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RESEARCH ARTICLE

Reproductive ecology of *Fungiacyathus marenzelleri* from 4100 m depth in the northeast Pacific Ocean

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Abstract *Fungiacyathus marenzelleri* (Vaughan, 1906) is a deep-water solitary coral, cosmopolitan in distribution that is found at depths of 300–6,328 m. This study examined gametogenesis, inter-annual variability and reproductive periodicity of *F. marenzelleri* collected from Station M (34°50′N, 123°00′W) in the northeast Pacific at a depth of 4,100 m. Samples were collected (May, June, October 1996; August 1998; February, June 2001; and June 2002) and histologically processed with spermatogenic stage, oocyte size and fecundity measured. Four stages of spermatogenesis were identified and all males contained multiple stages of sperm development in each seasonal sample. Three stages of oocyte development were identified; previtellogenic (<28–150 μm), vitellogenic (150–300 μm) and late vitellogenic (300–400 μm). Comparison of mean oocyte diameters among sampling dates showed there were no inter-annual variations or seasonal differences. Overall, fecundity was 1,290 (±407) oocytes polyp^{-1}, and with no significant differences between sample months. Fecundity was not polyp-size dependent. This study shows a similar quasi-continuous mode of reproduction to this species examined from the Northeast Atlantic Ocean, but the fecundity is reduced by 50%. The reproductive output may fluctuate in relation to the input of organic material at this site, as shown by non-significant trends in the oocyte size-frequency and fecundity data. A quasi-continuous output of gametes would promote successful fertilisation and wide dispersal of the lecithotrophic larvae.

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Introduction

Until recently, studies of coral reproductive ecology have largely centred upon shallow water scleractinian representatives of both hermatypic and ahermatypic forms. Having identified the main reproductive patterns of shallow water scleractinians, emphasis has moved toward exploring adaptive intraspecific and interspecific differences in reproductive mode, and the factors that may govern these differences. In this context, interest has moved concurrent with progress in marine exploration technology, which enables research in environments with more challenging conditions. One such research path is investigation of the reproductive biology of anthozoan and scleractinian inhabitants of the deep sea.

Both azooxanthellate and facultative zooxanthellate scleractinian corals have been found in both colonial and solitary forms at depths below the thermocline (Zibrowius 1980). The majority of ecological studies on deep-water, hermatypic scleractinians are centred on reef builders, such as *Lophelia pertusa* (Wilson 1979; Rogers 1999; Waller and Tyler 2005), *Oculina varicosa* (Reed 1980; Brooke and Young 2003), *Enallopsammia rostrata*, *Solenosmilia variabilis* and *Gonicorella dumosa* (Burgess and Babcock 2005; Adkins et al.

2004). In comparison to reef-building species, there is limited information on the biology of deep-water solitary corals even though they outnumber reef builders (Zibrowius 1980; Cairns 1982, 2001). While they may not be as long lived as their colonial counterparts, solitary deep-water corals are equally and perhaps more cosmopolitan in distribution (Zibrowius 1980). Like colonial species, solitary deep-water corals are often located on topographic highs such as seamounts, ridges and embayments. Here, the high current flow may be beneficial in two ways, enabling the feeding mechanisms of the inhabitants to achieve a high level of efficiency, and having important implications for larval dispersal in the deep sea, which as yet remains largely untracked.

Fungiacyathus marenzelleri is a deep-water solitary coral, cosmopolitan in distribution (Zibrowius 1980) found at depths of 300–6,238 m. Waller et al. (2002) examined this species from Station 'M' at 2,200 m depth in the NE Atlantic. This study found the gonochoric species to exhibit overlapping gametogenesis for both spermatocysts and oocytes, suggesting a quasi-continuous mode of reproduction. There was, however, some evidence for seasonal variation in intensity of reproduction and a high fecundity with strong size-dependency. It was suggested that a quasi-continuous reproductive pattern might benefit a deep-sea solitary coral, as an increased number of eggs increases the chances of fertilisation and aids wide dispersal (Waller et al. 2002).

