae, Halisarcida), *Myxilla incrustans* and *Iophon piceus* (Demospongiae, Poecilosclerida) From the White Sea

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Abstract. The reproductive development of the Demospongiae species *Halisarca dujardini* (Halisarcida), *Myxilla incrustans* and *Iophon piceus* (Poecilosclerida) from Chupa Inlet (Kandalaksha Bay, the White Sea) was studied histologically during 1982–1994 and 1997. These species are all viviparous. *Halisarca dujardini* inhabits shallow waters (1.5–5 m); *M. incrustans* and *I. piceus* are common in a more stable environment at depths between 15 and 25 m. Initiation of sexual reproduction stages is dependent upon water temperature. Reproductive effort is low in *Myxilla incrustans* and *I. piceus* (reproductive elements contribute 7.3% and 12% of maternal tissue volume respectively), but much higher in *H. dujardini* (up to 69% of the parental tissue volume). Reproduction leads to localized destruction of maternal tissue for *M. incrustans* and *I. piceus* and complete disorder of central and basal parts of the choanosoma of *H. dujardini* after each period of reproduction. *Myxilla incrustans* and *I. piceus* reproduce throughout the hydrological summer, but reproduction in *H. dujardini* is restricted to 3 weeks. The average life span of *M. incrustans* and *I. piceus* is more than 4 years, and that of *H. dujardini* is about 7–12 months. The data suggest that *M. incrustans* and *I. piceus* are *K*-strategists, whereas *H. dujardini* is an *r*-strategist.

Introduction

Sponges often dominate benthic communities. For instance, in the southwestern part of the Barents Sea, sponge biomass is about 54% of the total biomass of bottom biocoenoses (Ereskovsky, 1995b). The biocoenoses of *Halichondria panicea* and *H. sitiens* in shallow-water coastal regions of East Murman (Barents Sea) form 71.9% of the total biocoenoses biomass (Propp, 1971). Knowledge of the life history and reproduction cycles of sponges is important for understanding their evolution and role in marine ecosystems. Although some information on reproductive seasons of cold and temperate marine sponges is available (Elvin, 1976; Fell, 1976; Ivanova, 1978; Fell and Jacob, 1979; Chen, 1976; Fell *et al.*, 1979; Fell and Lewandrowsky, 1981; Barthel, 1986, 1988; White and Barthel, 1994), little is known about their reproductive efforts and patterns of anatomical-histological change. These studies have indicated that the examined species are generally *r*-strategists and are responsive to seasonal environmental changes, mainly in water temperature. According to E. R. Pianka (1978), species of sessile macrofauna may be divided into *r*- and *K*-strategists. The first are characterized by high rates of reproduction and growth, high reproductive efforts, and high invasion opportunities in an unstable environment, whereas the second have low reproductive rates, low reproductive efforts, and good adaptation to specialized ecological niches (mainly in stable conditions).

The embryonic development of *Halisarca dujardini* (Halisarcida), the gametogenesis of *Myxilla incrustans* and *Iophon piceus* (Poecilosclerida), and the larval development of *I. piceus* have already been studied (Levi, 1956; Korotkova and Ermolina, 1982; Korotkova and Ereskovsky, 1984; Ereskovsky, 1986; Efremova *et al.*, 1987a, b). This paper describes the reproduction cycles and dependence of different sexual reproduction stages on environmental factors in demosponge species *Halisarca dujardini, Myxilla*

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incrustans, and *Iophon piceus* from the White Sea (Arctic), with special attention to reproductive efforts (the parental contribution to each phase of reproduction) and maternal tissue state during reproduction.

Materials and Methods

The shallow-water (1.5–5 m) species *Halisarca dujardini* Johnston, 1842 (Ceractinomorpha, Halisarcida) was sampled monthly from December to May and weekly from June to August (1986–1989 and 1991–1994, 1997). *Myxilla incrustans* (Johnston, 1842) and *Iophon piceus* (Vosmaer, 1881) (Demospongiae, Poecilosclerida), found in deeper water (15–25 m), were sampled twice a month from June to September, 1982–1984. Occasional samples of these species were taken in spring and summer from 1985 through 1991 and in 1997. Subtidal sponges were sampled using scuba. For quantitative studies, 90 specimens of *H. dujardini* (sampled from January to August in 1986–1989) and 29 specimens of *I. piceus* and 25 specimens of *M. incrustans* (sampled from June to October in 1983–1984) were investigated. Other specimens of these three species were analyzed for the presence of sexual reproductive elements. To ascertain the minimum lifespan of the three species, in July 1992 a few specimens of each species were marked in their locality. Every year these specimens were monitored for survival.

Immediately after specimens were removed from the water, sponge fragments were fixed in Bouin's and Carnoy's fixatives for light microscopy. Tissue fragments were dehydrated through an ethanol series, placed in celloidin blended with castor oil and then in chloroform, and embedded in paraffin. Sections were cut to a thickness of 6 μm and Meier's hematoxylin, eosin, and Heidenhein ferric hematoxylin. Ten microscopic slides of each specimen were examined.

The number of gametes, embryos, and larvae in parental tissues were calculated using Elvin's equation (Elvin, 1976):

$$N = \delta N({}^{t}\!/\!_{D} + t)\mathrm{K}. \qquad (1)$$

where N is the number of objects per cubic millimeter of tissue; δN is the average number of objects (gametes, embryos, larvae and spermatic cysts) in the microscope field; t is the thickness of the histological section (here 0.006 mm); D is the diameter of the object; and K is a constant for converting the number of objects in a square millimeter to the number in a cubic millimeter; it is equal to 166.7.

Egg, spermatic cyst, embryo, and unreleased larva volumes were calculated using the equation:

$$V = ({}^{1}\!/\!_{6})\,D \qquad (2)$$

where V is an object volume and D is its diameter.

The volume of reproductive elements per cubic millimeter of parental tissue was obtained by multiplying N by V. The total sponge volume in breeding season was measured by immersing each specimen into a graduated cylinder filled with water. The volume of water displaced was a measure of the volume of the sponge tissue. Data are presented as mean ± standard error.

