Reproductive patterns in two deep-water solitary corals from the north-east Atlantic—\emph{Flabellum alabastrum} and \emph{F. angulare} (Cnidaria: Anthozoa: Scleractinia)

RHIAN G. WALLER\textsuperscript{1,2} and PAUL A. TYLER\textsuperscript{3}

\textsuperscript{1}National Oceanography Centre, University of Southampton, European Way, Southampton, SO14 3ZH, UK, \textsuperscript{2}Present address: School of Ocean and Earth Sciences and Technology, University of Hawaii at Manoa, 1000 Pope Road, Honolulu, HI 96822, USA, \textsuperscript{3}National Oceanography Centre, University of Southampton, European Way, Southampton, SO14 3ZH, UK

\textit{Gametogenesis and reproductive periodicity of the solitary scleractinians \textit{Flabellum alabastrum} (from the Rockall Trough) and \textit{F. angulare} (from the Porcupine Seabight) were investigated. Samples were collected between depths from 1370 to 2190 m for \textit{F. alabastrum} and 2412 to 2467 m for \textit{F. angulare}. Both species showed gonochorism with a 1:1 sex-ratio and broadcast spawning of gametes is inferred from the lack of brooded planulae. Oocyte sizes were large in both species (925 \mu m in \textit{F. alabastrum} and 1015 \mu m in \textit{F. angulare}), suggesting lecithotrophic larval development. Fecundity and periodicity of oocyte development differed between the two species. \textit{Flabellum alabastrum} produced a maximum of 2800 oocytes per polyp quasi-continuously, whereas the deeper species \textit{F. angulare} produced a maximum of 550 oocytes per polyp either seasonally or periodically. Both species showed size-dependent fecundity. The data show a decrease in oocyte size and fecundity with depth, in concordance with other deep-water scleractinian species.

Keywords: deep-water coral, reproduction, gametogenesis, seasonality, solitary coral, azooxanthellate

Submitted 16 August 2009; accepted 24 February 2010; first published online 17 June 2010

INTRODUCTION

Heightened scientific attention to the fragility and susceptibility of cold-water coral ecosystems has demonstrated our poor understanding of basic ecological functions in the deeper-living species. Almost 50\% of all scleractinian species known to date are azooxanthellate and over 41\% of these live at depths greater than 50 m (Cairns, 2007), yet data on shallow-water hermatypic coral ecology far outweighs that of ahermatypic scleractinians. Limited collections at deeper depths, single time point collections and difficulties with international transport of samples can all be attributed to this paucity of information (Cairns, 2007).

Understanding the reproductive biology of any organism is fundamental to understanding its population dynamics. At present however, there are just a handful of scientific papers examining the reproductive processes of cold-water azooxanthellate reef-building corals (Brooke & Young, 2003, 2005; Burgess & Babcock, 2005; Waller & Tyler, 2005) and solitary scleractinians (Waller et al., 2002, 2005, 2008; Flint et al., 2007). The majority of data on reproduction in scleractinians is based on observations and experiments from tropical zooxanthellate species (Fadlallah, 1983; Richmond & Hunter, 1990; Richmond, 1997; Goffredo et al., 2006). The limited studies on cold-water corals have shown different patterns of reproductive ecology, such as the high proportion of gonochorism and larger oocyte sizes (Waller, 2005) compared with the predominance of hermaphroditism and smaller oocyte sizes in tropical species (Fadlallah, 1983).