The present study examines the reproductive ecology of *F. marenzelleri* samples collected from 4,100 m in the NE Pacific (Station 'M'—34°50′N, 123°00′W). This abyssal area lies under the California Current upwelling region and is characterised by low relief (<100 m per 1,600 km^2) and clay sediments (Smith and Druffel 1998). Studies over 15 years have examined seasonal and inter-annual food falls and deep-sea community structure (Smith and Baldwin 1984; Lauerman et al. 1996; Baldwin et al. 1998; Beaulieu et al. 1998; Lauerman and Kaufmann 1998; Smith et al. 2001) documenting links between this flux and climate and productivity in the area (Smith and Kaufmann 1999; Ruhl and Smith 2004; Smith et al. 2006). The aim of the present paper is to determine the reproductive pattern in *F. marenzelleri* and investigate whether these traits are environmentally or phylogenetically determined. Comparisons of the observations with those of Waller et al. (2002) explore possible depth effects, as Station 'M' in the Pacific is at almost twice the depth of Station 'M' in the NE Atlantic, which in turn leads to numerous organic matter input and isolation differences.

Materials and methods

Field sampling

Samples were obtained using a semi-balloon otter trawl (5-m foot rope; 3.8-cm stretch mesh with 1.3-cm mesh cod-end liner), from the research vessel *New Horizon* at station 'M' in the eastern north Pacific. This station is at a depth of 4,100 m and is ~ 200 km off the central California coast. The specimens were initially preserved for histological processing in ~4% formalin then transferred to 70% alcohol. Samples collected are detailed in Table 1.

Histology

The general histological protocol used in this study was taken from Waller et al. (2002). By using this protocol, direct comparison with the results from *F. marenzelleri* collected from station 'M' in the Rockall Trough, northeast Atlantic Ocean (57° 18′N, 10°11′W) at 2,200 m depth was facilitated.

Each individual was weighed and skeletal dimensions measured. The specimens were individually submerged in Rapid Decalcifying Solution (concentrated HCl) for approximately 5–10 min until no carbonate skeleton remained. They were then left under running tap water for 12 h to remove acid traces, decalcified weight measurements were taken and the total number of mesenteries counted. Four–five mesenteries were dissected and dehydrated by four, 4 h submersions in 100% propanol, followed by clearing with xylene for approximately 12 h.

Polyp tissue was embedded in molten histology wax at 70°C for approximately 12 h, poured into standard molds and left for a minimum of 2 h to cool and harden. All blocks were sectioned at 5-μm intervals, with serial sections being taken of three randomly selected females per monthly sample. Sections were stained with Masson's Trichrome.

Table 1 *Fungiacyathus marenzelleri*. Specimens used for all analysis in this study

Month	Year	Male	Female	Total
February	2001	6	4 (4) *3*	10
May	1996	6	4 (3) *1*	10
June	1996	7	3 (3) *3*	10
June	2001	13	7 (6) *7*	20
June	2002	7	3 (2) *3*	10
August	1998	4	3 (3) *3*	7
October	1996	9	8 (3) *4*	17

Numbers in parenthesis indicate numbers of females used for oocyte-size frequency graphs. Numbers in italics indicate numbers of females used for fecundity analysis

Image analysis

Slides 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 diameter ("feret" diameter, the area if the oocyte was a perfect circle, was used). Spermatogenesis and oogenesis were staged and "fecundity" was calculated by counting all oocytes, regardless of size, in three mesenteries. This figure was then averaged and multiplied by the total number of mesenteries giving "realised fecundity".

Results

General morphology

Polyp diameters ranged from 2.2 to 2.7 mm (mean diameter is 2.42 mm) and decalcified weights from 0.50 to 1.80 g (mean weight is 1.051 g). All individuals examined were gonochoric with reproductive structures embedded in each of 42 ± 3 SD mesenteries. There were no obvious external morphological differences between sexes. Sex ratios averaged over the seven samples had a 1:1 ratio varying only slightly among months ($\chi^2 = 0.878$; $P = 0.01$).

