REPRODUCTIVE MORPHOLOGY OF THREE SPECIES OF DEEP-WATER PRECIOUS CORALS FROM THE HAWAIIAN ARCHIPELAGO: *GERARDIA* SP., *CORALLIUM SECUNDUM,* AND *CORALLIUM LAUUENSE*

Rhian G. Waller and Amy R. Baco

ABSTRACT

Three species of deep-sea corals were collected from several locations in the Hawaiian Archipelago. These species have been called "precious corals" because of their extensive use in the jewelry industry. Two octocorals *Corallium lauuense* Bayer, 1956 (red coral) and *Corallium secundum* Dana, 1846 (pink coral), and a zoanthid, *Gerardia* sp. (gold coral) collected between August and November in 1998–2004, were all histologically analysed for reproductive tissues. All three species of precious corals appear to be gonochoric (both males and females of all species being identified—though with *C. lauuense* more reproductive polyps are needed to conclusively confirm this), with the two species of *Corallium* having reproductive material contained within siphonozooids rather than the main polyp (autozoid). Maximum oocyte sizes were: *Gerardia* sp. ~300 μm, *C. secundum* ~600 μm, and *C. lauuense* ~660 μm. All three species are hypothesized to have spawned during the collection season. *Gerardia* was observed spawning during collection, and histological sections of the two *Corallium* species show areas where gametes appear to be missing. *Gerardia* sp. has a single cohort of gametes developing, which may suggest seasonal reproduction, and the two *Corallium* species show multiple sizes present in single individuals, suggesting a periodic or quasi-continuous reproductive periodicity.

The seamounts and slopes surrounding the Hawaiian Archipelago contain numerous species of deep-water corals at depths of around 300–600 m. Some of these species are classed as precious corals, and have been harvested in Hawaii for their skeletons since the mid-1960s (Grigg, 1976, 2002). These skeletons (along with antipatharians and bamboo corals) have been used in the jewelry industry both in the Hawaiian Islands and for export overseas (mainly to Asia). Often fetching many hundreds of dollars per kilogram, this fishery is potentially very lucrative. Three species have been the main focus of this fishing effort—the pink coral, *Corallium secundum* Dana, 1846; the red coral, *Corallium lauuense* Bayer, 1956; and the gold coral, an undescribed zoanthid in the genus *Gerardia* sp. (Fig. 1).

These fisheries have, however, gone through boom and bust periods, owing to both the cycles of over-harvesting new coral beds until no corals remain, and the high costs of collecting at deeper depths. A number of regulations have been implemented on deep-water coral harvests in the Hawaiian Archipelago over the years. The Federal Fishery Management Plan (FMP) allows only selected harvests with maximum collection quotas, for example, on the Makapuu bed off Oahu—2000 kg over 2 yrs with a 10-inch minimum size requirement for *C. secundum,* and a 600 kg limit of *Gerardia* sp. Then in late 2000, a Coral Reef Ecosystem Reserve was established in the NW Hawaiian Islands which protected roughly 84 million acres from harvests and effectively halted commercial collections of coral skeletons. This fishery is currently discontinued in Hawaii as the small number of coral beds in the south is not
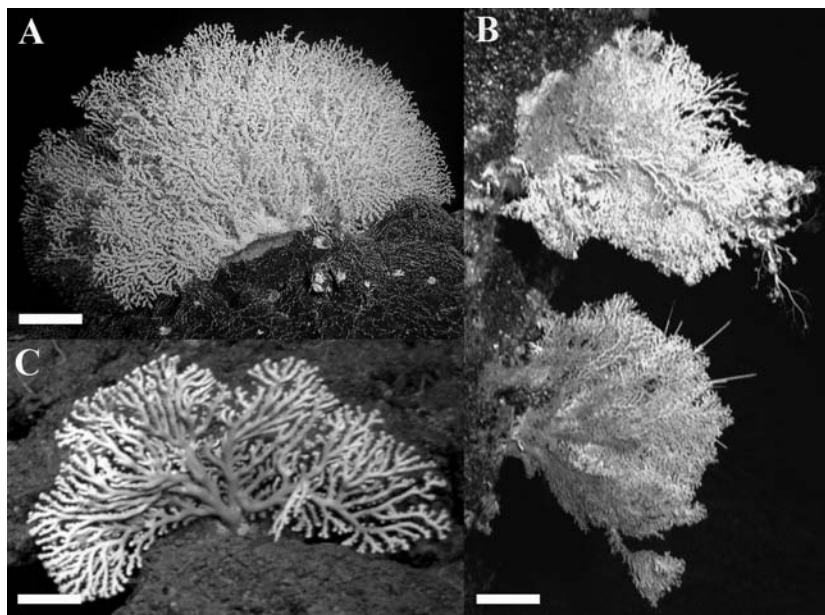
Figure 1. (A) *Gerardia* sp. colony; (B) *Corallium lauuense* colonies; (C) *Corallium secundum* colony.

