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The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean

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Abstract The reproductive ecology of colonies of *Lophelia pertusa* (Linné 1758) and *Madrepora oculata* Linné (1758) from the Porcupine Seabight (Thérèse Mound and South Porcupine Seabight site) and the Darwin Mounds (NE Rockall Trough—*L. pertusa* only) was investigated using histological techniques. Samples of *L. pertusa* exhibited seasonal reproduction, whereas the evidence for *M. oculata* is equivocal but suggests multiple cohorts of gamete production. *L. pertusa* produces a single cohort of around 3,000 oocytes, whereas *M. oculata* produces two cohorts, with a total fecundity of around 60 oocytes. The maximum observed oocyte size in *L. pertusa* was 140 µm and in *M. oculata* was 405 µm. From these oocyte sizes and the timing of reproduction, a lecithotrophic larva is expected, though not observed. This seasonality of reproduction fits with the phytodetrital food fall occurring around July in the Seabight area. *L. pertusa* was found to be non-reproductive at the Darwin Mound site. Though unable to be specifically tested, this may suggest that the increased trawling activity in this area might be keeping colonies below sexually viable sizes, as seen in numerous shallow water situations. All areas in the NE Atlantic are coming under threat from increased fishing and commercial exploration practices. This study shows that these highly seasonal reproducers could be sensitive to these fishing operations and care must be taken so as not to repeat the destruction that has occurred on shallower reefs.

Keywords Hermatypic · Azooxanthellate · Gametogenesis · *Lophelia pertusa* · *Madrepora oculata*

Introduction

Recently there has been an increase in the recognition of deep-water reefs as fragmented and biodiverse communities at bathyal depths around the globe (Rogers 1999). Though deep-sea scleractinians have been known for many decades (Cairns 1979; Zibrowius 1980), there has been little observation of their ecology owing to the difficulty and expense of deep-water collections.

Deep-water reefs, mounds, and banks are commonly found on continental margins and shelf breaks, as well as on seamounts and ridges, where high water flow is present. As in shallow-water, these flows may be necessary for the delivery of food and larvae to the area, as well as removing waste and excess sediment (Grigg 1974; 1984). Hard substrata are also necessary for reef formation in shallow-water, highly sedimented areas are not favoured possibly because of the risk of polyp suffocation (Dodge and Vaisnys 1977; Rogers 1990). Many deep-water reefs have been observed to begin from settlement on worm tubes, coral rubble, or mollusc shells, and so this need for hard substrate may also be necessary for these deeper living scleractinians (Wilson 1979).

There are many species of deep-water, reef-building scleractinians that occur throughout the world's oceans (Zibrowius 1980). *Goniocorella dumosa* occurs on the Campbell Plateau, New Zealand (Squires 1965), *Oculina varicosa* on the Florida continental shelf (Reed 1980; Brooke 2002), *Solenosmilia variabilis* from the South Pacific, SE Atlantic, and Cook Islands (Cairns 1982, 1995; Keller 1993), *Dendrophyllia cornigera* in the NE Atlantic (Zibrowius 1980), *Desmophyllum dianthus* off Chile (Cairns 1982), and *Enallopsammia rostrata* in New Zealand, *E. profunda* from the Western Atlantic and *E. marenzelleri* from the NE Atlantic, New Zealand, and Indonesia (Cairns 1995) are just a few. The most

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cosmopolitan deep-water scleractinian species are *Lophelia pertusa* and *Madrepora oculata* (Rogers 1999). *L. pertusa* is found in the Pacific, Atlantic, Indian, and Antarctic oceans. *M. oculata* in the Pacific, Atlantic, and Indian oceans.

Deep-water reefs are recognised as important biomes for many commercial and non-commercial species (Rogers 1999). Nearly 1,300 species of invertebrates and fishes have been found inhabiting the branches of *L. pertusa* in the NE Atlantic Ocean, and it is thought this figure will increase (M. Roberts, personal communication). *L. pertusa* is a cosmopolitan scleractinian. It can be found from depths of 50 m in the Norwegian fjords (Rogers 1999) to 3,600 m on the Mid-Atlantic Ridge (Bett et al. 1997) and in most of the world's oceans. Though many of these taxonomic references refer to the dead remains of *L. pertusa*, many new reefs are being discovered around the globe.