Oogenesis

Oocytes of varying stages occurred throughout all mesenteries (Fig. 1a). The maximum oocyte diameter was 750 μm. Previtellogenic oocytes <28 μm originated from the mesoglea of the mesentery. When these previtellogenic oocytes reached ~150 μm in diameter, vitellogenesis commenced with yolk accumulating up to a diameter of ~750 μm. Oocytes were termed 'late vitellogenic' when they possessed a cortical granular layer, at >300 μm in diameter. No planulae or brooded individuals were discovered during histological examination.

Spermatogenesis

Spermacysts of varying stages were located throughout all the mesenteries of all individuals on all seven sampling dates. Stage-one spermacysts were identified by their loosely packed aggregations within a cell membrane. Stage-two spermacysts were still loosely packed with the presence of some spermatozoa but their lumen was less distinct (Fig. 1b). Stage-three exhibited densely packed spermatocytes with lumens full of spermatozoa (Fig. 1c). Stage four was observed when only relict spermatozoa were observed.

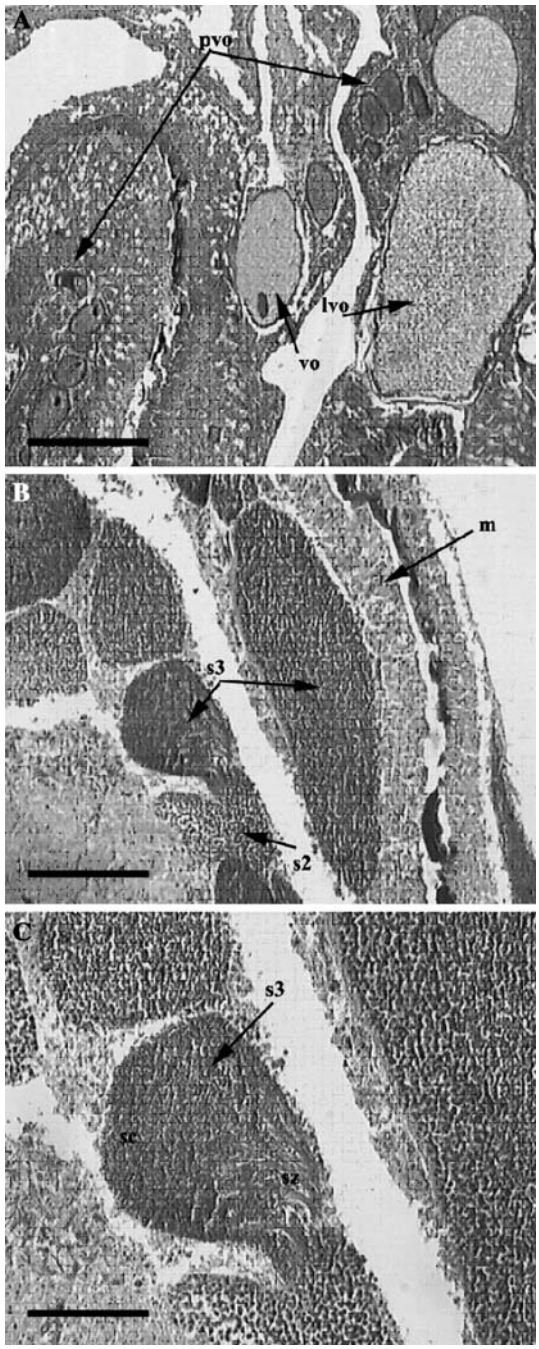

Fig. 1 *Fungiacyathus marenzelleri*. **a** Female mesentery, **b** male mesentery, and **c** spermacyst. *pvo* previtellogenic oocyte; *lvo* late vitellogenic oocyte; *vo* vitellogenic oocyte; *m* mesentery; *S3* stage 3 spermacyst; *S2* stage 2 spermacyst; *sc* spermatocyte; *sz* spermatozoa. Scale bars: **a**, 400 μm; **b** 400 μm; **c** 200 μm

Inter-annual variability

Mean oocyte diameters were assessed from histological examination for each sample group within the oocyte

size classifications described earlier. As there were three June samples collected (in 1996, 2001 and 2002), these values were plotted separately (Fig. 2a). No inter-annual variation was apparent in this plot. Oocyte size-frequency distributions were also plotted (Fig. 3) and showed no inter-annual variation.