adequate to keep up the cost of submersible equipment required for selective harvesting. However, as has happened in the past, if demand were to rise it could lead to economic conditions favorable for the reemergence of precious coral fisheries (Grigg, 2002).

Little is known of the biology and ecology of these commercially important species yet these data are an essential pre-requisite in producing effective fisheries management plan. Having an understanding of reproductive biology, and the associated processes of dispersal and recruitment, is essential for ecological studies of coral populations and communities (Harrison and Wallace, 1990). In this study, we examine the reproductive morphology of these three species of precious coral from various locations across the Hawaiian Ridge.

Methods

Collection.—Collections were made during six cruises to the Hawaiian Archipelago using the Pisces IV and V submersibles, operated by the Hawaiian Undersea Research Laboratory, Honolulu, Hawaii. Collections were made between August and November from Bank 8, Bank 11, Pioneer Bank, Cross Seamount, Raita Bank, Twin Banks, Makapuu, and Nero Seamount (Table 1). Pieces of coral were broken from main colonies of various sizes and placed in individual insulated bioboxes. Once on the surface corals were immediately fixed in 4% formaldehyde and later transferred to 70% isopropanol.

Histology.—A section of approximately 10 polyps was dissected from coral branches (see Table 1 for numbers of colonies analyzed) and placed in Bouins solution for ~2 hrs for decalcification. Polyps or siphonozooids were then dissected, weighed and placed in sequential dilutions of propanol for dehydration (50%, 75%, 95%, 100% × 3). Tissue was extracted and placed in molten histological wax overnight and subsequently embedded into standard molds. Ten sequential thin sections (5 μm) were taken of each block and then stained using Massons Trichrome. Sections were viewed using a Zeiss Axiopan 2 microscope with a Zeiss AxioCam

Table 1. Numbers of coral colonies sampled per location (with latitude and longitude below) analyzed for this study. Five polyps (or more) were sectioned per colony.

| | Bank 11 | Nero Seamount | Coral beds west to east | | | | | |
			Bank 8	Pioneer	Raita Bank	Twin Banks	Makapuu	Cross Seamount
	28°52'N, 179°34'W	27°56'N, 177°53'W	26°13'N, 174°31'W	25°49'N, 173°27'W	25°38'N, 169°19'W	23°16'N, 163°00'W	21°18'N, 157°33'W	18°44'N, 158°16'W
Gerardia sp.	5	5	7	4	2	7	4	4
Corallium secundum	3		10	7				6
Corallium lauuense	5		3			3		7