\textit{Flabellum alabastrum} Moseley 1873 and \textit{Flabellum angulare} Moseley 1876 are solitary deep-water scleractinians found only in the Atlantic (Cairns, 1999). \textit{Flabellum alabastrum} inhabits a depth-range from 401 to 2250 m in the north-east Atlantic (Zibrowius, 1980), whereas \textit{F. angulare} has a much narrower distribution, 1647 to 2857 m (Zibrowius, 1980). Both of these solitary scleractinians belong to the suborder Caryophylliina, Vaughan & Wells 1943, and the family Flabellidae, Bourne 1905. Within this family, the genus \textit{Flabellum}, Lesson 1831, has 42 species, all solitary azooxanthellate forms that are widely spread across all oceans (Cairns, 1999). The Flabellidae is a family with one of the highest numbers of species (Cairns, 1999), yet knowledge of any species ecology or physiology is sparse. Within the genus \textit{Flabellum}, there are only two published ecological studies, one on the feeding ecology of \textit{F. alabastrum} from the Newfoundland and Labrador continental slope (Sherwood et al., 2008) and one on the reproductive ecology of Antarctic \textit{Flabellum} spp. (Waller et al., 2008). This paper presents data on the reproductive ecology of these two azooxanthellate species.

MATERIALS AND METHODS

Samples for this study (Table 1) were used from the Discovery Collections (housed at the National Oceanography Centre, Southampton, UK), the SAMS Collections (housed at the
RESULTS

*Flabellum alabastrum*

*Flabellum alabastrum* is a gonochoristic species, with gametes clearly visible when the tissue is decalcified. The total sex-ratio is 1:1 with little deviation within months ($\chi^2 = 0.615, P = 0.01$). Putative size of first reproduction was 0.247 g polyp wet weight.

**Oogenesis**

Oogenesis (Figure 1A) can be divided into four stages:

- **Stage I**—oogonia (unobserved, but <100 μm), expected to bud from the mesenterial lamellae;
- **Stage II**—previtellogenic oocytes (<300 μm), containing a large nucleus;
- **Stage III**—vitellogenic oocytes (<800 μm), larger yolk granules can be observed;
- **Stage IV**—late vitellogenic oocytes (>800 μm), rarely observed, thick cortical granular layer present and a prominent nucleolus in the central nucleus observed.

Previtellogenic and vitellogenic oocytes were found within most females observed, late vitellogenic and oogonia were observed rarely. Females weighing less than 0.5 g polyp wet weight, contained only previtellogenic oocytes and so were not included in percentage size–frequency plots, as these are considered juveniles. The maximum oocyte size observed was 925 μm diameter, indicative of lecithotrophic larval development.

**Spermatogenesis**

In all months examined spermatocysts were at a late stage of development (Figure 1B), with spermatozoa tails clearly visible within the lumen. Spermatocysts appeared similar in morphology to that described for other deep-water scleractinians (Waller et al., 2002, 2005; Waller & Tyler, 2005).

**Periodicity**

Samples within a month sample were synchronous and so individual plots within a monthly sample were collated. Oocyte size–frequency diagrams (Figure 2), show little difference among monthly samples. Two cohorts appear to be developing and individuals are synchronous within populations. This suggests a quasi-continuous life history, with gametes being produced regularly. Male individuals were found only in the late stages of sperm development, this would also support a quasi-continuous pattern.

**Fecundity**

Fecundity is size-dependent and rises with polyp wet weight ($R^2 = 0.54; P = 0.01$). There was no significant difference between the average fecundity for the months analysed (Figure 4A). Monthly average fecundity reaches a maximum of 2800 oocytes per polyp.

### Table 1. Samples used for this study. Lat, latitude; Long, longitude; NR, non-reproductive.

<table>
<thead>
<tr>
<th>Species</th>
<th>Date</th>
<th>Cruise</th>
<th>Depth</th>
<th>Lat/Long</th>
<th>Female</th>
<th>Male</th>
<th>NR</th>
<th>Fecundity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Flabellum alabastrum</em></td>
<td>21 February 1991</td>
<td>'Challenger' 75/91</td>
<td>1908 m</td>
<td>56°56'N 09°50'W</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>10 March 1993</td>
<td>'Challenger' 101</td>
<td>1650 m</td>
<td>57°07'N 09°30'W</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>31 July 1983</td>
<td>'Challenger' 10/83</td>
<td>1705 m</td>
<td>57°56'N 12°21'W</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>17 August 1981</td>
<td>'Challenger' 12B/81</td>
<td>2190 m</td>
<td>56°00'N 13°58'W</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>21 November 1991</td>
<td>'Challenger' 86/91</td>
<td>1370 m</td>
<td>56°34'N 09°31'W</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><em>Flabellum angulare</em></td>
<td>1 October 2002</td>
<td>'Discovery' 266</td>
<td>2443–2452 m</td>
<td>50°04'N 12°45'W</td>
<td>7</td>
<td>6</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>11 March 2002</td>
<td>'Discovery' 260</td>
<td>2412 m</td>
<td>49°57'N 12°42'W</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>21 September 2000</td>
<td>'Discovery' 249</td>
<td>2454–2467 m</td>
<td>50°02'N 12°42'W</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>
**Flabellum angulare**