Reproductive periodicity

As a result of the lack of inter-annual variation among the June samples, a mean value was collated and utilised with data from five different sampling dates. Analysis of the distribution of the three stages of oocyte development (Fig. 2b) or the monthly oocyte size-frequency data (Fig. 4) gave no evidence of a marked annual reproductive periodicity. This suggests that at Station 'M' in the northeast Pacific, *F. marenzelleri* is reproducing quasi-continuously.

Fecundity estimation

The fecundity of each individual within a month's sample was averaged, producing an estimate of mean monthly fecundity. Overall average fecundity was 1,290 ± 407 SD oocytes. It is apparent (Fig. 5) that there were fluctuations in fecundity measurements among the different sampling dates This could reflect variation in reproductive output, with an apparent maximum being reached in February. It is important to note that the standard deviations in the mean fecundity values calculated for individuals within a sample were very large (Fig. 5). The poor quality of some of the slides resulted in fecundity counts not being done on some individuals and, in some cases, oocyte diameter analysis was also not possible (the total numbers of females used per fecundity sample were: May 1996, 1; June 1996, 3; October 1996, 4; August 1998, 3; February 2001, 3; June 2001, 7; and June 2002, 3), These very low sample sizes are likely the cause of this large standard deviation. Fecundity was not size-dependent (Fig. 6).

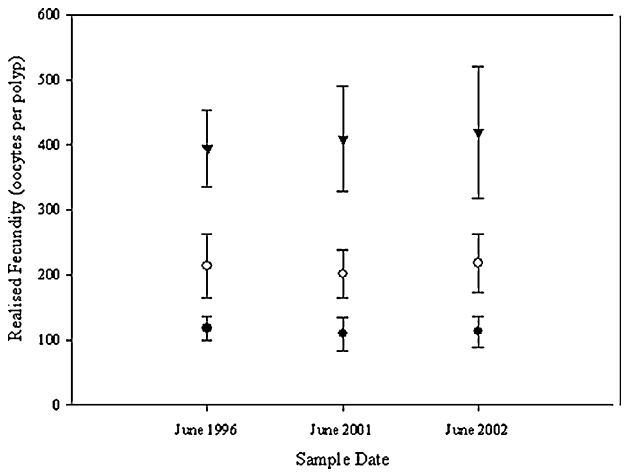

Fig. 2 Fungiacyathus *marenzelleri.* Mean feret diameters for previtellogenic, vitellogenic and late vitellogenic oocytes in June 1996, 2001 and 2002*: filled circles* previtellogenic; *open circles* vitellogenic; *filled inverted triangles* late vitellogenic; *error bars* ±SD

