REPORT

R.G. Waller · P.A. Tyler · J.D. Gage

Reproductive ecology of the deep-sea scleractinian coral *Fungiacyathus marenzelleri* (Vaughan, 1906) in the northeast Atlantic Ocean

Abstract The reproductive biology and its seasonality were examined in the deep-water, solitary coral *Fungiacyathus marenzelleri* from 2,200 m depth in the NE Atlantic, using histological techniques. A total of 186 corals were collected using either an Otter trawl (semi-balloon) or Agassiz trawl from the research vessel RRS *Challenger* between 1979 and 1991. All individuals were gonochoric, with all 48 mesenteries being fertile. A high fecundity was recorded (2,892 ± 44.4 oocytes per polyp) with strong size-dependency. This species is a quasi-continuous reproducer with overlapping gametogenesis for both spermacysts and oocytes. No planulae were observed and broadcasting of gametes is inferred, with the large egg size (max. 750-μm diameter) suggesting lecithotrophic development. There is a non-significant trend towards a synchronous spawning event during June/July. Asexual fission was observed, though in low numbers.

Keywords Ahermatypic · Azooxanthellate · Solitary coral · Gametogenesis

Introduction

Zooxanthellate corals form one of the best-recognized marine ecosystems on earth. These corals, however, are limited to the warm, sunlit waters of the tropics and subtropics, and by depth. Below the permanent thermocline in many parts of the world's oceans, particularly at bathyal depths, large accumulations and small patches of colonial, azooxanthellate corals, such as *Lophelia pertusa*, occur (see Rogers 2000). Solitary ahermatypic corals can also be found on soft sediments at both bathyal and abyssal depths.

Information on reproduction in deep-sea anthozoans is limited. For actinarians, Van Praet et al. (1990) have described the gametogenic biology of two species of *Phelliactis*; Bronsdon et al. (1993) described the gametogenic periodicity of the bathyal epizoite *Amphianthus inornatus* and the abyssal epizoite hermaphrodite *Kadosactis commensalis*. Muirhead et al. (1986) observed gametogenesis in two zooanthid species, the bathyal *Epizoanthus paguriphilus* and the abyssal *E. abyssorum*. In the Alcyonaria, the gametogenic pattern has been described for a variety of species of pennatulid (Rice et al. 1992; Tyler et al. 1995). From these limited studies, it appears that there is no gametogenic pattern 'typical' of deep-sea anthozoans.

Information on reproduction in shallow-water scleractinians is much more extensive. The majority of species are hermaphroditic, with just 25% known to be gonochoric (Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; Hall and Hughes 1996; Richmond 1997). The pattern of reproduction is also known for several solitary corals from shallow depths, of which the majority are gonochoristic, brooding species (Fadlallah 1983). Goffredo et al. (2000, 2002) reported on the hermaphroditic brooder *Balanophyllia europaea* and Krupp (1983) reported that *Fungia scutaria* is a gonochoristic solitary coral that spawns gametes during the late summer. More recently, there has been interest in the reproduction of corals from high latitudes (Harii et al. 2001). However, nothing is known at present about the gametogenic biology of deep-sea scleractinians.

In this paper we report on the gametogenic development of the deep-water coral *Fungiacyathus marenzelleri* in the NE Atlantic Ocean. *F. marenzelleri* (Vaughan, 1906) is a solitary, deep-sea scleractinian, which is known to occur from 730 to 5,870 m depth

R.G. Waller (✉) · P.A. Tyler
Southampton Oceanography Centre,
European Way, Southampton,
SO14 3ZH, UK
E-mail: rhian@soc.soton.ac.uk
Tel.: +44-2380-592557
Fax: +44-2380-596247

J.D. Gage
Scottish Association for Marine Biology,
Dunstaffnage Marine Laboratory,
Oban, Argyll, PA34 4AD, UK