Figure 2. Histological sections of *Gerardia* sp.: (A) mesenterial lamella with previtellogenic oocytes; (B) vitellogenic oocyte with prominent nucleolus; (C) folded female mesentery with multiple oocytes; (D) spawned mesentery of a female individual; (E) Stage 3 spermacysts; and (F) male mesentery with multiple spermacysts. Pv = previtellogenic oocyte; l = lamellae; vo = vitellogenic oocyte; m = mesentery; s = spermacyst; Scale bars: A, 100 μm; B, 100 μm; C, 300 μm; D, 300 μm; E, 100 μm; F, 300 μm

video camera attachment. Images were grabbed using Openlab 3.1.5 and further analyzed using SigmaScan Pro v. 4 to calculate feret diameters of oocytes (diameter if the oocyte was a perfect circle). Only oocytes with a nucleus were measured (to prevent re-measuring the same oocyte) and all oocytes in all sections were measured. Sections were also used for staging oocytes and spermacysts and for producing size-frequency graphs. Owing to observations of spawning on collection, no fecundity estimates could be calculated for these samples.
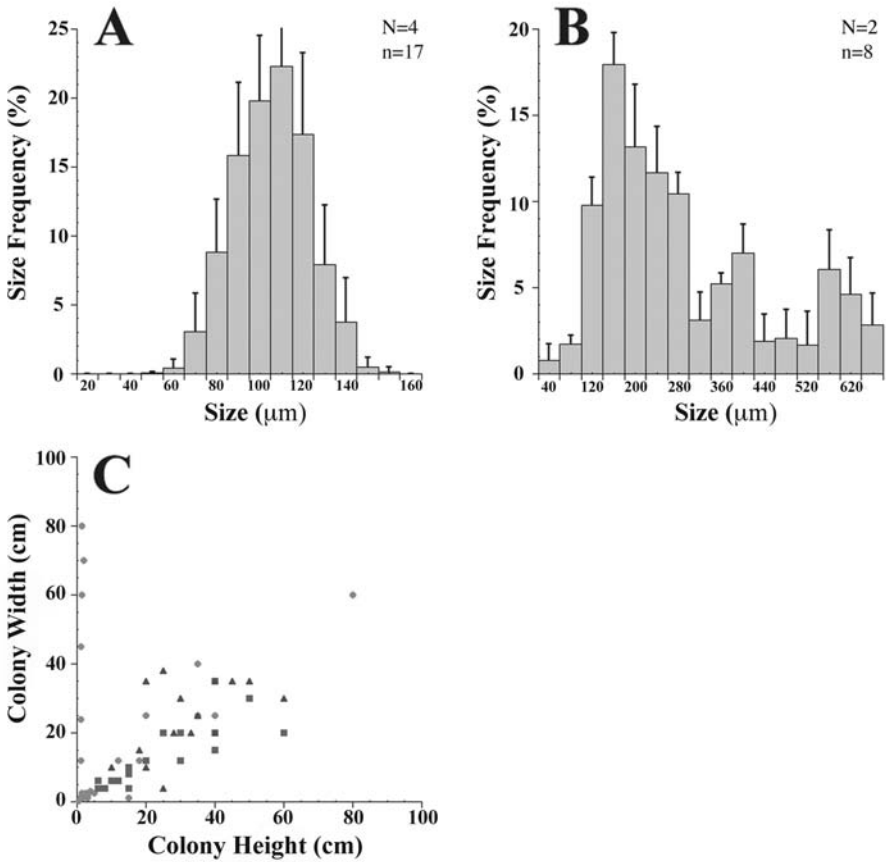
Figure 3. (A) Oocyte size-frequency graph for *Gerardia* sp. from Bank 8, (B) Oocyte size-frequency graph for *Corallium secundum* from Bank 8; (C) Sizes of colonies analyzed for this study (circles, *Gerardia*; triangles, *C. secundum*; squares, *Corallium lauuense*) N, Number of colonies analyzed; n, number of individuals analyzed

Results

Gerardia sp. (Fig. 2)

Like other deep and shallow water hexacorals, *Gerardia* sp. has gametes contained in a string along the length of the mesenteries. This species is gonochoric with no hermaphroditic polyps or colonies observed in the thirty eight samples analyzed. Previtellogenic and vitellogenic oocytes were observed in this species (Fig. 2A–C), though only late stage spermacysts were present (Fig. 2E,F). A small number of individuals (X = 5) had empty or nearly empty mesenteries (Fig. 2D), consistent with the observation of spawning during the onboard processing. Colonies of various sizes were chosen for analysis (Fig. 3C). The smallest polyp found to be producing gametes was approximately 5 mg wet weight, and reproductive material was found in the smallest colonies analyzed (Fig. 3C).