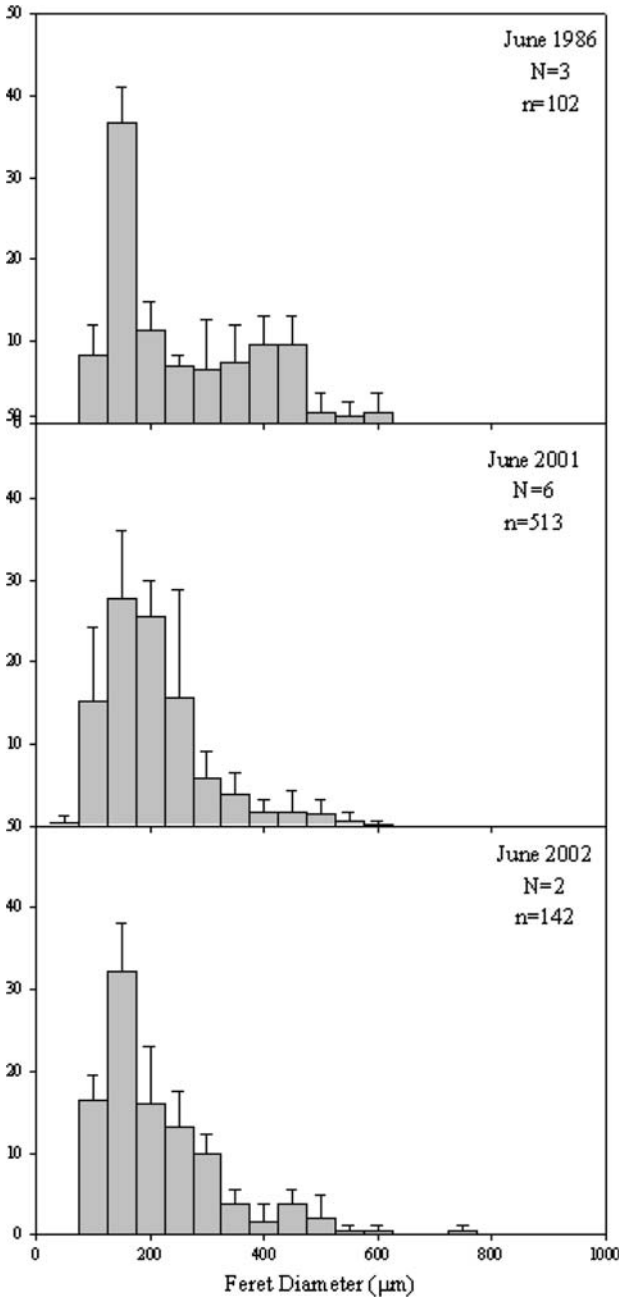

Fig. 3 *Fungiacyathus marenzelleri* . Oocyte size-frequency graphs for June 1996, 2001 and 2002 samples. *N* number of individuals; *n* number of oocytes measured