A hydrologic thermometer was used to measure water temperature during sampling. Additional information on

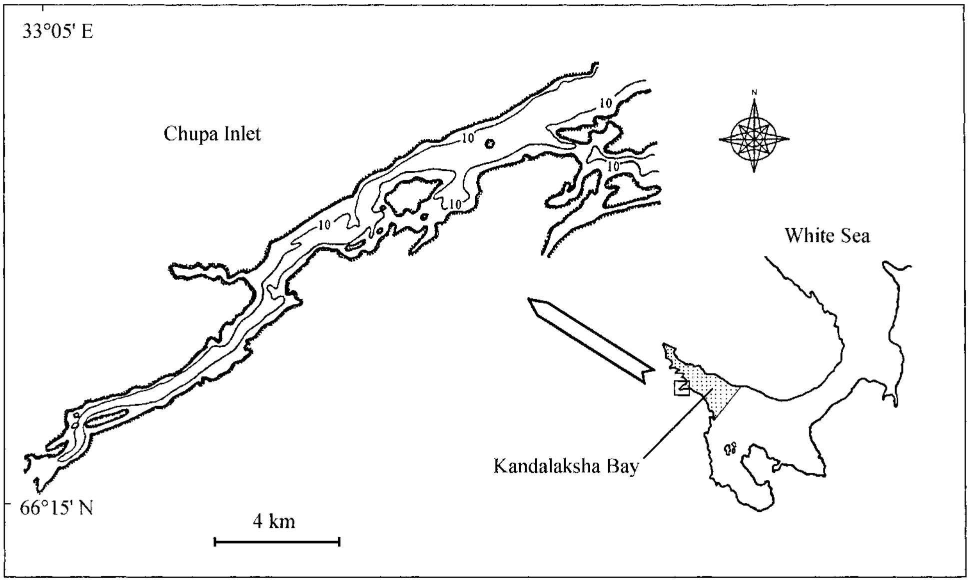

Figure 1. Chupa Inlet, showing the 10-m depth contour; inset illustrates the location of the Inlet in Kandalaksha Bay of the White Sea.

seasonal temperature changes at different depths in Chupa Inlet (the White Sea) was obtained from the White Sea Biological Station, Zoological Institute, Russian Academy of Sciences.

Study Area

Seasonal sampling was performed in the Chupa Inlet located in the innermost part of the Kandalaksha Bay, the White Sea (Fig. 1). All oceanologic and climatic data were obtained from Babkov (1982, 1984) and Babkov and Golikov (1984). The region has a long, severe winter and a short, relatively warm summer. From December until mid-May, Chupa Inlet is covered with ice. The average annual water temperature in the Inlet, which has a mean depth of about 20 m, is about 5°C, ranging from −1.5°C in winter to 17°C in summer (Fig. 2a). In autumn and spring the water column is homothermal: the temperature throughout all layers in November does not exceed +2°C and in March ranges from −1.0° to −0.5°C (Babkov, 1982).

Except for the open part of the Kandalaksha Bay, Chupa Inlet is characterized by reduced salinity. The seasonal variation in the 10-m surface layer is between 15‰ and 26‰; fluctuations decrease with depth, and in the bottom layer are not more than 1‰. The minimum surface-layer

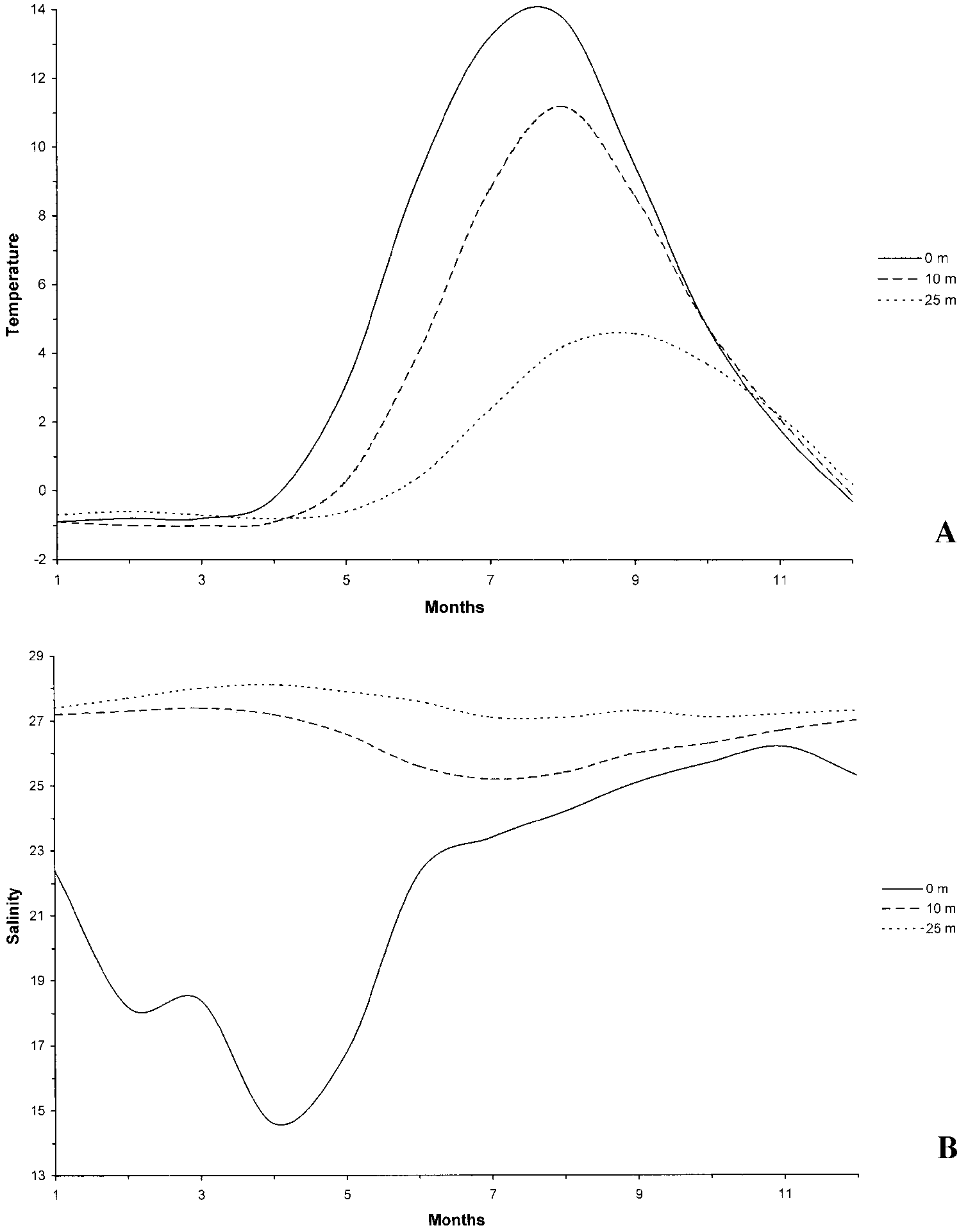

Figure 2. Seasonal changes in temperature (A) and salinity (B) at different depths in Chupa Inlet.

salinity was detected in April, and the maximum in November (Fig. 2b) (Babkov, 1982).