Only a single cohort of oocytes was observed in this species (Fig. 3A), with a maximum oocyte size of ~300 μm. Oocyte size frequency charts were constructed of
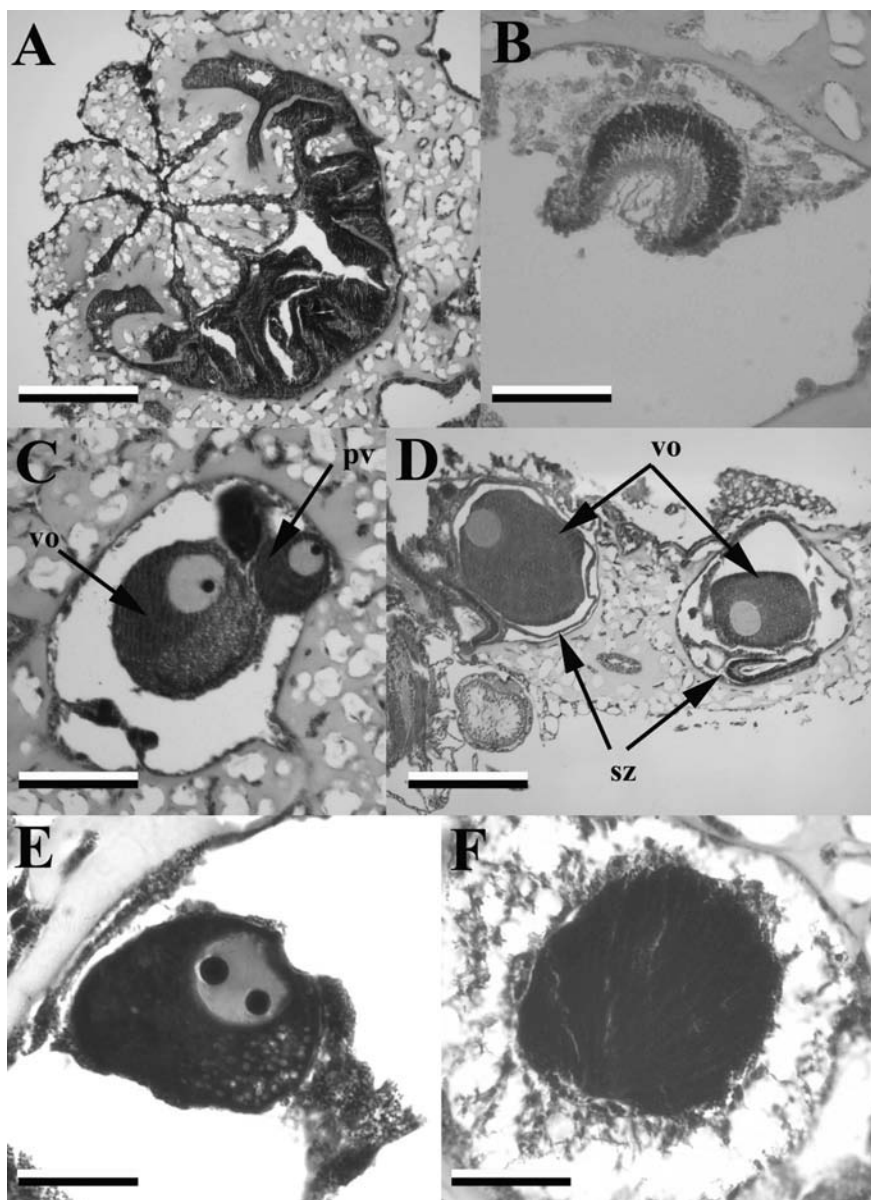
Figure 4. Histological sections of *Corallium secundum*: (A) Autozoid polyp; (B) siphonozooid polyp; (C) siphonozooid polyp containing previtellogenic and vitellogenic oocytes; (D) multiple female siphonozooids; (E) vitellogenic oocyte showing amphinucleolus; and (F) Stage 3 spermacyst. Vo = vitellogenic oocyte; pv = previtellogenic oocyte; sz = siphonozooid; Scale bars: A, 500 μm; B, 200 μm; C, 300 μm; D, 500 μm; E, 300 μm; F, 300 μm