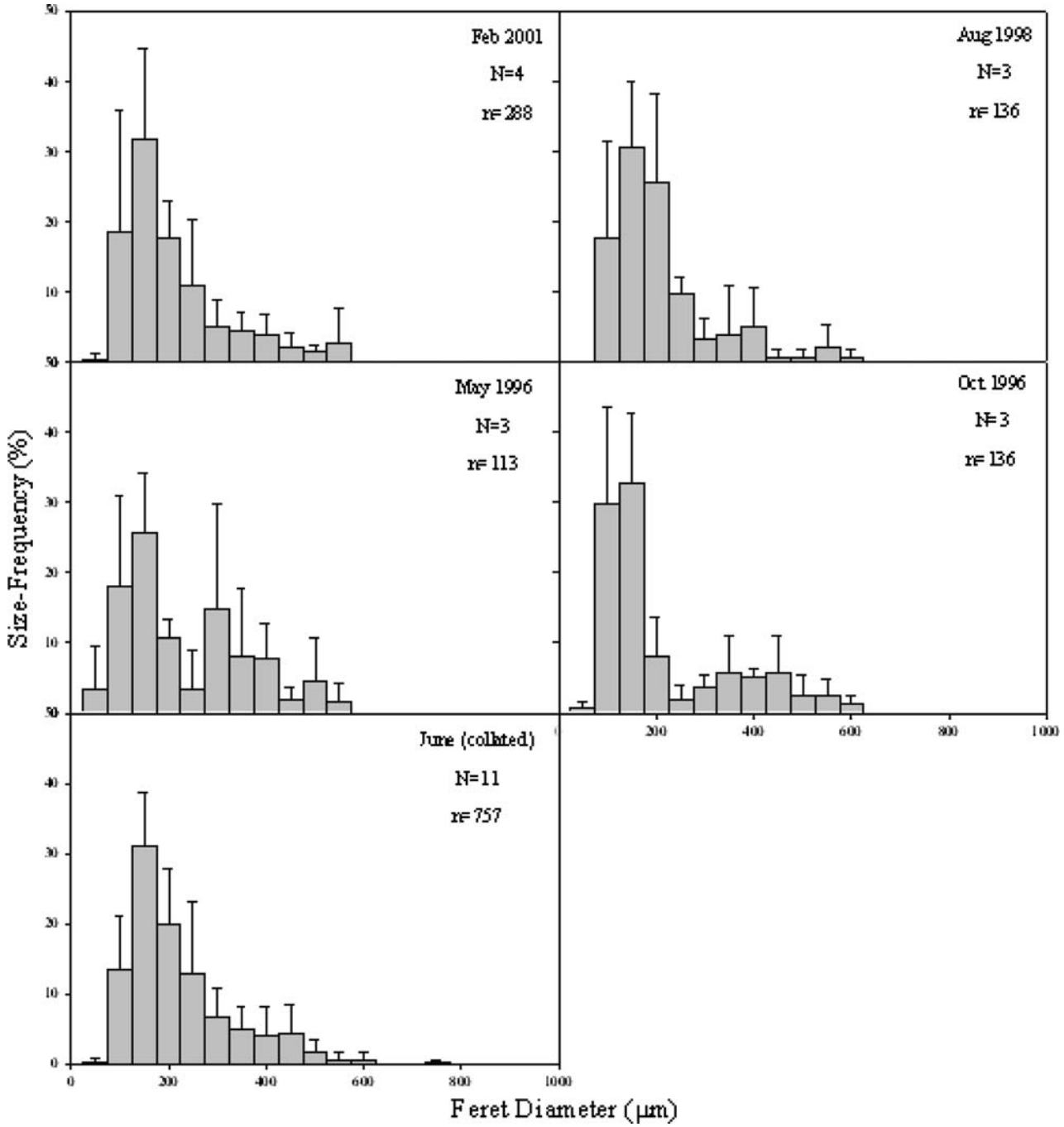

Fig. 4 *Fungiacyathus marenzeller.* Monthly oocyte size-frequency diagrams. *N* number of individuals; *n* number of oocytes measured

Discussion and conclusions

Monthly oocyte size-frequency diagrams were constructed to determine whether *Fungiacyathus marenzelleri* at Station M in the NE Pacific had a seasonal reproductive cycle or maintained a quasi-continuous output of gametes. The lack of variation observed among the mean oocyte diameters within each size classification provides a strong indication of a quasi-continuous output. The presence of all stages of oocyte development in five different months analysed suggests a basal output of gametes. Further resolution was obtained when the oocyte size classification bins were broken down into smaller increments and displayed in an oocyte size/frequency distribution plot.

There appears to be some indication of variation occurring as the oocytes grow and progress up through the size classes. The greatest percentages of oocytes

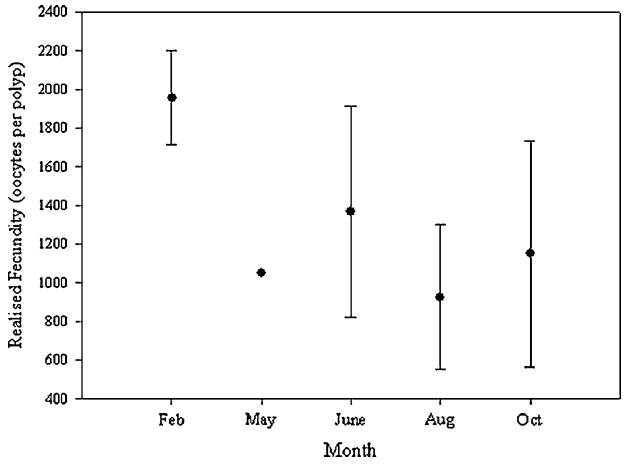

Fig. 5 *Fungiacyathus marenzelleri.* Average monthly realized fecundity. *Error bars* ±SD

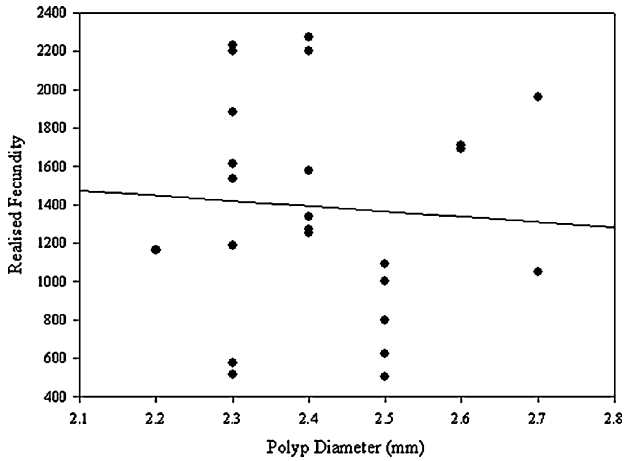

Fig. 6 *Fungiacyathus marenzelleri.* Individual realised fecundity plotted against polyp diameter of all individuals in which fecundity was measured