(Zibrowius 1980) and has a wide distribution, occurring in the Atlantic (personal observations) and the Pacific (Lauerman et al. 1996). Although the morphology of this species has been well described (Cairns 1979; Zibrowius 1980), little is known of its biology, ecology, or life history. Three species of *Fungiacyathus* inhabit the NE Atlantic, *F. crispus*, *F. fragilis*, and *F. marenzelleri*. *F. crispus* is the smallest, reaching a maximum of 9 mm in diameter and is found at the shallowest depths ($<1,500$ m) (Zibrowius 1980). *F. fragilis* inhabits depths from 366 to 2,200 m, and coexists with *F. marenzelleri* at $\sim 2,000$ m (Zibrowius 1980). *F. fragilis* and *F. marenzelleri* have similar morphologies and so from depths around 2,000 m must be carefully distinguished by septal differences described by Zibrowius (1980).

Methods

All specimens were obtained using either a 3-m Agassiz trawl or a semi-balloon Otter trawl with 14-m aperture, from RRS *Challenger* in the area around station 'M' (57°18′N, 10°11′W; Gage and Tyler 1982; Table 1). This station is at a depth of 2,200 m. The material was preserved in 4% formalin and later transferred to 70% alcohol. The July 1983 sample was fully processed, but the data were not used due to the poor condition of the preserved tissue of the specimens. For histological processing, all individuals were submerged for approximately 4 h in rapid decalcifying solution (conc. HCl) until no carbonate skeleton remained. They were then rinsed in running tap water for 24 h to remove acid traces.

Individuals were dehydrated by three, 4-h submersions in 100% propanol, followed by clearing with Histoclear for approximately 12 h. The diameter of each individual was then measured and recorded. Around a quarter of the polyp tissue was embedded by being left for 6–12 h in molten histology wax at 70 °C, which was then poured into standard molds. All wax blocks were serially sectioned at 5 μm, leaving 75 μm in between slices, which were mounted on slides and stained with Masson's Trichrome stain.

For fecundity estimation, all slides of female tissue were examined. After decalcification, mesenteries from 20 whole individuals, from varying months, were counted and had their structure noted. Sections of each individual were then examined using an Olympus BH2 compound microscope with video camera attachment. Images were captured using Matrox Rainbow Runner and analyzed using SigmaScan Pro version 4 to calculate oocyte diameters ('feret' diameter, the area if the oocyte was a perfect circle, was used). Spermatogenesis and oogenesis were staged. All previtellogenic, vitellogenic, and late vitellogenic oocytes were counted in two mesenteries from each female. The number of oocytes in the two mesenteries were averaged and that number is hereby referred to as the 'realized fecundity.' 'Potential fecundity' is the realized fecundity multiplied by the number of mesenteries. Mean realized fecundity was calculated for each sample.

Results

Mesenterial structure

Forty-eight mesenteries are present, arranged in cycles of four, reducing in number towards the anterior. The mesenterial mesoglea is thick at the periphery of the polyp, and reduces in width towards the small central oral cavity. All individuals of *F. marenzelleri* examined were gonochoric. Sex ratios averaged over the 9 months analyzed show a 1:1 ratio, varying only slightly among months ($\chi^2 = 0.882$; $P = 0.01$). Reproductive tissue was found in high densities at the base of the individual, reducing in occurrence towards the anterior. Only five individuals did not have either oocytes or spermacysts present on all mesenteries. Each mesentery produces embedded reproductive structures, though there is no obvious external morphological difference between males and females.

Asexual reproduction

F. marenzelleri undergoes asexual reproduction by a form of fission (Fig. 1), followed by complete detachment of the new polyp when it reaches a certain size (>6 mm diameter, as this was the smallest found). The new polyp grows on the anterior surface of the coral. Both sexes were observed to undergo fission. The asexually produced polyp buds from a single mesentery (Fig. 1) and is composed of mesenteries with a central oral area. No more than one bud was found on any individual. There was a low incidence of asexual reproduction in the samples studied. The maximum number of individuals undergoing asexual fission in any month's sample was two, with 4 months' samples having no budding individuals. There was no temporal pattern in the monthly incidence of asexual reproduction in polyps.