Temperature-salinity-analysis reveals two bodies of water in the region: surface water—boundary depth between 10 and 25 m, yearly temperature average 11°C, salinity not exceeding 27.0‰; and bottom water—water temperature not more than 5°–6°C, salinity exceeding 27‰ (Babkov, 1982; Babkov and Golikov, 1984).

Results

Halisarca dujardini

In the White Sea, *Halisarca dujardini* dwells at depths from 1.5 to 10 m, mainly on the algae *Fucus vesiculosus* and *Laminaria saccharina* and, rarely, on stones. Its body shape is irregular: encrusting, pillowy or clotted in form. Its size varies from 3 to 40 mm in width and from 2 to 6 mm in height. The volume of specimens averages 0.25 to 0.40 cm^3. The body surface is smooth and slimy. Oscules are small, one or several in a specimen. Color varies from milky to greyish-brown.

Halisarca dujardini is a gonochoristic organism. Spermatogenesis occurs at a water temperature of around −0.8°C and lasts for about 4 months. Spermatic cysts containing spermatocytes can be found in the male mesohyl in about the middle of December at a water temperature of about −0.08°C. Male generative cells appear to originate from choanocytes that migrate into the lumen of choanocyte chambers, where spermatogenesis takes place. Choanocyte chambers thereby transform into spermatic cysts with a diameter between 40 and 90 μm. During intensive spermatogenesis (January–March), the mesohyl of the mature male differs greatly from that of an immature individual. It contains neither choanocyte chambers nor channels and pores. At this time the volume of spermatic cysts containing male generative cells amounts to 0.65 ± 0.5 mm^3/mm^3 of tissue (Fig. 3). In March and April, spermatic cysts contain only mature spermatozoa. From mid-December until mid-April, the volume of total reproductive elements (male and female) is nearly equal to the volume of spermatic cysts, differing from it only by the minute volume contributed by early oocytes (Fig. 3). Spermatogenesis and, thereafter, fertilization cease by April or the first week of May.

Early oocytes, 15 to 35 μm in diameter, are first observed during the last third of December, at a water temperature of about −0.6°C. Cytoplasmic growth is recorded until the beginning of June; however, vitellogenesis begins in May, when water temperature is about +2°C. Mature eggs, 110–130 μm in diameter, appear in females at the end of May; their number increases rapidly and their total volume

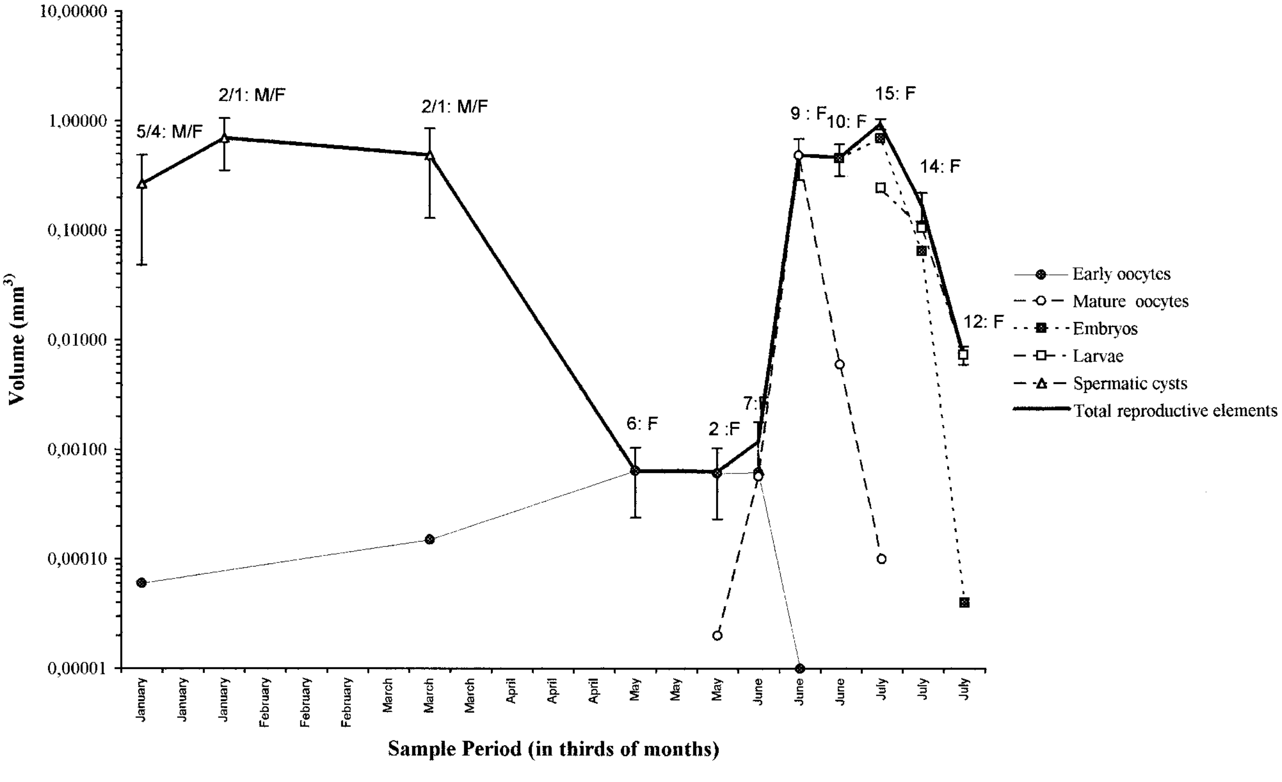

Figure 3. Mean volumes of gametes, embryos, and larvae per cubic millimeter of parental tissue in *Halisarca dujardini* during the reproduction seasons for 1986–1989. Numbers indicate individuals (males/females) analyzed. Vertical bars designate standard errors of the values for total reproductive elements.

reaches 0.49 ± 0.011 mm^3/mm^3 of tissue in mid-June (Fig. 3, 4a).