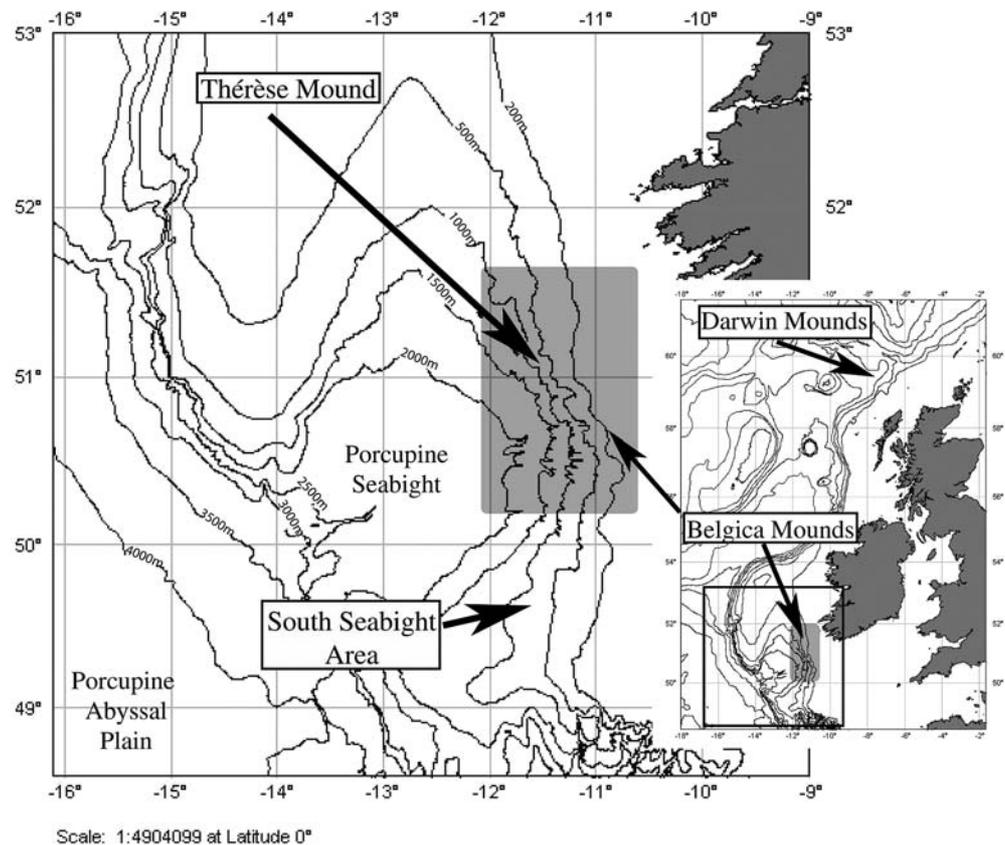
M. oculata is less cosmopolitan than *L. pertusa* and has only been found as a co-species with other reef-forming scleractinians. *M. oculata* and *L. pertusa* are frequently found together off New Zealand (Cairns 1995), the Aegean Sea (Vafidis et al. 1997), SE Atlantic (Keller 1993), and the NE Atlantic (Keller 1993; Bett et al. 1997; Wilson 1997; Rogers 1999).

There are a few data on reproduction of deep-water scleractinians. The reef building *Oculina varicosa* is a seasonal gonochoristic broadcast spawner with small

ooocytes ($<100\ \mu\text{m}$) and a high fecundity (1,000–4,800 oocytes per cm^2 skeletal area) (Brooke 2002). *Fungiacyathus marenzelleri* is a solitary deep-water scleractinian found in sedimentary environments in the NE Atlantic. This species is a non-seasonal gonochoristic broadcast spawner with high fecundity (2,900 oocytes per polyp) and large oocytes (750 μm) (Waller et al. 2002). Three deep-water *Caryophyllia* species from the NE Atlantic Ocean have also been examined (Waller et al. 2005, in press). *Caryophyllia ambrosia*, *C. seguenzae*, and *C. cornuformis* all exhibited cyclical hermaphroditism.

The present study focuses on *L. pertusa* and *M. oculata* from three sites at bathyal depths in the NE Atlantic Ocean (Fig. 1). The Darwin Mounds are series of several hundred mounds, each approximately 100 m in diameter and 5 m high, found within the NE segment of the Rockall Trough (Bett 2001). Thérèse Mound is a large (100 m relief) coral mound found within the Belgica Mound system in the Eastern Porcupine Seabight. The third site is an area on the south side of the Porcupine Seabight (SPS). All the sites are between 800 and 1,000 m depth. This study is part of the interdisciplinary European project 'Atlantic Coral Ecosystem Survey' (ACES). This project began in April 2000, to examine the biology, oceanography, and geology of the reefs and mounds at bathyal depths round the European margin.

Fig. 1 NE Atlantic Ocean. Showing bathymetry and location of Darwin Mounds in the Rockall Trough, Thérèse Mound within the Belgica Mounds, and the Southern Seabight Area. Map generated using GEBCO software



Methods

Field sampling

All specimens were obtained using a 0.5 m² box core, 3 m Agassiz Trawl, or an Otter Trawl Semi-Balloon (OTSB), between 2000 and 2002 from the RRS Discovery in the NE Atlantic (Table 1, Fig. 1). Corals from Thérèse Mound were solely collected by box core, corals from the Darwin Mounds were collected by Agassiz Trawl, and the South Seabight area was a sample collected by OTSB. Different collection methods were used for the different physical and environmental conditions found at the sites. For Thérèse mound, the corals are too large to trawl, as the net is easily broken. The Darwin Mounds were unable to be box cored because of their small size, though this was repeatedly attempted. The South Seabight area was a fortuitous coral sample from an OTSB trawling for benthic invertebrates. As this sample was also collected within the Porcupine Seabight, and at similar depths to Thérèse mound, these two samples are pooled herein so as to give a better overall picture of reproduction in the Seabight. No site was able to be sampled more than twice in a season, thus limiting the availability of material.

The corals were preserved in 4% formalin and later transferred to 70% alcohol. Specimens of each species were selected at greater than 30-cm colony width, and are referred to herein as putative colonies. Large specimens were selected to try to ensure the collection of sexually viable material. In trawled corals, colonies were selected that had dissimilar appearance (i.e. skeletal shading, orientation of polyps, and thickness of skeleton) to attempt to minimise sampling of the same colonies within the trawl haul, though this cannot be ruled out entirely. Any major differences in appearance (such as colouration) were noted.

Histology

For histological processing, large pieces of the putative colonies of *L. pertusa* (Fig. 2a) and *M. oculata* (Fig. 4a)

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. *L. pertusa* polyp tissue were weighed at this stage.