*Flabellum angulare* is also a gonochoric species with a 1:1 sex-ratio \( (\chi^2 = 0.719, \ P = 0.01) \), deviating little within monthly samples. Gametes were also clearly visible post-decalcification within and throughout mesenteries. Size of first reproduction is putatively 1.379g polyp wet weight.

**Oogenesis**

Oogenesis can be divided into four stages (Figure 1C), similar to *F. alabastrum*. Oogonia \(<100 \ \mu\m\) as in *F. alabastrum*, were rarely observed. Previtellogenic \(<350 \ \mu\m\) and vitellogenic \(<900 \ \mu\m\) were present in all female individuals examined. Late vitellogenic oocytes were also rarely observed \(>900 \ \mu\m\). The maximum oocyte diameter observed was 1015\ \mu\m, indicative of lecithotrophic larval development.

**Spermatogenesis**

In contrast to *F. alabastrum* there were four stages of spermatogenesis observed in *F. angulare* samples (Figure 1D):

- **Stage I**, Early—loosely packed aggregations of spermatocytes within spermatocyst. Empty lumen;
- **Stage II**, Maturing—some spermatozoa present, still largely empty lumen;
- **Stage III**, Late—lumen packed with spermatozoa;
- **Stage IV**, Spent—relict spermatozoa can be seen.

Mainly maturing and late stages of spermatogenesis could be observed in single individuals, though all males in September were at stages I and II.

**Periodicity**

Individual oocyte size–frequency diagrams were collated monthly, as individuals were synchronous. Oocyte size–frequency diagrams show a similar bimodal tendency in March and September, but less of a second peak in October (Figure 5). These data, together with the fecundity data, suggest a release of oocytes before or during September. Although the data are limited we interpret this as either seasonality or periodic synchrony of gamete release.

**Fecundity**

Fecundity is size-dependent in *F. angulare*, increasing numbers of oocytes are produced as wet weight increases \((Figure 3B) R^2 = 0.528, \ P = 0.01\). Figure 4B shows a marked variation in fecundity, with significant numbers of oocytes in October and March \((U = 39.0, \ P = 0.032)\) and a significant decrease in September \((U = 30, \ P = 0.036)\). Monthly average fecundity reaches a maximum of 550 oocytes per polyp for March samples.

**Discussion**

Both species in this study are gonochoric, with no hermaphroditic individuals being found. The random selection of
males and females within size-classes militates against the likelihood of sequential hermaphroditism. No brooded planulae were observed in any specimen examined (Table 1), and thus we suggest both species broadcast-spawn gametes. This is a strategy found widely in cold-water scleractinians examined to date (Waller, 2005).

Two oocyte cohorts were present in all samples of *F. alabastrum*. There was no marked difference in fecundity among samples. In males, spermatogenesis is nearly always in the late stages of development. These factors all contribute to the pattern of quasi-continuous release of gametes into the water column. Vitellogenic oocytes in *F. angulare*, however, were present in larger numbers in March and September, than in October, and fecundity was significantly lower in September than in March or October, suggesting vitellogenic oocytes were spawned before or throughout late September. Previtellogenic oocytes are then produced to increase the fecundity found in October. One important factor that is unable to be assessed in this study is interannual variability, which may have caused an offset in these results.