The development of larvae, namely cleavage and morphogenesis, occurs within a fortnight, from late June until July. During this period water temperature averages about 10°C. The even, asynchronous cleavage results in a coeloblastula, which transforms into a disphaerula larva (Ereskovsky and Gonobobleva, 1999), with a diameter between 120 and 150 μm (Fig. 4b, c). Larvae of *H. dujardini* (disphaerula), consisted of two flagellated sphaeras: external and internal; the internal sphaera was formed by invagination of laternal cells. The disphaerula was completely flagellated—sparsely so on the posterior pole (Ereskovsky and Gonobobleva, 1999). The volume of reproductive elements (cleaving embryos and prelarvae) reaches its maximum from the end of June to the beginning of July and amounts to about 0.69 ± 0.20 $mm^3/1\ mm^3$ of the tissue (*i.e.*, 69.5% of the total sponge volume; Fig. 3). This period is marked by the complete disorder of central and basal parts of the choanosoma, which are now filled with developing larvae (Fig. 4c). Normal tissue organization persists only in the narrow marginal zone of the sponge. Larval emergence occurs rapidly, within about a fortnight, begining before mid-July at a water temperature of about 12°C.

Slow postmetamorphic development of the new generation and postreproduction rehabilitation of parental sponges continues until December. Some parental sponges died and underwent disruption after larval emergence. A general life-history scheme of *H. dujardini* in the White Sea is shown in Figure 5.

Myxilla incrustans *and* Iophon piceus

White Sea populations of two Myxillidae species, *Myxilla incrustans* and *Iophon piceus*, are similar in their main life-history stages. Both species are simultaneous hermaphrodites: oogenesis and spermatogenesis occur at the same time. Gametogenesis and embryogenesis take place only in the choanosoma.

Iophon piceus, in the White Sea, dwells at depths from 3 to 172 m on stony-muddy substrates where the water temperature ranges from −1.15° to 11.5°C and the salinity from 18.6‰ to 29.12‰. The body is irregular—lumpy or flattened and uneven—with a wrinkled and porous surface. The oscules average 0.5 cm in diameter. The body height ranges from 6 to 12 cm and the diameter from 7 to 10 cm. The volume of observed individuals averages 11–16 cm^3. All stages of embryogenesis and gametogenesis in *I. piceus*, including new gonia formation, occur simultaneously (Fig. 6).

Generative cell development in *I. piceus* is usually initiated during February for female elements, and April–May for male elements. Male and female gametogenesis becomes active in mid-May at depths of 15–25 m at an

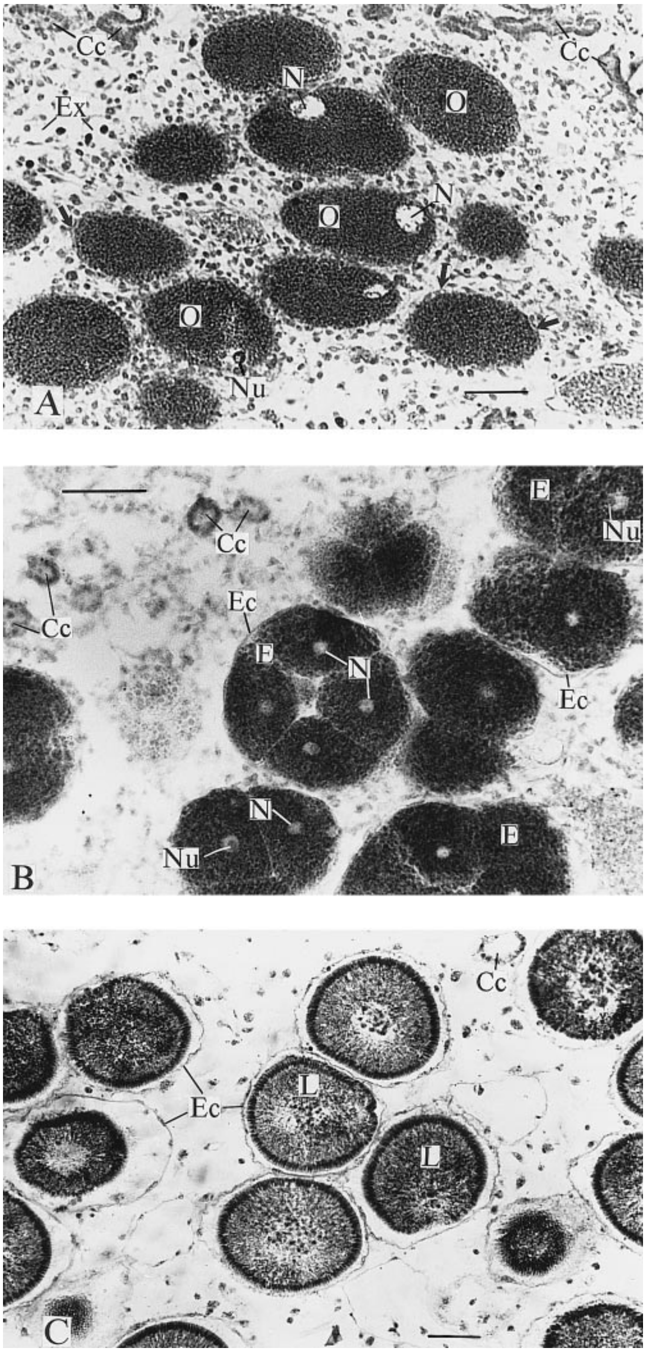

Figure 4. The central part of the choanosoma of *Halisarca dujardini*, showing stages of vitellogenesis, cleaving embryos, and mature larvae. (A) Oocytes (O) in late vitellogenesis, still with prominent nucleus (N) and nucleolus (Nu), are surrounded by cells forming embryonic capsules (arrows). The aquiferous system in this part of the choanosoma is destroyed. There are remnants of exhalant channels (Ex) and choanocyte chambers (Cc) in upper marginal parts of the choanosoma. Scale bar = 50 mm. (B) Cleaving embryos (E) enclosed in embryonic capsules (Ec). As in (A), choanocyte chambers (Cc) remain in upper marginal parts of the choanosoma. Note the nucleus (N) and nucleolus (Nu) of blastomers. Scale bar = 50 μm. (C) Larvae (L) before emission with well-differentiated ciliated cells at their periphery. Scale bar = 50 mm.