present in any individual in any month were previtellogenic (i.e. <150 μm). Apparent troughs in late vitellogenic oocyte output frequency were seen in the February sample, then mid to late summer, (the figure is still diminishing from a May peak, through June to August) and again after the October peak. Waller et al. (2002) found a quasi-continuous gamete release pattern at Station M in the Rockall Trough (NE Atlantic) specimens of *F. marenzelleri.* If the variations in the intensity of gamete output against the background of a continuous basal gamete output all year round suggested in the current study are real, the *Fungiacyathus marenzelleri* in this study may possess a gamete release pattern similar to their NE Atlantic counterparts. Corresponding troughs were documented in Waller et al. (2002) for February, August, and November samples and it was similarly suggested that individuals may have spawned prior to, or during, trawl collection.

In shallow-water corals, spawning and planulation events are triggered by external cues such as lunar phase cycles, photoperiod length or temperature changes (Richmond and Hunter 1990). Examples of differences in spawning or planulation periodicity have been found to occur intra-specifically over a species' distribution range, a pattern thought to be adaptation to local environmental parameters and cues (Richmond and Hunter 1990). Yet below the permanent thermocline there is little seasonal fluctuation in either temperature or salinity and no light cues from lunar or solar sources. Flux of organic matter to the deep sea floor provides a strong seasonal signal to its inhabitants (Billett et al. 1983; Tyler et al. 1993, 1995; Herring 2002). Lauerman et al. (1996) described time-lapse camera data at Station "M" in the NE Pacific that illustrated the highest densities of detrital aggregates in summer and autumn corresponding to periods of high particulate organic matter flux. If *F. marenzelleri* individuals were increasing reproductive effort in response to a seasonal food input cue, peaks should occur in late May and October. Such a reproductive pattern would produce an increased intensity of egg development and/or release at a time when there is good food availability thereby increasing the chances of high recruitment. At the same time, a continuous output of gametes all year round may facilitate successful fertilisation. Such a pattern has been observed in other deep-water anthozoans (Van Praet et al. 1990; Rice et al. 1992; Waller et al. 2002; Burgess and Babcock 2005; Waller and Tyler 2005; Waller et al. 2005), with a large oocyte size suggesting a lecithotrophic larva, it is likely that they are not reliant on food fall until later stages of development.

Average potential fecundity for NE Pacific individuals for all monthly samples was 1290 ± 407 (mean ± SD). This is approximately half the mean potential fecundity calculated for *F. marenzelleri* from Station 'M' (size corrected) in the Rockall Trough (Waller et al. 2002). It could be suggested that this is also a depth-related effect owing to food availability at this depth and the coral's resource allocation trade-off between reproduction and growth. This decrease in fecundity with depth has been observed in many deep-sea invertebrates (Gage and Tyler 1991). Although there appears to be a pattern, the fecundity data also suggest a quasi-continuous production of gametes. A maximum does occur in February, which correlates with the postulated increase in gamete production intensity before the food fall. There is, however, no evidence of a corresponding peak in October, although the fecundity data have large standard deviations. Lauerman et al. (1996) reported densities of *F. marenzelleri* of 0.0181–0.293 m^{-2} from towed camera

surveys at Station M (Pacific), but there are no other data on the density distributions of solitary deep-water scleractinians.

The life history pattern of a species is characterised by numerous physiological traits and environmental limits. *F. marenzelleri* from the NE Pacific at 4100 m has the same quasi-continuous reproductive habit, yet fecundities that are significantly lower than those found by Waller et al. (2002) for the same species from the NE Atlantic at 2200 m. From this study it is suggested that the environmental effects of depth (such as decreased food availability) decrease this species' reproductive output, but that the overall reproductive pattern is genetically controlled.