Sexual reproduction

Spermatogenesis

Ovoid spermacysts occurred throughout, and in all the mesenteries. Each mesentery contained many spermacysts at varying stages of differentiation. There appeared

Table 1 Colonies analyzed

Cruise no.	Date	Longitude	Latitude	No. analyzed
Challenger 1A/79	15 Jan 79	57°20′N	10°27′W	20
Challenger 75	17 Feb 91	57°19′N	10°23′W	20
Challenger 4/80	03 Mar 80	57°16′N	10°17′W	30
Challenger 6A/81	12 April 81	57°22′N	10°19′W	20
Challenger 9/80	29 May 80	57°18′N	10°16′W	20
Challenger 10/83	24 July 83	57°07′N	09°23′W	0 – poor condition
Challenger 12B/81	18 Aug 81	57°21′N	12°02′W	20
Challenger 15A/81	19 Oct 81	57°27′N	11°10′W	16
Challenger 86	19 Nov 91	57°18′N	10°24′W	25
Challenger 74	14 Dec 90	57°15′N	10°21′W	15

Fig. 1 a Early asexually produced bud in female *F. marenzelleri* polyp; **b** early asexually produced bud in male *F. marenzelleri* polyp. *Ap* Asexual polyp; *Lv* late vitellogenic oocyte; *S* spermacyst; *scale bars* 40 μm

to be no specific arrangement of spermacysts within the mesenteries. Spermatogenesis can be divided into four stages:

Stage 1

Loosely packed aggregations of spermatocytes contained within a cell membrane. Empty lumen can be seen (Early, Fig. 2a).

Stage 2

Some spermatozoa present, still loosely packed. Lumen less distinct (Maturing, Fig. 2a,b).

Stage 3

Densely packed with spermatocytes and lumen packed with spermatozoa (Mature, Fig. 2c).

Stage 4

Relict spermatozoa can be seen (Spent, Fig. 2d).

Oogenesis

Oogonia arise from the mesoglea of the mesentery and develop into 'previtellogenic' oocytes at < 28 μm (Fig. 3a). These early oocytes, which have a central nucleus, are attached to the lamellae of the mesentery and are surrounded by follicle cells. Previtellogenic oocytes then undergo vitellogenesis at ~150 μm diameter, and continue to accumulate yolk up to the maximum of 750 μm diameter (Fig. 3a–d), and are classed as 'vitellogenic.' At < 300 μm a cortical granular layer is devel-

Fig. 2 a Arrangement of spermacysts within *F. marenzelleri* mesenteries; **b** stage II and III spermacysts; **c** stage III spermacysts; **d** stage III and IV spermacysts. *M* Mesentery; *SI* stage I spermacyst; *S2* stage II spermacyst; *S3* stage III spermacyst; *Me* mesoglear envelope; *Sz* spermatozoa; *Sc* spermacyst; *S4* stage 4 spermacyst; *scale bars* **a** 200 μm; **b** 40 μm; **c** 20 μm; **d** 40 μm

Fig. 3 a *F. marenzelleri* mesentery with previtellogenic, vitellogenic, and late vitellogenic oocytes; **b** section showing young oocyte attachment to *F. marenzelleri* mesentery; **c** vitellogenic oocyte; **d** thick cortical layer. *Fc* Follicle cells; *N* nucleus; *V* vitellogenic oocyte; *M* mesentery; *Ml* mesentery lamellae; *Pv* previtellogenic oocyte; *Lv* late vitellogenic; *Cl* cortical layer; *scale bars* **a** 200 μm; **b** 200 μm; **c** 20 μm; **d** 20 μm

oped (Fig. 3c). These oocytes were classed as 'late vitellogenic.' Large yolk vacuoles and a prominent nucleolus in the central nucleus can now also be observed.

Oocytes of varying stages occurred throughout and in all the mesenteries (Fig. 3a), though ten polyps (of all those examined) contained only previtellogenic or vitellogenic oocytes. No planulae or brooded individuals were found during histological examination.