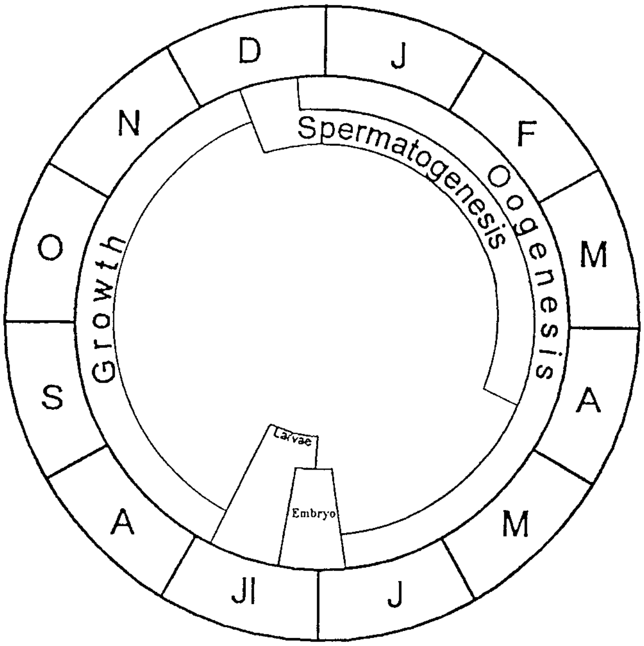

Figure 5. Scheme of the life history of *Halisarca dujardini* at Chupa Inlet, White Sea.

average water temperature of +0.1°C. Egg vitellogenesis and cleavage occur in late June and early July, when water temperature is about +4.2°C. During the last third of June the total volume of reproductive elements in this species amounts to about 0.05 ± 0.021 mm^3/mm^3 of tissue, whereas during the last third of July it amounts to 0.096 ± 0.028 mm^3 (Fig. 7).

The first larvae in *I. piceus* tissues are recorded at the end of July. These are typical parenchymulae common to the order Poecilosclerida. Their oval or oviform body (200×260 μm) is evenly covered (except the tailpiece) by flagella that are all of the same length (Ereskovsky, 1986). Larval emergence lasts from the first third of August (when water temperature is about 8°C) to early October, when the larvae constitute the total volume of reproductive elements. In the initial period of this process, the volume of the generative cells and larvae reaches 0.118 ± 0.01 mm^3/mm^3 of tissue (about 12%).

It is notable that only local disintegration of the parental tissues is observed during the period of larval emergence in *I. piceus:* the adjacent choanocyte chambers are destroyed, and some of the choanocytes degenerate. In this case, the ratios of mesohyl cell elements are modified around the region of larvae development (Fig. 6). However, the general anatomical and histological organization of the parental sponge is not changed. Marked specimens of *I. piceus* remained alive (survived) from 1992 to 1995, so their lifespan is more than 4 years. The life-history scheme of White Sea *I. piceus* individuals is represented in Figure 8.

Myxilla incrustans, in the White Sea, inhabits stony-muddy or gravelly-muddy substrates chiefly at depths from 1.5 to 150 m within the temperature range of −0.9° to 14.5°C and the salinity range of 23.3‰ to 28.93‰. The body is irregular, usually lumpy- or pillowy; the surface is uneven, wrinkled, and porous. The average oscule diameter is about 0.8 cm. Specimens are at most 8 cm in height and 7 cm in width. The volume of investigated individuals averaged 7 to 9 cm^3.

Early oocytes are found in *M. incrustans* in late February, and the first spermatic cysts are seen in April-May. Gametogenesis increases in mid-June at a water temperature of about +1.7°C.

During this period, the development of male and female generative cells is continuous (Fig. 9). Vitellogenesis and cleavage persist from mid-July until the beginning of August at a water temperature of about 6°C. At the beginning of this period, the total volume of reproductive elements amounts to 0.019 ± 0.006 mm^3/mm^3 of tissue (Fig. 10). The number of embryos in maternal sponges rapidly increases as the relative amount of fully formed oocytes decreases. By the beginning of August, spermatic cysts are no longer found.

The first larvae are recorded in August. Larvae (typical parenchymulae) are released from September until early October, at water temperatures from 2.5° to 4°C. The volume of all reproductive elements during larval release averages 7.3% (0.73 ± 0.21 mm^3). The general anatomical and histological organization of *M. incrustans* is unchanged after larval release. Marked specimens of *M. incrustans,* like those of *I. piceus,* survived from 1992 to 1995; their lifespan also exceeds 4 years. The life-history scheme of *M. incrustans* in the White Sea is represented in Figure 11.

Rehabilitation processes and vegetative growth occur

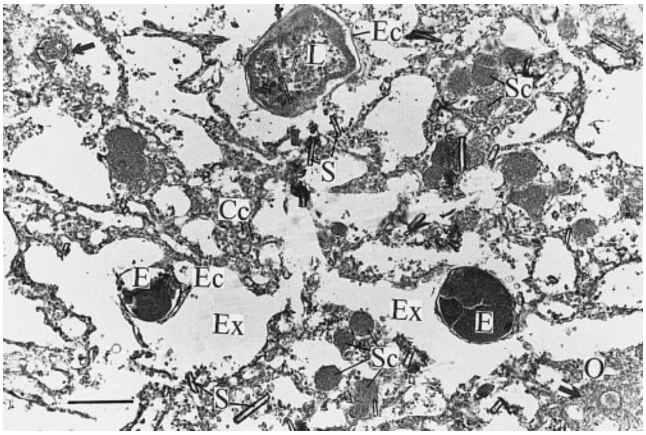

Figure 6. The choanosoma of the simultaneous hermaphrodite *Iophon piceus* during the reproductive period. Vitellogenic oocytes (O) are surrounded by nurse cells (arrows). Cleaving embryos (E) and larvae (L), enclosed in embryonic capsules (Ec) are located close to exhalant channels (Ec). Many spermatic cysts (Sc) can also be seen. Note choanocyte chambers (Cc) and spicules (S). Scale bar = 100 μm.