the different locations where samples were collected (see Fig. 3A for the oocyte-size frequency chart for Bank 8). Analysis of oocyte size-frequency distributions revealed no significant difference among locations sampled (K = 5.01, P = 0.1). This pattern of oocyte distribution suggests a seasonality of reproduction rather than a continuous or quasi-continuous production. Additional monthly samples are required however, to conclusively investigate seasonal gamete development and test the intensity of reproduction in this species.

Corallium secundum (Fig. 4)

Corallium secundum had both autozoids and siphonozooids present in the colony. Autozoids were sterile and siphonozooids fertile (Fig. 4A,B). Colonies appear to be gonochoric as no hermaphrodites were found in this study. Previtellogenic and vitellogenic oocytes were observed within the same siphonozooid (Fig. 4C,D) and some oocytes had amphinucleolus (Fig. 4E). Only late stage spermacysts were observed (Fig. 4F).

Sections appeared to have gametes missing from the siphonozooid (partial oocytes observed in some specimens, empty areas in the siphonozooid where tissue would be expected) suggesting either problems with preservation and histology or spawning at time of collection. However, multiple cohorts were still observed in size-frequency diagrams (Bank 8 site–Fig. 3B), though in numerous individuals not enough oocytes were located to construct diagrams. Maximum oocyte size was ~600 µm. This multiplicity of cohorts suggests either a periodic or quasi-continuous life history. Colonies of different sizes were analyzed (Fig. 3C) and there appeared to be no pattern between colony size and reproductive state, although this may be confounded by missing gametes in some of the specimens (through spawning, preservation, or processing).

Corallium lauuense (Fig. 5)

This species also had both autozoids and siphonozooids, with only the siphonozooids being fertile. Tissue was not well preserved in this species and there appeared to be gametes missing from the tissue sections (as described above), and so limited data could be extracted. However, all colonies analyzed appeared to be gonochoric with multiple stages of oocytes present (Fig. 5A), and only late stage spermacysts were found (Fig. 5B). Maximum oocyte size was ~650 µm.

Too few oocytes were present in preserved samples to obtain oocyte-size frequency charts, however, the presence of both very large vitellogenic and very small previtellogenic oocytes in this species suggests a similar reproductive strategy to *C. secundum*.