For both species, 20 individual polyps of varying sizes from each colony were separated and dehydrated by three, 4-h submersions in 100% propan-2-ol, followed by clearing with xylene for a maximum of 12 h. Whole polyp tissue was embedded in molten histology wax at 70°C for 6–12 h and then poured into standard moulds. All wax blocks were serially sectioned at 5 µm, leaving 50 µm in between slides, and then stained with Masson's Trichrome stain. Remaining polyps were stored in 70% propan-2-ol. Sections of each individual were examined using an Olympus BH2 compound microscope with video camera attachment. Images were captured using Matrox Rainbow Runner and analysed using SigmaScan Pro Version 4 to calculate oocyte feret diameter ('feret' diameter is the diameter of an oocyte if it was perfectly round). Between 50 and 100 random oocytes were measured from each individual polyp. Percentage size frequency charts were constructed for each individual polyp and subsequently polyps were combined within and between colonies to give a percentage oocyte size-frequency and variance for each month. For *M. oculata*, few polyps produced more than 50 oocytes and so data were pooled between polyps. Spermatogenesis and oogenesis were staged to determine their sexual state.

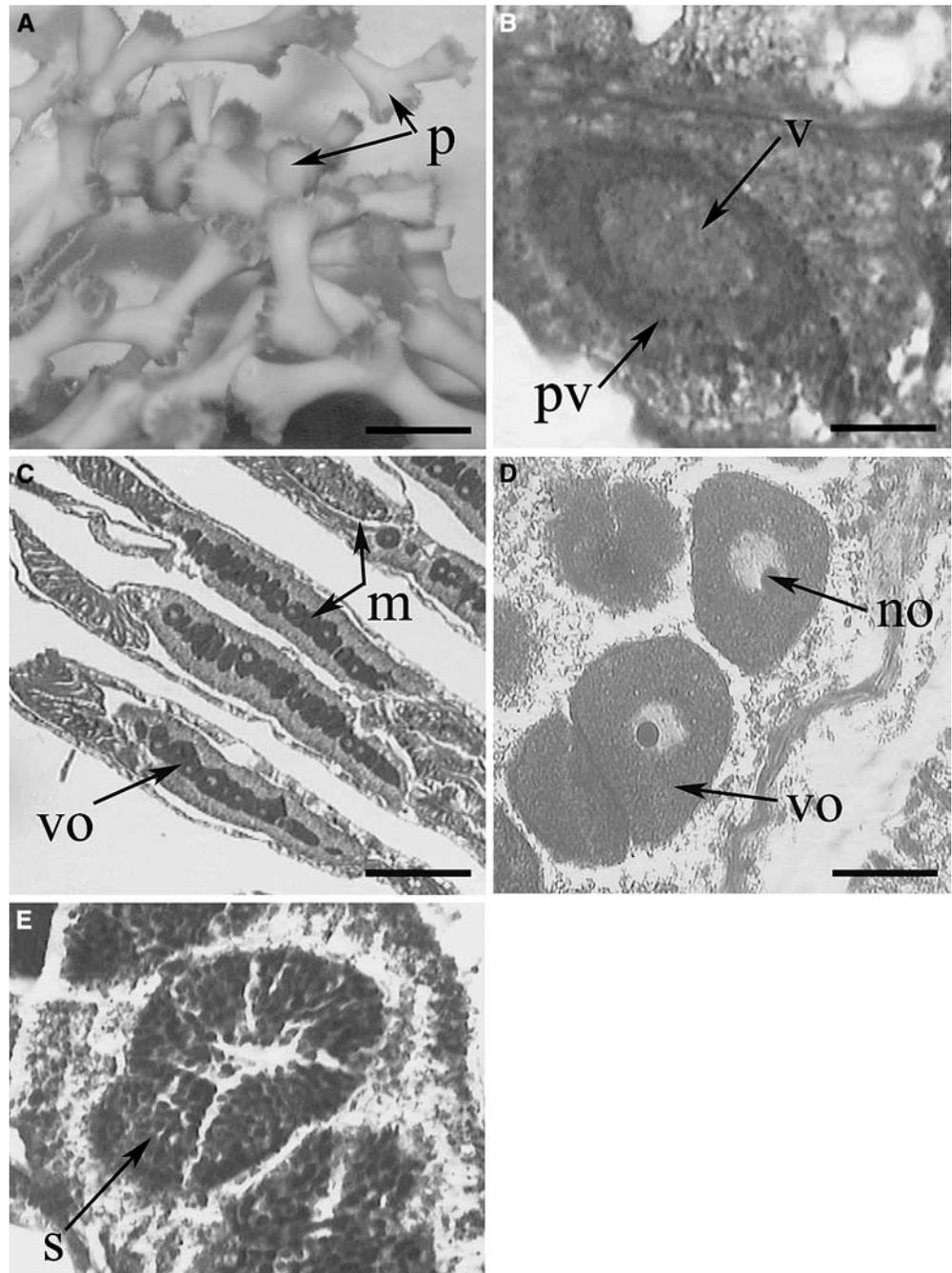
Fecundity

For fecundity estimation of *L. pertusa*, five polyps were dissected from August to October. The wet weight of each polyp was measured and the total number of mesenteries recorded. Five mesenteries were dissected and embedded using the procedure above. Blocks were serially sectioned and all visible vitellogenic, vitellogenic, and late vitellogenic oocytes

Table 1 Collections made of *Lophelia pertusa* and *Madrepora oculata* in the NE Atlantic Ocean

Species	Area	Depth (m)	Cruise	Coordinates	Date
<i>L. pertusa</i>	Darwin Mounds	980	248	59°N 48.88 07°W 17.99	16/07/2000
	Thérèse Mound	870	248	51°N 25.67 11°N 46.41	06/08/2000
		870	266	51°N 25.67 11°N 46.41	30/9/2002
		870	260	51°N 25.67 11°N 46.41	08/03/2002
	South Porcupine Seabight	785–925	260	44°N 40.00 11°W 30.70	18/10/2002
<i>M. oculata</i>	Thérèse Mound	870	248	51°N 25.67 11°N 46.41	06/08/2000
		870	260	51°N 25.67 11°N 46.41	08/03/2002
	South Porcupine Seabight	785–925	266	44°N 40.00 11°W 30.70	18/10/2002