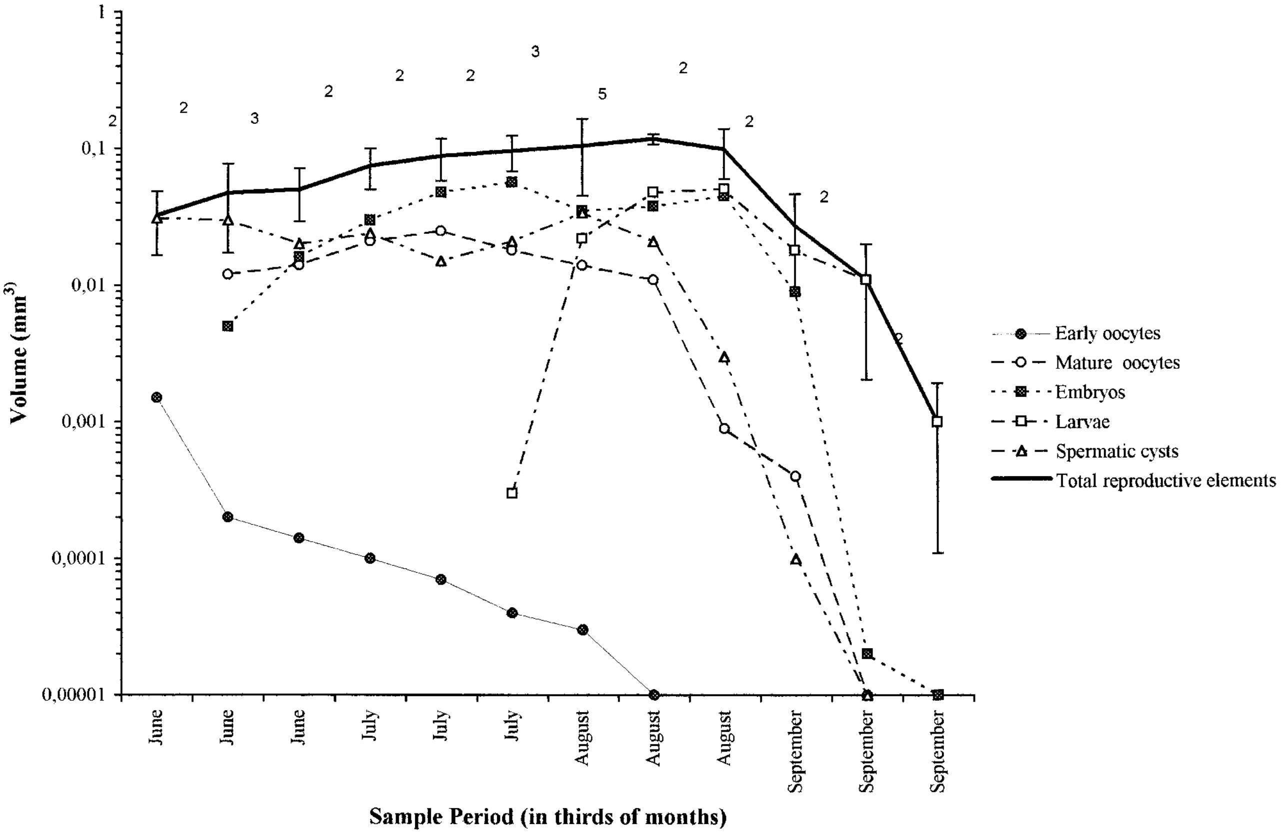

Figure 7. Mean volume of gametes, embryos, and larvae per cubic millimeter of tissue in the hermaphrodite *Iophon piceus* during the reproductive seasons for 1983–1984. For legend, see Figure 4.

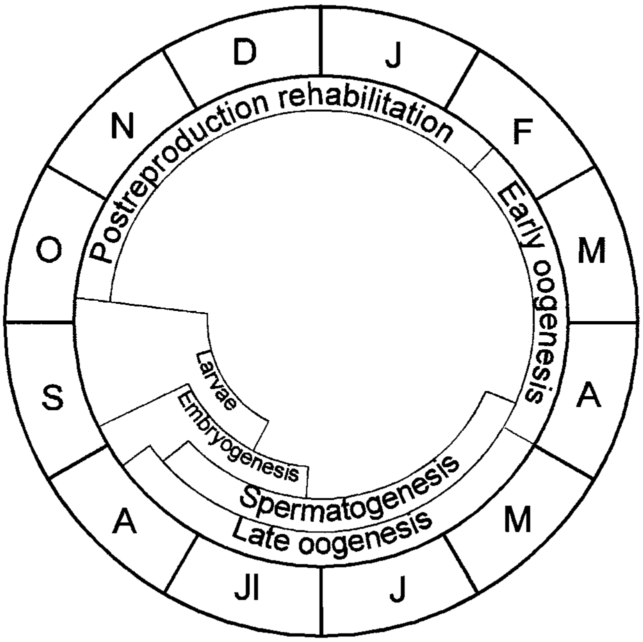

Figure 8. Life-history scheme of *Iophon piceus* in the White Sea.

during the postreproduction period of both *I. piceus* and *M. incrustans.*

Discussion

As evident from previous investigations (Ereskovsky, 1995b), only eurybiont sponges were able to settle in the White Sea where low salinity and temperature stratification are common. *H. dujardini, I. piceus,* and *M. incrustans* are thus subjected to seasonal fluctuations in temperature, salinity, and nutrition. The influence of these factors is different in the shallow waters populated by *H. dujardini* than in the deeper waters occupied by *I. piceus* and *M. incrustans.* Consequently, these populations have a special set of adaptations, including life and reproduction tactics.