Discussion

All three species in this study are thought to be gonochoric (though with *C. lauuense*, more reproductive polyps are needed to fully confirm this). *Gerardia* sp. contains gametes within the mesenteries of the polyp, with oocytes and spermacysts forming long chains through the mesentery, similar to other deep-water anthozoan species (Van-Praet, 1990; Van-Praet et al., 1990; Waller et al., 2002, 2005; Brooke and Young, 2003; Waller and Tyler, 2005). The two species of *Corallium,* however, contain gametes within siphonozooids, showing more similarity with reproduction in *Anthomastus* species (Alcyonacea) (Jungersen, 1927; Cordes et al., 2001). Octocorals of the closely related octocoral family Paragorgiidae also have both autozoids and siphonozooids (Sanchez, 2005), but the reproductive morphology of this family has not yet been described. From non-quantitative observations, *Gerardia* sp. appears to have a much higher fecundity per polyp than that of the two *Corallium* species.
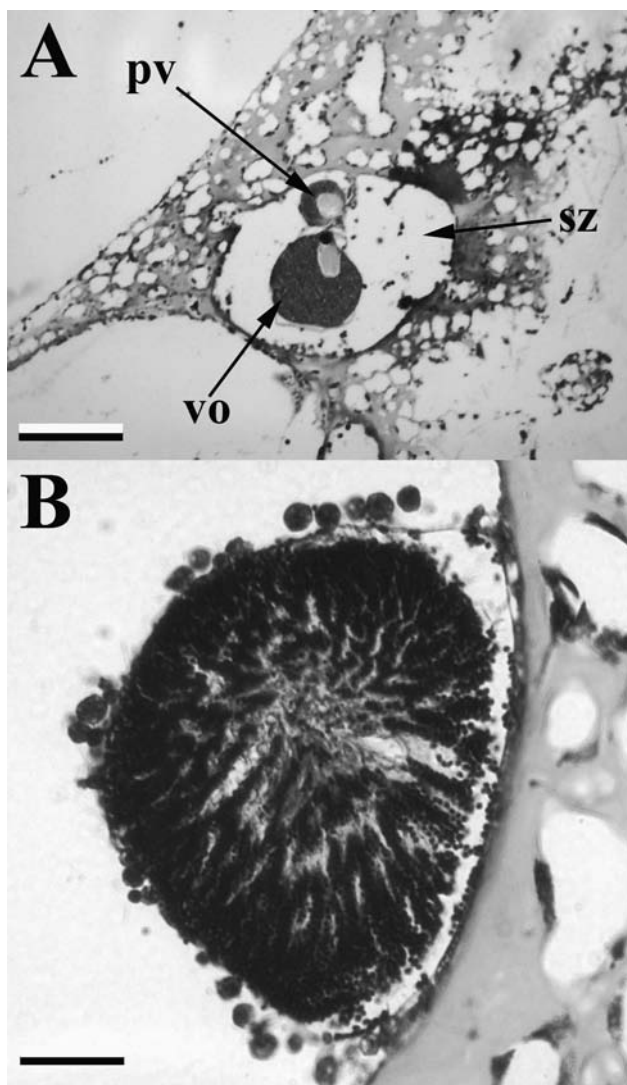
Figure 5. Histological sections of *Corallium lauuense*: (A) Siphonozooid containing previtellogenic and vitellogenic oocytes; (B) spermacyst. Pv = previtellogenic oocyte; vo = vitellogenic oocyte; sz = siphonozooid; Scale bars: A, 500 μm; B, 300 μm

The observation of spawning during collection, as well as empty areas in the tissue sections (where gametes are potentially missing) suggest that all three of these precious coral species may be spawning during the fall. Although no brooded larvae were observed, possibly because of these missing areas, further investigation is needed into the full reproductive cycle of these two *Corallium* species. *Anthomastus ritteri* Nutting, 1909, a species that also produces gametes in the siphonozooids, broods larvae in these structures and releases them quasi-continuously throughout the year (Cordes et al., 2001) and so there is the possibility that these *Corallium* species may be similar. While this study was not designed to test seasonality, certain initial observations were possible based on oocyte sizes. *Gerardia* sp. had just a single cohort, a pattern distinctive of seasonal reproducers, whereas oocytes of varying sizes were

found in the two *Corallium* species, more suggestive of a periodic or quasi-continuous reproduction (Gage and Tyler, 1991; Tyler et al., 1993; Waller et al., 2002; Waller and Tyler, 2005). *Corallium secundum* has previously been reported as being a seasonal reproducer, with spawning occurring in June or July (Grigg, 1976), and so more seasonal samples of this species are needed to test this conflicting evidence. Reproduction in the deep-sea is often related to food fall (Billett et al., 1983; Tyler et al., 1992, 1993; Waller and Tyler, 2005) with few other seasonal cues existing at depths below the thermocline, so no doubt this is also a factor in these species survival. As none of these species showed obvious differences in oocyte size or stage among the different seamounts, they may experience similar environmental factors or at least no significant difference that might lead to a long term change in reproductive habit (Eckelbarger and Watling, 1995).