Fig. 2 **a** *L. pertusa* colony. **b** Previtellogenic oocyte undergoing vitellogenesis. **c** Female mesenteries containing vitellogenic oocytes. **d** Vitellogenic oocytes. **e** Stage 2 spermacyst. *p* polyp, *v* vitellogenesis, *pv* previtellogenic, *vo* vitellogenic oocyte, *m* mesentery, *no* nucleolus, *s* spermatocytes. Scale bars **a** 2 cm; **b** 25 μ m; **c** 125 μ m; **d** 50 μ m



were counted in each mesentery. For fecundity estimation of *M. oculata*, serially sectioned slides from five to ten female polyps were examined and all oocytes counted. All polyp measurements were size-corrected to the average polyp size for that species. The tin foil method was used to calculate the number of polyps per cm² skeletal area (Marsh 1970). An area of 10 cm² foil was used for *L. pertusa*, and 5 cm² for *M. oculata*. This number of polyps per cm² was then used to calculate the number of oocytes per unit area of skeletal surface.

Results

Lophelia pertusa

Morphology

L. pertusa has two major skeletal colour morphologies: white and orange. The white morph appears less prolific in the areas sampled, as it was only obtained from the South Seabight during the October 2002 cruise.

This species is gonochoristic with all mesenteries fertile. Gametes are in two to three pockets throughout the mesentery and two to three oocytes per spermacysts wide (Fig. 2b–e). These pockets contain gametes at the same stage of development. The number of mesenteries per polyp varied between 13 and 24.

Gametogenesis

Gametes were observed in colonies sampled during August–October from the Porcupine Seabight only. No gametes were found in colonies sampled in August from the Darwin Mound site, or in March from the Porcupine Seabight. Males were only found in the October sample at this site, and only in the white morph. All results, therefore, are only from the Porcupine Seabight.

Female

All female colonies were of the orange morph. Only three stages of oogenesis were observed, but a fourth is inferred from previous azooxanthellate coral studies (Fig. 2b–e). Oocytes appear to develop from the lamellae of the mesentery.

Stage I: Oogonia— $< 5 \mu\text{m}$ diameter bud from the mesenterial lamellae.

Stage II: Previtellogenic Oocytes— $5\text{--}30 \mu\text{m}$ diameter small oocytes with thin wall and a basophilic cytoplasm (Fig. 4c).

Stage III: Vitellogenic Oocytes— $> 30 \mu\text{m}$ diameter (Fig. 2c, d).

Stage IV (Inferred): Late Vitellogenic Oocytes— $> 140 \mu\text{m}$ oocytes become heavily granulated and have a thick cortical layer around the periphery of the ooplasm.

The total March sample revealed two small oocytes ($\sim 50 \mu\text{m}$) that appeared to be reabsorbing. These were not measured or counted for fecundity estimations. Previtellogenic oocytes were observed in August, but not September or October.

Male

Only one sample of a male colony was found in the October 2002 sample. All spermacysts were at the same stage of development (Fig. 2e). Using the same staging scale as Waller et al. (2002), all spermacysts appear to be at stage 2. Numerous spermatocytes were present, with a few spermatozoa beginning to congregate around the lumen (Fig. 2e).

Fecundity

There was no significant difference between fecundity estimations for August and October ($U=8$; $P < 0.05$). It is expected that further oogonia have developed into

oocytes between August and October. Fecundity for the March sample is taken as 0, as no developing oocytes or oogonia were observed and the only oocytes present were few and being reabsorbed. Individual polyps in August had an average fecundity of 3,146 oocytes per polyp ($\pm 1,688$), and in October had an average fecundity of 2,308 oocytes (± 818).

No evidence of gametogenesis was found in polyps below 0.08 g, suggesting that this is the size of first