Within its area, *H. dujardini* colonized algae and stones only in littoral-medial vertical zones (0–35 m) having salinities between 16‰ and 35‰ and temperatures from −0.8° to 26.5°C (Ereskovsky, 1993, 1994b, 1995a). It is a widespread subtropical-boreal species, common in the Atlantic Ocean from Mediterranean shallow waters along the Atlantic coast of Europe to the Barents and White Seas, and along the North American coast from Cape Hatteras to the Gulf of Maine (Ereskovsky, 1993, 1994a). *Halisarca dujar-*

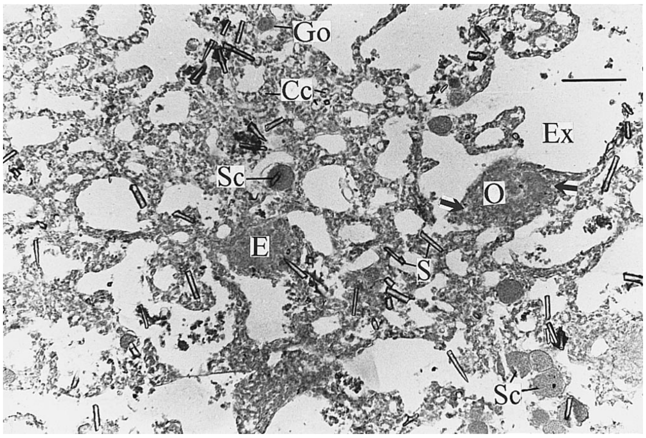

Figure 9. The choanosoma of the simultaneous hermaphrodite *Myxilla incrustans* at the stage of gametogenesis. The growing oocyte (Go) appears to be migrating in mesohyle; a vitellogenic oocyte (O) is surrounded by nurse cells (arrows) and located near the exhalant channel (Ex). Spermatic cysts (Sc) are dispersed in the choanosoma. Note choanocyte chambers (Cc) and spicules (S). Scale bar = 100 µm.

dini inhabits very fluctuating shallow-water environments. This report concerns the northern boundary area of the species—*i.e.*, the circumlittoral zone of the Barents and White Seas where variations in temperature and salinity are acute.

Correlations between different stages of the reproductive cycle and environmental conditions (chiefly temperature) in the White Sea population of *H. dujardini* have been noted here. Gametogenesis starts at an average water temperature of −0.8°C. The connection of spermatogenesis with minimal water temperatures has also been recorded in *H. dujardini* on the Atlantic coast of the United States (Chen, 1976). The onset of vitellogenesis in White Sea sponges correlates with a spring temperature change in May. The disappearance of male spermatic cysts in April suggests that oocytes are fertilized during their cytoplasmic growth. Penetration of the oocyte by sperm during meiotic prophase has been described in the nematode *Brachycoelium*, the annelids *Dinophilus* and *Histriobdella*, and the onychophora *Peripalopsis* (Austin, 1965).

Halisarca dujardini releases larvae during the period of temperature maximum. This is typical for marine hydrobionts in cold waters; the release of their larvae is timed to the momentary summer period of warmest water (Kaufman, 1977; Kasyanov, 1989). Embryogenesis, larval development, and metamorphosis in the White Sea population of *H. dujardini* occupy only about 3 to 4 weeks—from the end of June to the middle of July.

White Sea populations of *M. incrustans* and *I. piceus* dwell mostly in more stable and predictable conditions. Eurybathic circumlittoral-highbathyal (1.5–500 m) *M. incrustans* and *I. piceus* (Ereskovsky, 1995a) inhabit chiefly stony-muddy substrates. The boreal-arctic species *M. incrustans* is eurychoric: it is found in all Arctic Seas; the southern Pacific boundary of its area is the northern part of

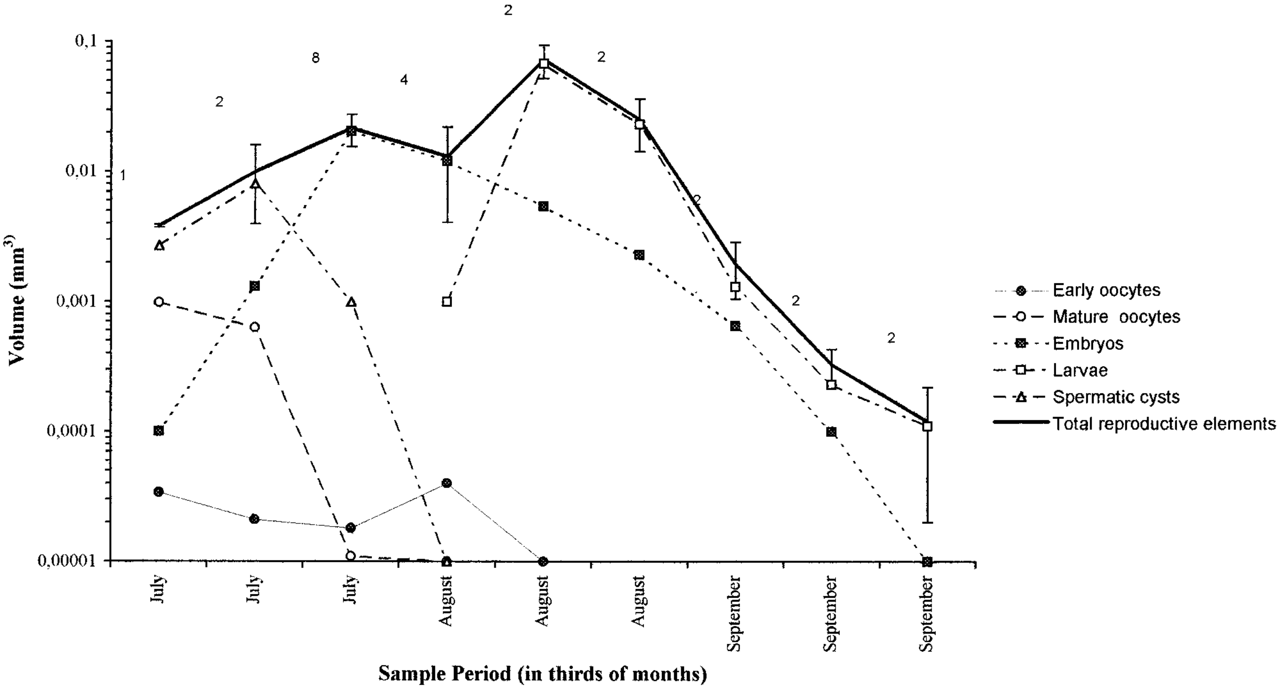

Figure 10. Mean volume of gametes, embryos, and larvae per cubic millimeter of tissue in the hermaphrodite *Myxilla incrustans* during the reproductive seasons for 1983–1984. For legend, see Figure 4.