This initial investigation suggests that a long term seasonal study should be undertaken to more fully understand the timing and reproductive potential of these commercially important species. Should another boom in the jewelry industry begin, a better understanding of the reproduction of these species would benefit the design of a new sustainable management plan.

Acknowledgments

Literature Cited

Billett, D. S. M., R. S. Lampitt, A. L. Rice, and R. F. C. Mantoura. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302: 520–522.

Brooke, S. and C. M. Young. 2003. Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf. Cont. Shelf. Res. 23: 847–858.

Cordes, E. E., J. W. Nybakken, and G. VanDykhuizen. 2001. Reproduction and growth of *Anthomastus ritteri* (Octocorallia: Alcyonacea) from Montery Bay, California, USA. Mar. Biol. 138: 491–501.

Eckelbarger, K. J. and L. Watling. 1995. Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. Invertebr. Biol. 114: 256–269.

Gage, J. D. and P. A. Tyler. 1991. Deep-sea biology, a natural history of organisms at the deep sea floor. Cambridge University Press, Cambridge. 504 p.

Grigg, R. W. 1976. Fishery management of precious and stony corals in Hawaii. SeaGrant Technical Report 490. 48 p.

_____. 2002. Precious corals in Hawaii: discovery of a new bed and revised management measures for existing beds. Mar. Fish. Rev. 64: 13–20.

Harrison, P. L. and C. C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. Pages 133–207 *in* Z. Dubinsky, ed. Ecosystems of the world: coral reefs, Vol 25. Elsevier, Amsterdam, Oxford, New York, Tokyo.

Jungersen, H. F. E. 1927. *Anthomastus*. Pages 1–20 *in* The Danish Ingolf-Expedition, Vol 5 (11), Bianco Luno, Copenhagen.

Sanchez, J. A. 2005. Systematics of the bubblegum corals (Cnidaria: Octocorallia: Paragorgii-dae) with descriptions of new species from New Zealand and the eastern Pacific. Zootaxa 1014: 1–72.

Tyler, P. A., L. S. Campos-Creasey, and L. A. Giles. 1993 Environmental control of quasi-continuous and seasonal reproduction in deep-sea benthic invertebrates. Pages 158–178 *in* C. Young and K. Eckelbarger, eds. Reproduction, larval biology and recruitment of the deep-sea benthos. Columbia University Press, New York.

_____, J. D. Gage, G. J. L. Paterson, and A. L. Rice. 1993. Dietary constraint on reproductive periodicity in two sympatric deep-sea species. Mar. Biol. 115: 267–277.

_____, R. Harvey, L. A. Giles, and J. D. Gage. 1992. Reproductive strategies and diet in deep-sea nuculanid protobranchs (Bivalvia: Nuculoidea) from the Rockall Trough. Mar. Biol. 114: 571–580.

Van-Praet, M. 1990. Gametogenesis and the reproductive cycle in the deep-sea anemone *Paracalliactis stephensoni* (Cnidaria: Actiniaria). J. Mar. Biol. Assoc. U.K. 70: 163–172.

_____, A. L. Rice, and M. H. Thurston. 1990. Reproduction in two deep-sea anemones (Actiniaria); *Phelliactis hertwigi* and *P. robusta.* Prog. Oceanogr. 24: 207–222.

Waller, R. G. and P. A. Tyler. 2005. The reproductive biology of two deep-sea, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24: 514–522.

_____, _____, and J. D. Gage. 2002. The reproductive ecology of the deep-sea solitary coral *Fungiacyathus marenzelleri* (Scleractinia) in the NE Atlantic Ocean. Coral Reefs 21: 325–331.

_____, _____, and _____. 2005. Sexual reproduction of three deep water *Caryophyllia* (Anthozoa: Scleractinia) species from the NE Atlantic Ocean. Coral Reefs 24: 594–602.

Addresses: (R.G.W.) *MS#33, 2-34 Redfield, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.* (A.R.B.) *MS#33, 2-50 Redfield, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.* Corresponding Author: (R.G.W.) *E-mail: <rwaller@whoi.edu>*

BMS