ELSEVIER

Deep-Sea Research II 53 (2006) 972–984

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Observations of asexual reproductive strategies in Antarctic hexactinellid sponges from ROV video records

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Received 11 January 2005; accepted 14 February 2006
Available online 5 July 2006

Abstract

Hexactinellid sponges are one of the structuring taxa of benthic communities on the Weddell Sea shelf (Antarctica). However, little is known about their reproduction patterns (larval development, release, settlement, and recruitment), particularly in relation to sexual and asexual processes in sponge populations. Video stations obtained during several expeditions covering a wide depth range and different areas recorded a high frequency of asexual reproductive strategies (ARS) (bipartition and budding) among hexactinellids. Analysis of seabed video strips between 108 and 256 m depth, representing an area of 1400 m^2, showed that about 28% of these sponges exhibited ARS. The *Rossella nuda* type dominated most of the video stations and exhibited the highest proportion of budding (35%). This proportion increased with the size class. Size class >20 cm exhibited in all the stations a mean value of 8.3 ± 0.7 (SE) for primary and of 2.5 ± 0.2 (SE) for secondary propagules per sponge, respectively. Results from a shallow station (Stn 059, 117 m depth) showed the highest relative abundance of *R. nuda* type and budding (>20 cm ~72%, 10–20 cm ~60%, 5–10 cm ~12%, and <5 cm ~3%). A potential influence of iceberg scouring disturbance on the occurrence of budding and number of propagules also was investigated. We conclude that asexual reproduction in hexactinellid sponges may be more frequent than has been thought before and it may greatly influence the genetic structure of populations.

Keywords: Antarctica; Asexual reproduction; Hexactinellida; ROV; Sponges

1. Introduction

Recruitment, either through larvae or asexual propagules, is one of the fundamental factors in determining population success in marine benthic communities (''supply-side ecology''; Grosberg and Levitan, 1992; Levin, 1986; Underwood and Fairweather, 1989; Young, 1990). Recruitment represents the input of new individuals into a population or community. This process is fundamental for understanding a wide range of ecological descriptors, from the genetic structure of populations through to population dynamics and community structure (Ayre and Hughes, 2000; Caley et al.,

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doi:10.1016/j.dsr2.2006.02.008

1996; Hughes, 1990; Roughgarden et al., 1987). Recruitment also is recognized as an important determinant for the establishment and maintenance of populations affected by disturbance events (Connell and Keough, 1985; Menge and Sutherland, 1987; Sousa, 2001).

Clonal benthic invertebrates (constituted by modules/polyps or zooids) such as sponges, cnidarians, bryozoans, and ascidians disperse by both sexual (as offspring or larvae) and asexual means (as fragmentation, regrowth of existing colonies, internal gemmules, and as external propagules) (Jackson, 1986; Hughes, 1989; Wulff, 1985; 1986). Variations in the life histories of both modular and solitary organisms are associated with a number of factors such as age and/or body size at sexual maturity, sex ratios, and the compromise of number, size, protection, and survival of the offspring (Hall and Hughes, 1996; Stearns, 1992). There have been many discussions on the evolution of sexual versus asexual strategies regarding their costs and benefits of energy allocation under different regimes of mortality (e.g., Jackson and Coates, 1986; Stearns, 1992; Williams, 1975). The relative contribution of sexual and asexual reproduction to the recruitment of new individuals into populations may vary considerably; however, the survival of asexual propagules is considerably higher than for most larval recruits (Highsmith, 1982; Jackson and Coates, 1986; Karlson, 2002).

Sponges exhibit various modes of reproduction, larval types, dispersal abilities, and life-history traits that may have had major evolutionary consequences (Ayling, 1980; Wulff, 1991). The most common types of asexual reproduction forms found in sponges are gemmule formation, budding, and fragmentation of the adult (Simpson, 1984). Budding is the formation of new individuals from primordial tissue by growth and cellular differentiation, without division from the parent (Hughes, 1989). This phenomenon is not very common in sponges although it occurs in some phylogenetically distant species, e.g., on the hispidating spicule bundles of *Tethya* spp. (Hadromerida) (Connes, 1968; Bergquist, 1978) and *Mycale contarenii* (Poecilosclerida) (Uriz, 1983) and along the spicule rhizoids and the medium zone of *Thenea muricata* (Astrophorida) (Boury-Esnault et al., 1994).

The Hexactinellida or glass sponges mainly inhabit the deep oceans (500–3000 m), but there are at least four shallow locations (< 50 m) where they occur: along the coast of British Columbia and Alaska, in submarine caves in the western Mediterranean, in the fjords of southern New Zealand, and in the Ross Sea (Antarctica) (Boury-Esnault and Vacelet, 1994; Dayton, 1979; Leys et al., 2004). Hexactinellids are one of the most dominant groups constituting the benthic communities of the Ross and Weddell seas (Barthel and Gutt, 1992; Bullivant, 1967; Dayton et al., 1974). Although only represented by few species (28 species) (Barthel and Tendal, 1994), hexactinellids are important structural agents by means of their epi-and endobiotic relationships with other organisms and substrate formation by generation of spicule mats (Barthel et al., 1991; Barthel and Gutt, 1992; Kunzmann, 1996). They greatly contribute to the total abundance and biomass of the Antarctic benthic fauna (Gerdes et al., 2003; Teixidó et al., 2004). Hexactinellid sponges are abundant and reach large sizes in areas of low ice disturbance (Teixidó et al., 2004), and exhibit very low growth rates and long life spans (Dayton, 1979). However, little is known on their reproduction patterns (larval development, release, settlement, and recruitment), particularly on the extent of the sexual and asexual processes. They are thought to reproduce year round by larvae and only at long-time intervals (Barthel and Tendal, 1994; Dayton, 1979). The most comprehensive studies on sexual reproduction of hexactinellids were performed by Okada (1928) on *Farrea sollasi* and by Boury-Esnault et al., 1994 on a single population of *Oopsacas minuta* living in a Mediterranean cave. Asexual reproduction by budding has been observed regularly in *Rossella racovitzae*, which forms dense patches of small individuals on Antarctic soft bottoms (Barthel and Gutt, 1992; Barthel and Tendal, 1994; Dayton, 1979).

Remote imaging techniques have provided valuable information of Antarctic benthic communities on the Weddell Sea shelf (Gutt and Piepenburg, 2003; Starmans et al., 1999; Teixidó et al., 2004). From a collection of images acquired during several expeditions covering a wide depth range and different areas, we observed a high plasticity of asexual reproduction modes in hexactinellid sponges (Fig. 1). Moreover, we noted a high abundance of the hexactinellid *Rossella nuda*/*Anoxycalyx* (*Scolymastra*) *joubini* type (both named as *R. nuda* type) with spectacular propagules (buds) on their surface at a shallow station (Stn 059, 117 m depth) in Atka Bay (eastern Weddell Sea). This phenomenon also was recorded at deeper stations on the Weddell Sea shelf, but the abundance of this