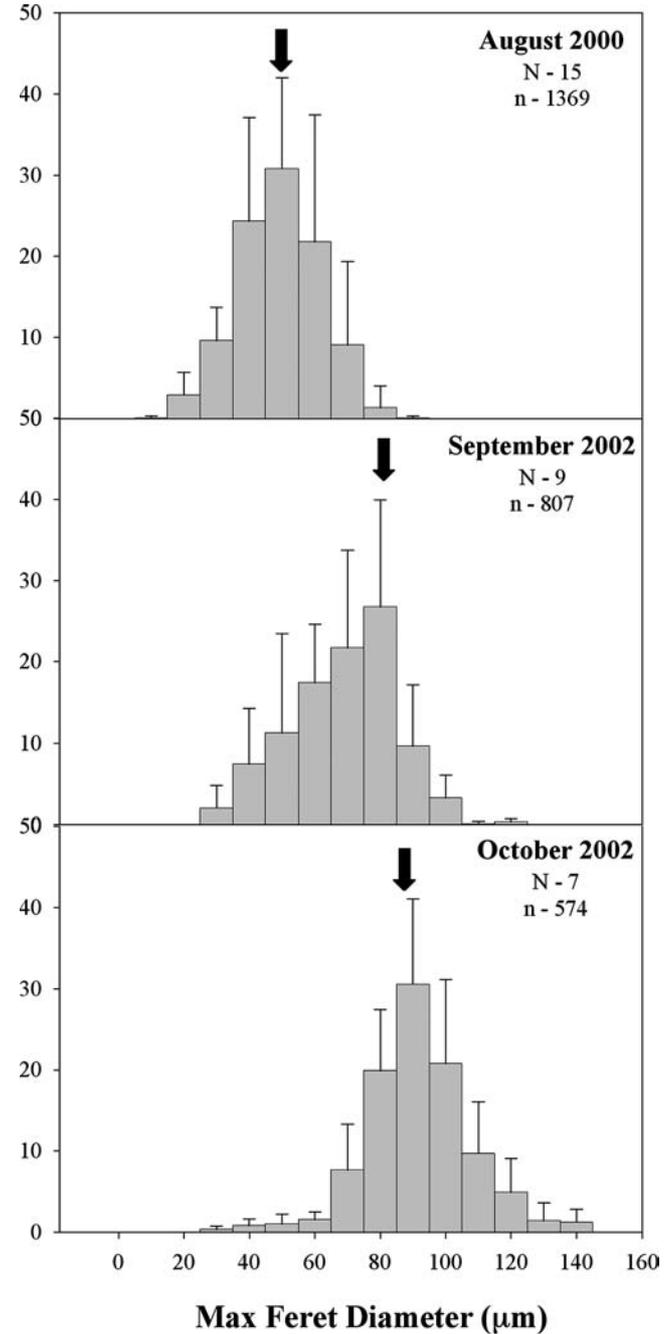
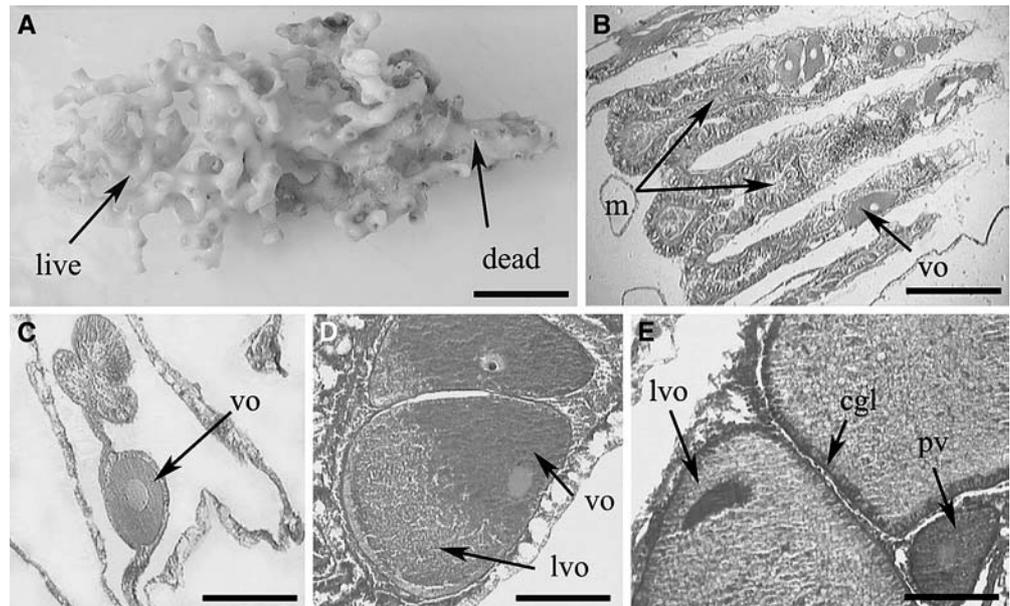


Fig. 3 *L. pertusa* oocyte-size frequency diagrams for pooled samples from the NE Atlantic Ocean in August 2000, September 2002, and October 2002. *N* Total number of polyps, *n* Total number of oocytes measured, *Arrow* mean oocyte diameter

Fig. 4 **a** *M. oculata* colony showing dead and live polyps. **b** Female polyp showing position of vitellogenic oocytes. **c** Vitellogenic oocyte within mesentery. **d** Vitellogenic oocyte undergoing change to late vitellogenic oocyte. **e** Late and previtellogenic oocytes. *m* mesentery, *vo* vitellogenic oocyte, *lvo* late vitellogenic oocyte, *cgl* cortical granular layer, *pv* previtellogenic oocyte. Scale bars **a** 2 cm; **b** 400 μ m; **c** 300 μ m; **d** 150 μ m; **e** 250 μ m

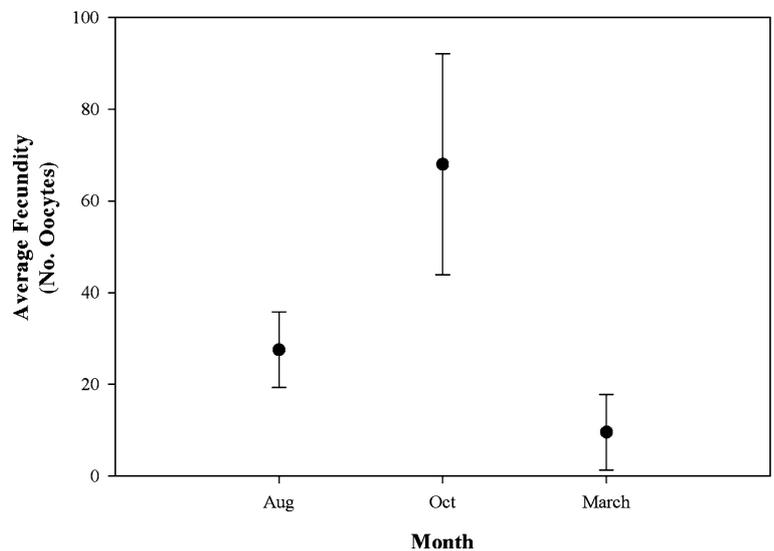


reproduction. There was no significant relationship between weight of polyp and fecundity ($R^2=0.4$ $P= > 0.05$). Colony fecundity was recorded at approximately 3,300 oocytes per cm^2 ($\pm 1,103$). This would give a colony of around 30 cm^2 and an approximate total fecundity of 99,800 oocytes.

Reproductive periodicity

Oocyte size-frequency analysis shows there was a single cohort of developing oocytes in the population (Fig. 3). There appears to be rapid growth of oocytes, feret diameter doubles between August and October (41.3 μ m for August, 64.3 μ m for September, and 88.7 μ m for October). Maximum oocyte size is 139 μ m.