Fig. 4 Monthly mean previtellogenic, vitellogenic, and late vitellogenic oocyte diameters for *F. marenzelleri* sampled between 1979 and 1991. *Triangles* Late vitellogenic; *solid circles* vitellogenic; *open circles* previtellogenic; *error bars* ±1 SD

Analysis of the distribution of the three stages of oocyte development (Fig. 4) or the oocyte size/frequency (Fig. 5) gave no evidence of a marked annual reproductive periodicity. There was no significant difference between any of the mean oocyte diameters for the different months. This suggests that *F. marenzelleri* is a quasi-continuous reproducer. All three cohorts appear to develop simultaneously, though during February, August, and November no late vitellogenic oocytes were found, suggesting they had spawned prior to, or during, collection. The presence of all levels of sperm development in spermacysts within the same mesentery (overlapping gametogenesis) suggests a quasi-continuous release of gametes. The lack of late vitellogenic oocytes in the summer months suggests there may be a variation in the intensity of gamete production rather than a true seasonality (sensu Harrison 1988).

Fecundity

The realized fecundity of each individual within a month's sample was averaged, producing an estimate of mean, per colony fecundity. This number varied significantly among months (Fig. 6). The data suggest an annual periodicity in fecundity, with a maximum being reached during April, and spawning during May/June, suggesting a variation in intensity of reproduction within a year. The average potential fecundity [realized fecundity per mesentery multiplied by the

Fig. 5 Oocyte size/frequency distribution for *F. marenzelleri* monthly samples from the Rockall Trough, NE Atlantic Ocean. *Error bars* ±1 SD

number of mesenteries (48)] for all 10 months was 2,892 (±44).

The size at first reproduction was approximately 10 mm polyp diameter, because both non-reproductive and reproductive individuals were found at this size. No reproduction was observed below this size. Fecundity is size dependent (Fig. 7) and rises as a second-order polynomial ($r^2 = 0.713$).

Discussion

This is the first reproductive investigation of the solitary coral *F. marenzelleri*, and of any deep-water scleractinian. All samples were obtained from station 'M' in the Rockall Trough (Gage and Tyler 1982) between the Anton Dohrn Seamount and the Hebrides Shelf in the northeast Atlantic, an area known for its high species diversity (Gage 1979). Examination of the reproductive biology of a wide variety of marine invertebrates has shown that different species show quasi-continuous, seasonal, or opportunistic reproductive patterns (Tyler and Young 1992). In addition, there are good environmental data from this site (Dickson et al. 1986; Ellett et al. 1986; Holliday et al. 2000).

Fig. 6 Average realized fecundity of *F. marenzelleri* monthly samples collected between 1979 and 1991. *Error bars* ±1 SD

In shallow-water scleractinians, gametes develop within the lamellae of the mesenteries and subsequently migrate into the mesoglea, to develop as oogonia (Szmant-Froelich et al. 1980; Fadlallah 1983). Oogonia of *F. marenzelleri* were first observed attached to the lamella. We believe that the gametes of *F. marenzelleri*

Fig. 7 Polyp diameter of *F. marenzelleri* plotted against average realized fecundity with a fitted second-order polynomial curve. [$n = 83$, $r^2 = 0.7132$ ($y = 32.071x^2 - 63.089x + 53.235$)]

also originate in this area and then migrate into the mesoglea, in common with other corals and anthozoans (Fadlallah and Pearse 1982; Fadlallah 1983).

All the developing individuals examined were found to be gonochoric, whereas the majority of scleractinians are hermaphrodites (Fadlallah 1983; Harrison et al. 1984; Szmant 1986). The random mixture of males and females among size classes mitigates against sequential hermaphroditism. Although gonochorism has been suggested as a more primitive strategy than hermaphrodism (Goffredo et al. 2000), it has been shown to be important for genetic diversity of populations (Szmant 1986). There are certain restrictions, however, in being a gonochoristic individual: spawning must occur synchronously and densities of both individuals and gametes must be sufficiently high to allow successful fertilization. Because of its lack of mobility as an adult, an individual that settles and grows at very low density is less likely to pass its genes on to the next generation than an individual in a high-density population. The spatial relationships between individuals of *F. marenzelleri* are critical in understanding this species' reproductive success. Lauerman et al. (1996) report densities of 0.0181 to 0.293 m at 4,100 m depth off California.