Most zooxanthellate and shallow water azooxanthellate scleractinians have some form of reproductive periodicity, usually either lunar or temperature-dependent (Fadlallah, 1983; Richmond & Hunter, 1990; Goffredo et al., 2002, 2006). Within this study, *F. alabastrum*, the shallower species, appears quasi-continuous, and *F. angulare* appears to reproduce periodically. Though these species are found below the permanent thermocline, there have been many
instances of reproductive cues in the deep-sea (Tyler et al., 1982, 1992, 1993; Billet et al., 1983) and have even been related to deep-water scleractinians (Waller & Tyler, 2005). Eckelbarger & Watling (1995) proposed that increased food in the environment could affect reproduction in three ways: (1) it can initiate gametogenesis followed soon after by spawning; (2) it can initiate spawning for planktotrophic larvae; or (3) it can initiate and synchronize gametogenesis, with a spawning event occurring after a time period. Seasonal phytoplankton blooms reaching the benthos in the Porcupine Seabight occur around July (Lampitt et al., 2001), and so in F. angulare, which spawns in late August/September, this food fall could be the seasonal cue to induce vitellogenesis (Fadlallah, 1983; Richmond & Hunter, 1990). Indeed in Lophelia pertusa, a reef building cold-water scleractinian, this same bloom is thought to initiate gametogenesis (Waller & Tyler, 2005). Sherwood et al. (2008) have shown F. alabastrum to have a mixed to carnivorous diet, and so is unlikely to be limited to feeding primarily within phytodetrital food falls. With this feeding strategy, F. alabastrum is likely to have food available year around, and this could explain its non-seasonal reproductive habit. There is unfortunately no data on the feeding ecology of F. angulare, but with its seasonal reproductive habit, there is the potential that this species has a more selective diet (perhaps to fresher phytodetritus) that is only supplied to the deep sea seasonally.

Coral, including scleractinians, are also renowned for their reproductive plasticity. Within a genus there are often differing reproductive patterns (Hartnoll, 1977; Fadlallah, 1983; Szmant-Froelich, 1984; Szmant, 1986; Richmond & Hunter, 1990), and even the same species having differing patterns (poecilogeny) in different locations (Richmond & Jokiel, 1984; Kruger et al., 1998). So it is not unusual within the Cnidaria for F. alabastrum to be quasi-continuous and F. angulare to be seasonal, and this is likely to be a consequence of environmental conditions being different at these different depths (Eckelbarger & Watling, 1995). Indeed the only other published reproductive study within the genus Flabellum (or the family Flabellidae) showed Antarctic species of Flabellum to be quasi-continuous brooders, a pattern frequently observed in invertebrates from Antarctic waters (Waller et al., 2008).

During trawls from RRS ‘Discovery’ between 2000 and 2002 it was noted that the two species were mutually exclusive.
in each trawl (personal observation). Although Zibrowius (1980) has shown their depth-ranges to be very similar, the different depth-range in a specific area may have led to allopatric speciation, emphasized by the slight differences in reproductive pattern. Such speciation has been observed in shallow sympatric populations of the echinoid Echinometra (Palumbi & Metz, 1991). More detailed surveys of the distribution of the two species of Flabellum in the north-east Atlantic would provide interesting insights into their population ecology.

ACKNOWLEDGEMENTS

This research was supported by the European Union ‘Atlantic Coral Ecosystem Study’ contract No. EVK3-CT1999-00008. Dave Billett, I.G. (Monty) Priede and the captains and crew of the RSS ‘Discovery’ were all instrumental in obtaining specimens for this study. We also thank John Gage†, Peter Lamont and Murray Roberts for samples obtained from DML, Oban. R. Waller is currently supported by a SOEST Young Investigator fellowship from the University of Hawaii at Manoa, and this paper is SOEST contribution number 7893.

REFERENCES


and


Correspondence should be addressed to:
R.G. Waller
School of Ocean and Earth Sciences and Technology
University of Hawaii at Manoa, 1000 Pope Road,
Honolulu, HI 96822, USA
email: rwaller@hawaii.edu