Fig. 5 *M. oculata* average fecundities (number of oocytes per polyp) for pooled samples from the NE Atlantic Ocean in August 2000, October 2002, and March 2002. All animals' size corrected to 1,661 μ m polyp diameter



Madrepora oculata

Morphology

There are also white and orange skeletal morphs of *M. oculata* (ACES 2003), though none were obtained in our sampling programme. *M. oculata* is gonochoristic, with all mesenteries fertile (Fig. 5). Oocytes develop from the lamellae of the mesentery.

Gametogenesis

No male *M. oculata* were found during this study. In the female previtellogenic, vitellogenic, and late vitellogenic oocytes were present within a single mesentery in the October sample.

Stage I: Oogonia— $> 37 \mu\text{m}$ small female gametes budding off the mesenterial lamellae.

Stage II: Previtellogenic— $37\text{--}200 \mu\text{m}$ small oocytes with thin wall and a basophilic cytoplasm (Fig. 4e).

Stage III: Vitellogenic— $200\text{--}350 \mu\text{m}$ larger granulated oocytes with thin wall (Fig. 4b–d).

Stage IV: Late Vitellogenic— $> 350 \mu\text{m}$ large, highly granulated, with thick cortical granule layer, presumably ready for spawning (Fig. 4d–e).

Fecundity

The average fecundity varied over the months studied (Fig. 5). The lowest fecundity recorded was during March, with an average of 10 oocytes per polyp (± 8.26). In August, 28 oocytes per polyp (± 8.26) were recorded and in October 68 oocytes per polyp (± 24.15).

The smallest reproductive individual had a polyp diameter of 1.24 mm. However, non-reproductive individuals were found up to a polyp width of 1.7 mm. There was no significant relationship between polyp diameter and fecundity ($R^2 = 0.07$ $P = > 0.05$).

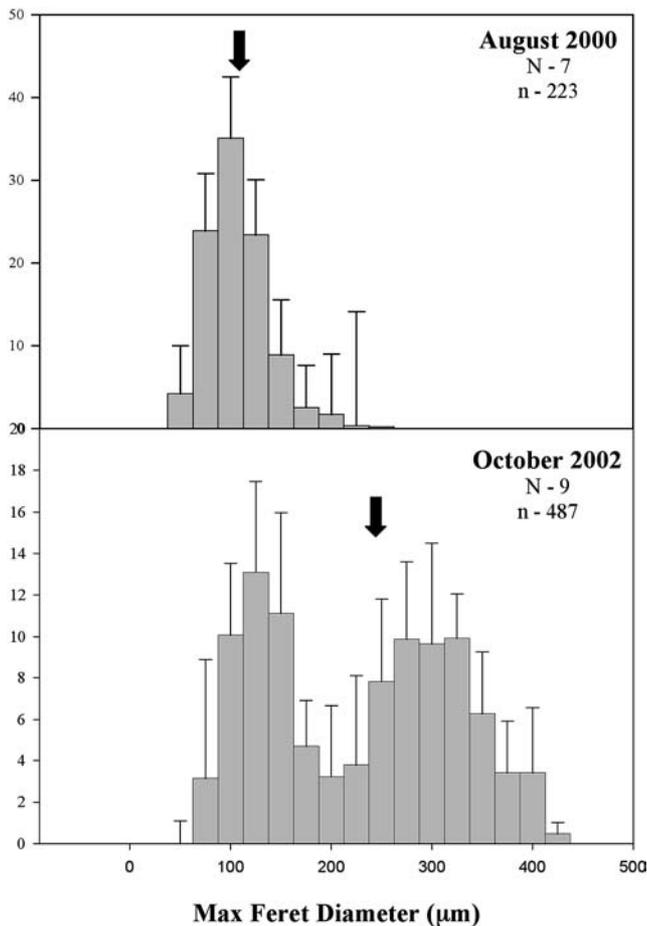


Fig. 6 *M. oculata* oocyte size-frequency diagrams for pooled samples from the NE Atlantic Ocean in August 2000 and October 2002. *N* Total number of polyps, *n* Total number of oocytes measured, *Arrow* mean oocyte diameter

Colony fecundity was recorded at 36 oocytes per cm^2 (± 2) for March, 104 oocytes per cm^2 (± 6.2) for August, and 256 oocytes per cm^2 (± 12) for October. This gives a colony of around 30 cm^2 surface area, a fecundity of 7,680 oocytes in October.

Reproductive periodicity

One cohort could be seen in the August sample (Fig. 6), whereas in the October sample two distinct cohorts could be seen. Oocyte growth appears rapid, more than doubling in size between August and October. Maximum oocytes size is $405 \mu\text{m}$. The March sample did not produce enough oocytes for size-frequency analysis.⁷

Discussion

There are two main reproductive patterns in marine invertebrates, the production of small numbers of large oocytes, and the production of large numbers of small oocytes (Gage and Tyler 1991). In shallow reef-building scleractinians, Harrison and Wallace (1990) demonstrated an inverse relationship between oocyte size and fecundity. In the bathyal scleractinians from the NE Atlantic sampled here, *L. pertusa* produces relatively large numbers of small oocytes (an average of 3,300 oocytes per cm^2 , $140 \mu\text{m}$ maximum diameter); whereas, *M. oculata* produces small numbers (an average of 256 oocytes per cm^2 skeletal area) of large oocytes ($405 \mu\text{m}$ max). *L. pertusa*'s pattern is similar to that observed in *O. varicosa*, which also produces large numbers (1,000–4,800 oocytes per cm^2 skeletal area) of small oocytes ($< 100 \mu\text{m}$ diameter) (Brooke 2002).