Asexual reproduction in reef-building corals is an important adaptation for rapid colonization of locally available areas, since competition for space is high (Szmant-Froelich et al. 1980; Fadlallah 1983; Hall and Hughes 1996). In solitary species this need would appear to be limited, especially within the deep-sea sedimentary environment where space is not limited. The solitary coral *Fungia scutaria*, which lives in shallow reef areas, has been found to asexually reproduce by budding, and possibly from tissue fragments (Krupp 1983). Population genetic studies have also shown that most of a local population is of the same genotype (Krupp 1983). In *F. marenzelleri* asexual proliferation appears in such low

densities to suggest that this would be the secondary mode of reproduction, with sexually produced polyps comprising the majority of the population.

Planulation in deep-sea species is difficult to observe without in vitro cultures. However, histological evidence suggests that *F. marenzelleri* spawns gametes rather than broods. This is inferred by both the lack of planulae and the varying stages of gamete development within a single polyp. The release of eggs and sperm as the normal mode of reproduction in the Cnidaria has been well documented for a number of species (Kojis and Quinn 1981; Bothwell 1982; Fadlallah and Pearse 1982; Fadlallah 1983; Harrison et al. 1984; Szmant 1986; Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997). Stimson (1978) proposed that deeper-living (deep fore-reef) corals should broadcast gametes to facilitate a wide dispersal range required at depths. Rinkevich and Loya (1979) proposed that large polyped species would spawn large numbers of large eggs. Szmant (1986) also noted that the larger-polyp species of Caribbean corals were gonochoristic broadcasters. The extra energy required for growth, defense, and maintenance of the large polyp suggests that the energy required to produce a brooded planula would not be available. *F. marenzelleri* appears to fit both of these hypotheses. The large egg size suggests a lecithotrophic development rather than planktotrophic early development (Fadlallah 1983; Gage and Tyler 1991). Lecithotrophic development, contrary to earlier suggestions, is now recognized as an adaptation for wide dispersal in oligotrophic environments such as the deep sea (Shilling and Manahan 1994).

Body size, in most invertebrates and some vertebrates, usually has a major effect on reproductive output (Gage and Tyler 1991; Hall and Hughes 1996). *F. marenzelleri* has a strong size-dependent reproduction with a size of 10 mm diameter for first reproductive output. The fecundity of a single polyp is high when compared to both the polyp and colony fecundities of other scleractinian species. The Great Barrier Reef coral *Goniastrea retiformis* has a polyp fecundity of 46 oocytes and a colony fecundity of around 360 oocytes (Hall and Hughes 1996).

The majority of scleractinian corals have some form of reproductive periodicity, usually lunar or temperature controlled (Fadlallah 1983). The individuals of *F. marenzelleri* sampled for this study came from ~2,200 m depth, an area below the permanent thermocline, and so there is little seasonal fluctuation in either temperature or salinity (Holliday et al. 2000). There are, however, data that suggest a marked seasonal flux of surface primary production to the deep sea bed at this station, and elsewhere in the NE Atlantic, which has an influence on the reproductive biology of both infaunal and epibenthic invertebrates (Billett et al. 1983; Tyler et al. 1992, 1993). Although there is some evidence for a seasonal variation in intensity of reproduction in *F. marenzelleri*, most of the evidence, such as large egg size and lack of significant oocyte variation between

samples, suggests quasi-continuous reproduction. This reproductive strategy may benefit a deep-sea solitary coral, as an increased number of eggs broadens the chances of fertilization and aids wide dispersal (Szmant-Froelich et al. 1980).

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