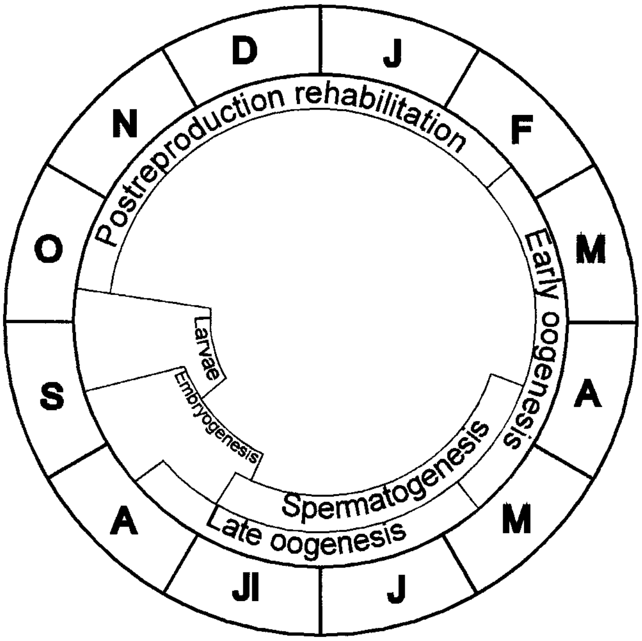

Figure 11. Life-history scheme of *Myxilla incrustans* in the White Sea.

the Sea of Japan and the California bathyal zone; in the Atlantic Ocean it extends south to the western Mediterranean and Cape Cod (Ereskovsky, 1994a).

Thus, *M. incrustans* is apparently a eurythermic (−1.9°–16.2°C) and euryhaline (25‰–35.5‰) species (Ereskovsky, 1994b).

The area of the Pacific highboreal-Arctic species *Iophon piceus* is not so broad. *I piceus* is circumarctic; in the Pacific Ocean it is found near the Northern Kurile Islands, in the Sea of Okhotsk and near Vancouver Island; in the Atlantic Ocean it extends south to Baffin Sea and the Faeroe Islands. Like *M. incrustans,* this species is eurythermic (−1.6°–12.5°C) and euryhaline (25.6‰–35.5‰) (Ereskovsky, 1994b).

It is clear from the reported data that different stages of the sexual cycles in the investigated species correlate well with seasonal environmental changes. Most significantly, the dependence of the main stages of oogenesis (a complicated multi-stage process) upon water temperature should be noted. Thus, deutoplasm growth begins within hydrological spring in all of the populations investigated. Vitellogenesis and egg maturation, as well as embryogenesis, end during hydrological summer—*i.e.,* the warmest season. A similar dependence on temperature has been noted for the developmental stages of some tropical sponge species (Fromont, 1994; Fromont and Bergquist, 1994).

Larval emission in some species is timed to a specific hydrological season in their habitat. On one hand, this relationship is modified by peculiarities of larval development and ecology since organisms are more temperature-sensitive during early ontogenesis than later (Kinne, 1963). On the other hand, the relationship is determined by the species genotype, and larvae are released when the temperature is close to the optimum for the species. But dependence of larval release upon water temperature is further mediated by biogeographical characteristics of the species. For poikilotherms, the temperature of the environment during speciation influences cell and tissue thermoresistance, which is considered to be a species-specific feature (Ushakov, 1989). As a result, temperatures optimal for both life and larval release are closely connected with the conditions that prevailed during the origin of the species and, consequently, with its zoogeographic position (Golikov and Scarlato, 1972; Mileikovsky, 1981). Maximal annual average temperatures most favorable for larval development are recorded within this period (Babkov, 1984).

In this study, special attention was given to the state of maternal tissues in different sexual reproduction stages in each of investigated species. It became evident from previous studies (Ereskovsky and Korotkova, 1997) that sexual and somatic morphogenesis correlate closely in sponge ontogenesis. Thus, somatic tissue state is important for the attainment of different sexual reproductive stages. Sexual and somatic morphogenesis either take place as successive life-cycle stages or occur in parallel, but they vary in correlation with each other due to their equal dependence on internal integrative mechanisms (Simpson and Gilbert, 1974; Fell *et al.,* 1979; Korotkova, 1988).

Owing to the vertical stratification in the Kandalaksha Bay, deep-water *M. incrustans* and *I. piceus* are less exposed to seasonal environmental fluctuations than is the shallow-water *H. dujardini.* It could be suggested then that *M. incrustans* and *I. piceus* are *K*-strategists, whereas *H. dujardini* is an *r*-strategist. Some features of these species may provide additional evidence for such conclusions:

1. Reproductive effort (the contribution by the organism to all parts of reproduction) is low in Myxillidae (about 7.3% of the maternal tissue volume in *M. incrustans* and about 12% in *I. piceus*) but high in *H. dujardini* (69.5% in females and 65% in males).
2. These different levels of reproductive effort result in different degrees of destruction of maternal tissue: only localized destruction in Myxillidae (both *I. piceus* and *M. incrustans*), but widespread destruction in *H. dujardini.*
3. Embryogenesis and larval development last over the hydrological summer in Myxillidae, but only 3 or 4 weeks in *H. dujardini.*
4. The average life span is more than 4 years in *M. incrustans* and *I. piceus* and about 7–12 months in *H. dujardini.*
5. *M. incrustans* and *I. piceus* inhabit a more stable environment than *H. dujardini.*

Similar ecological and reproductive characteristics have been reported for sponges inhabiting different regions. Thus, the volume of reproductive elements in the eurybiont *r*-strategist *Mycale* sp. amounts to 7.5%–20% under stressful conditions in Discovery Bay, Jamaica (Reiswig, 1973). Similar characteristics have been reported for other *r*-strategists such as littoral specimens of *Haliclona permolis* from the Oregon coast of the United States (Elvin, 1976) and the estuarine species *Haliclona loosanoffi* and *Halichondria* sp. (Fell, 1976; Fell and Jacob, 1979; Fell *et al.*, 1979; Fell and Lewandrowsky, 1981; Lewandrowsky and Fell, 1981). Shallow-water *Halichondria panicea* from the Barents (Ivanova, 1978), Baltic (Barthel, 1986, 1988), and White Seas (Ereskovsky, unpubl.) could be classified as a typical opportunist species and an *r*-strategist.

A comprehensive study of marine ecosystems is impossible without data on the reproductive cycles of the species of which they are composed. Knowledge of the peculiarities of both the reproduction strategies of the species and the reproduction tactics of the populations in different regions is thus of great value. The concept of reproduction strategies in sponges is still under development. In analyzing sponge reproduction, it is necessary to consider the maternal tissue state and reproductive effort of the specimens throughout the period of reproduction.

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