The presence of previtellogenic oocytes in the August sample of *L. pertusa*, followed by rapid oocyte development (with only mature vitellogenic oocytes being observed in September and October), suggests that oogenesis is likely to be initiated in late summer. The oocyte size-frequency samples for *L. pertusa* for August–October show an increasing mean size of oocyte. This, together with the absence of developing gametes, and the observation of two reabsorbing oocytes in the March sample of *L. pertusa* suggests that this species has an annual gametogenic cycle with spawning around January/February. Such a gametogenic pattern in a bathyal species would be coincident with other deep-sea seasonally spawning species in the NE Atlantic (Tyler and Young 1993). Oocyte size-frequency diagrams, and the large oocyte size in *M. oculata*, also suggest a seasonal pattern of gametogenesis. There is, however, evidence of multiple cohorts of developing oocytes not usually found within seasonal reproducers. This would in turn suggest a periodicity of reproduction, rather than true seasonality. *M. oculata* may be environmentally cued into producing and spawning gametes, when conditions are suitable for reproduction.

Most shallow-water scleractinians spawn in response to environmental cues (Fadlallah 1983; Richmond 1997). In shallow-water species, this can be temperature, lunar phases, tidal cycles, or in synchronous spawners, the presence of other gametes in the water. For deep water species the cues are less obvious. There is little temperature variation at depths below 800 m, and there is no solar radiation. Studies in the NE Atlantic have shown that seasonal blooms of surface primary production sink rapidly to the deep-sea floor (Billett et al. 1983; Lampitt 1985; Thiel et al. 1989) and can have an effect on the reproductive biology of benthic invertebrates (Billett et al. 1983; Tyler et al. 1992, 1993). Seasonal phytoplankton blooms in the Porcupine area occur in July (Lampitt et al. 2001), and this could be the cue for *L. pertusa* and *M. oculata* to initiate gametogenesis. At this time there would be a substantial increase in the availability of particulate organic matter, and so may coincide with the, energetically expensive, production of gametes in both these species. No samples were obtained during this time, and so the precise date of the beginning of reproduction in both these species from this area is unknown.

It is also unknown precisely what these species feed on, though as they are sessile and unable to scavenge actively for food, it is likely that they rely heavily on food fall to these bathyal depths. A lecithotrophic larva would appear the most suitable for such conditions. The extra energy and nutrients put into producing larger planulae serves as a food store until settlement takes place. In the deepwater coral *O. varicosa*, settlement has been observed to occur between 20 and 35 days in the laboratory (Brooke 2002). Lecithotrophic larvae have also been shown to be suitable for long distance dispersal (Shilling and Manahan 1994) and hence may explain both of these species' wide distribution. No planulae were observed in this study and so it is hypothesised that neither of these species brood.

In *M. oculata*, polyp size overlapped for non-reproductive and reproductive polyps, suggesting that a factor other than size controls gametogenesis. It has been reported in shallow-water corals that total colony size can determine mode of reproduction (Kojis and Quinn 1982; Szmant 1986; Hall and Hughes 1996). A small colony would reproduce asexually, extending total size until large enough to overcome size-related mortality, and then proceed to sexual reproduction. Due to collection methods in this study this aspect was not observed, though is likely to be an important aspect of these two species' ecologies, as both do not show polyp size-related fecundity. Using box cores and trawls, total colony size is unable to be established as the sample is broken, sometimes into many pieces, before retrieval. In situ methods, such as submersibles and remotely operated vehicles, are required to investigate this factor in deep-water scleractinian ecology.

No reproductively active polyps were observed in *L. pertusa* taken from the Darwin Mounds. This area has been observed to be extensively damaged by trawl-

ing operations (Bett 2001; Hall-Spencer et al. 2003; Wheeler et al. 2005, in press). Wheeler et al. (2005, in press) observed multidirectional trawl door scars using a high-resolution sidescan sonar, and 28 trawl scars were observed within a 5 km towed video camera track. Many areas within the Darwin Mounds were also assessed to be 100% trawled between trawl door scars (Wheeler et al. 2005, in press). Many scleractinian colonies have to reach a certain size before reaching reproductive maturity (Szmant-Froelich 1985; Szmant 1986; Richmond 1997). Brown and Howard (1985) also observed that stress could also reduce reproductive output, and even cause death in some cases (Ward 1995; Rinkevich and Loya 1989). It is hypothesised that the intense trawling in this area may keep the *L. pertusa* colonies at a size that is below necessary for gametogenesis to occur. Rinkevich and Loya (1989) observed that removal of even 23% of a colony of *Stylophorapillata* causes sterility for up to a year. Trawling has been shown to remove both corals, and disturb colonies from these mounds (Wheeler et al. 2005, in press). There is also the possibility of polyp suffocation from increased sediment suspension as in shallow water, Dodge and Vaisnys (1977) have shown that extended dredging operations have had a destructive effect on coral communities. Genetic analysis of populations in the Darwin Mound area also support these findings, showing that there is little sexual reproduction occurring (LeGoff-Vitry et al. 2004). In this study using microsatellite markers and the ITS1 and ITS2 regions, the Darwin Mounds had the least genetic diversity of any of the sites in the NE Atlantic.