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References

Adkins J, Henderson GM, Wang SL, O'Shea S, Mokadem F (2004) Growth rates of the deep-sea scleractinian *Desmophyllum cristagalli* and *Enallopsammia rostrata*. Earth Planet Sci Lett 227:481–490

Baldwin RJ, Glatts RC, Smith KL (1998) Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: Composition and fluxes. Deep-Sea Res II 45:643–666

Beaulieu S, Baldwin RJ (1998) Temporal variability in currents and the benthic boundary layer at an abyssal station off central California. Deep-Sea Res II 45:587–615

Billett DSM, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302:520–522

Brooke SD, Young CM (2003) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf. Cont Shelf Res 23:847–858

Burgess S, Babcock RC (2005) Reproductive Ecology of three reef-forming, deep-sea corals in the New Zealand region. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, New York, pp 701–713

Cairns SD (1982) Antarctic and Subantarctic Scleractinia. Biology of the Antarctic Seas XI: Antarct Res Ser 34:1–74

Cairns SD (2001) A brief history of taxonomic research on azooxanthellate Scleractinia. Bull Biol Soc Wash 10:191–203

Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge

Herring P (2002) The biology of the deep ocean. Oxford University Press, London

Lauerman LML, Kaufmann RS (1998) Deep-sea epibenthic echinoderms and a temporally varying food supply: results from a one year time series in the N.E. Pacific. Deep-Sea Res II 45:817–842

Lauerman LML, Kaufmann RS, Smith K (1996) Disribution and abundance of epibenthic megafauna at a long term time-series station in the abyssal northeast Pacific. Deep-Sea Res 43:1075–1103

Reed JK (1980) Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bull Mar Sci 30:667–677

Rice AL, Tyler PA, Paterson GJL (1992) The pennatulid *Kophobelemnon stelliferum* (Cnidaria: Octocorallia) in the Porcupine Seabight (North-east Atlantic Ocean). J Mar Biol Assoc UK 72:417–434

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean the Tropical Pacific and the Red Sea. Mar Ecol-Prog Ser 60:185–203

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Ruhl HA, Smith KL (2004) Shifts in deep-sea community structure linked to climate and food supply. Science 305:513–515

Smith KL, Baldwin RJ (1984) Seasonal fluctuations in deep-sea sediment community oxygen consumption: central and eastern North Pacific. Nature 307:624–625

Smith KL, Druffel ERM (1998) Long time-series studies of the benthic boundary layer at an abyssal station in the NE Pacific. Deep-Sea Res II 45:573–586

Smith KL, Kaufmann RS (1999) Long term discrepancy between food supply and demand in the deep eastern North Pacific. Science 284:1174–1177

Smith KL, Baldwin RJ, Carlucci AF (2001) Pelagic-benthic coupling in the abyssal eastern North Pacific: an eight year time-series study of food supply and demand. Limnol Oceanogr 46:543–556

Smith KL, Baldwin RJ, Ruhl HA, Kahru M, Mitchell BG, Kaufmann RS (2006) Climate effect on food supply to depths greater than 4,000 meters in the northeast Pacific. Limnol Oceanogr 51:166–176

Tyler PA, Bronsdon SK, Young CM, Rice AL (1995) Ecology and gametogenic biology of the Genus *Umbellula* (Pennatulacea) in the North Atlantic Ocean. Int Rev Hydrobiol 80:187–199

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

Van Praët M, Rice AL, Thurston MH (1990) Reproduction in two deep-sea anemones (Actiniaria); *Phelliactis hertwigi* and *P. robusta*. Prog Oceanogr 24:207–222

Waller RG, Tyler PA (2005) The reproductive ecology of two deep-water reef building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Waller RG, Tyler PA, Gage JD (2002) 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 of three deep water *Caryophyllia* (Anthozoa: Scleractinia) species from the NE Atlantic Ocean. Coral Reefs 24:594–602

Wilson JB (1979) The distribution of the coral *Lophelia pertusa* (L.) [*L. Prolifera* (Pallas)] in the North-East Atlantic. J Mar Biol Assoc UK 59:149–164

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mem de l'institut Oceanogr Monaco 11:22–27