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References

- Bett BJ et al (1997) RRS Charles Darwin Cruise 101C Leg 2, 14 Jul-20 Aug 1996. Atlantic Margin Environmental Survey; seabed survey of the shelf edge and slope west of Shetland. Southampton Oceanography Centre, Southampton
- Bett BJ (2001) UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Res* 21:8-10
- Billett DSM, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302:520-522
- Brooke SD (2002) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa* from the South East Florida Shelf. PhD Thesis, School of Ocean and Earth Science, Southampton Oceanography Centre, Southampton, 160pp
- Brown BE (1987) Heavy metals pollution on coral reefs. In: Salvat B (ed) *Impacts des activites humaines sur les recifs coralliens: connaissances et recommandations*
- Brown BE, Howard LS (1985) Assessing the effects of stress on reef corals. *Adv Mar Biol* 22:1-63

- Cairns SD (1979) The deep-water Scleractinia of the Caribbean Sea and adjacent waters. Studies on the Fauna of Curacao and other Caribbean Islands, vol 57, 341 pp
- Cairns SD (1982) Antarctic and Subantarctic scleractinia. Biol Antarctic Seas XI: Antarctic Res Ser 34:1–74
- Cairns SD (1995) The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). New Zealand Oceanography Institute Memoirs, vol 103, 210 pp
- Dodge RE, Vaisnys JR (1977) Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J Mar Res 35:715–730
- Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals: A review. Coral Reefs 2:129–150
- Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, p 504
- Grigg RW (1974) Distribution and abundance of precious corals in Hawaii. Proceedings of the 2nd international symposium on coral reefs, vol 2
- Grigg RW (1984) Resource management of precious corals: a review and application to shallow water reef building corals. Pubblicazioni della Stazione zoologica di Napoli I: Mar Ecol 5:57–74
- Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef building corals. Ecology 77:950–963
- Hall-Spencer J, Allain V, Fossa JH (2003) Trawling damage to North East Atlantic ancient coral reefs. Proc R Soc Lond 269(1490):507–511
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky (ed) Ecosystems of the world: coral reefs. Elsevier, New York, pp 133–207
- Keller NB (1993) New records of deep-sea madreporarian corals in the southern parts of the Atlantic and Indian oceans. In: Vinogradova NC (ed) Novye nakhodki glubokovodnykh madreporarij v yuzhnoj chasti Atlanticheskogo i Indijskogo okeanov, pp 89–96
- Kojis BL, Quinn NJ (1982) Reproductive ecology of two faavid corals (Coelenterata: Scleractinia). Mar Ecol Prog Ser 8:251–255
- Lampitt RS (1985) Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep Sea Res 32:885–897
- Lampitt RS, Bett BJ, Kiriakoulakis K, Popova EE, Ragueneau O, Vangriesheim A, Wolff GA (2001) Material supply to the abyssal seafloor in the Northeast Atlantic. Prog Oceanogr 50:1–4
- LeGoff-Vitry M, Rogers AD, Baglow D (2004) A deep-sea slant on the molecular phylogeny of the Scleractinia. Mol Phylogenet Evol 30:167–177
- Reed JK (1980) Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bull Mar Sci 30:667–677
- Richmond RH (1997) Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 175–197
- Rinkevich B, Loya Y (1989) Reproduction in regenerating colonies of the coral *Stylophorapistillata*. In: Luria M (ed) Environmental quality and ecosystem stability, pp 257–265
- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202
- Rogers AD (1999) The biology of *Lopheliapertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406
- Rogers CS, McLain L, Zullo E (1988) Damage to coral reefs in Virgin Islands National Park and Biosphere Reserve from recreational activities. In: Proceedings of the 6th international coral reef symposium, vol 2
- Shilling FM, Manahan DT (1994) Energy metabolism and amino acid transport during early development of antarctic and temperate echinoderms. Biol Bull 187:398–407
- Squires D (1965) Deep-water coral structure on the Campbell Plateau, New Zealand. Deep Sea Res 12:785–788
- Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–54
- Szmant-Froelich A (1985) The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). In: Proceedings of the 5th international coral reef congress, vol 4, pp 295–300
- Thiel H, Pfannkuche O, Schriever G, Lochte K, Gooday AJ, Hemleben C, Mantoura RFC, Turley CM, Patching JW, Riemann F (1989) Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. Biol Oceanogr 6:203–239
- Tyler PA, Harvey R, Giles LA, Gage JD (1992) Reproductive strategies and diet in deep-sea nudulanid protobranchs (Bivalvia: Nuculoidea) from the Rockall Trough. Mar Biol 114:571–580
- Tyler PA, Gage JD, Paterson GJL, Rice AL (1993) Dietary constraints on reproductive periodicity in two sympatric deep-sea astropectinid seastars. Mar Biol 115:267–277
- Vafidis D, Koukouras A, Voultziadou-Koukoura E (1997) Actinaria, Corallimorpharia, and Scleractinia (Hexacorallia, Anthozoa) of the Aegean Sea, with a checklist of the eastern Mediterranean and Black Sea species. Isr J Zool 43:55–70
- Waller RG, Tyler PA, Gage JD (2002) The reproductive ecology of the deep-sea scleractinian coral *Fungiacyathus marenzelleri* (Vaughan, 1906) in the Northeast Atlantic Ocean. Coral Reefs 21:325–331
- Waller RG, Tyler PA, Gage JD (2005) Sexual reproduction in three hermaphroditic deep-sea *Caryophyllia* species (Anthozoa:Scleractinia) from the NE Atlantic Ocean (in press)
- Ward S (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 187:193–206
- Wheeler AJ, Bett BJ, Billet DSM, Masson D, Mayor D (2005) The impact of demersal trawling on the NE Atlantic deep-water coral habitats: the case of the Darwin Mounds, UK. In: Thomas J, Barnes P (eds) Benthic habitats and the effects of fishing. American Fisheries Society, Bethesda (in press)
- Wilson JB (1979) The distribution of the coral *Lophelia pertusa* in the North East Atlantic. J Mar Biol Assoc UK 59:149–164
- Wilson JB (1997) The deep-water coral *Lophelia pertusa* in the north-east Atlantic with particular reference to the west and north-west of Scotland and on the eastern margin of Rockall Bank. A report prepared for Greenpeace UK Ltd
- Zibrowius H (1980) Les Scleractiniaires de la Mediterranee et de l'Atlantique nord-oriental. Mem Inst Oceanogr Monaco 11:247