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Gonad morphology and gametogenesis in the deep-sea jellyfish *Atolla wyvillei* and *Periphylla periphylla* (Scyphozoa: Coronatae) collected from Cape Hatteras and the Gulf of Mexico

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Observations on gonad morphology and the structure of ovaries and testes of the coronate scyphozoans Atolla wyvillei *and* Periphylla periphylla *are described based on samples collected from the Gulf of Mexico and Cape Hatteras (north-western Atlantic). In* A. wyvillei*, gonads of distinguishable sex were observed in medusae as small as 17 mm bell diameter (BD). Spermatogenesis occurred within follicles (average 366 × 254 μm) that were evenly distributed throughout the gonad. Oocytes in different stages of development were observed in all the females with gonads. Oocytes arise from the gastrodermis and migrate into the mesoglea to develop from early-mid to late vitellogenic oocytes characterized by a large nucleus and granular (organic-rich) cytoplasm. The largest oocytes measured were 543 μm and 263 μm from the Gulf of Mexico and Cape Hatteras respectively. Possible reasons for this difference are discussed. In* P. periphylla *gonads were also initially observed in medusae 17 mm BD, although not all larger medusae had obvious gonads. Unlike* A. wyvillei *sperm follicles were arranged in long convoluted rows normally only one follicle thick. The organization of ooytes in female* P. periphylla *was very similar to* A. wyvillei*, although the gonads were small and the number of oocytes present in each gonad very low (<22). The largest oocyte measured was 777 μm in a 53 mm BD medusa. Although medusae were collected from one time period only (September) in this study, our findings appear to be in agreement with literature evidence indicating that coronate jellyfish produce few eggs continuously over a long time period. Aspects of gonad development and gametogenesis are discussed with respect to potential differences in site productivity and species identification.*

Keywords: jellyfish, *Atolla*, *Periphylla*, gametogenesis, oocytes, sperm follicles, continuous reproduction

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INTRODUCTION

The coronate jellyfish (class Scyphozoa, order Coronatae) are composed of five families, three of which, the Atollidae, Paraphyllinidae and Periphyllidae, are considered to exclusively comprise deep sea species (Arai, 1997; Jarms *et al.*, 2002). Of the two other families, the Linuchidae are found in shallow water only, while the Nausithoidae have jellyfish in both the deep sea and shallow waters, including caves (see Jarms *et al.*, 1999; Morandini & Silveira, 2001).

Of the deep sea jellyfish, *Periphylla periphylla* (Péron & Lesueur, 1810) and *Atolla* spp. are the most well-known. *Periphylla periphylla* is widely distributed at mesopelagic depths in several oceans from the Arctic to Antarctic (e.g. Mauchline & Harvey, 1983; Larson *et al.*, 1991; Mianzan & Cornelius, 1999; Donnelly *et al.*, 2006; Osborn *et al.*, 2007; Gershwin & Zeidler, 2008; Youngbluth *et al.*, 2008). Abundance estimates from net tows and ROVs are in the region of 1 ind 1000 m^{-3} to 2 ind 100 m^{-3} (Pagès *et al.*, 1996; Dalpadado *et al.*, 1998; Youngbluth *et al.*, 2008). Permanent and highly abundant populations up to 2–3 orders of magnitude greater than open ocean environments have also been observed in several Norwegian fjords, and research into these populations has greatly increased our understanding of the biology and ecology of this species (e.g. Youngbluth & Båmstedt, 2001; Riemann *et al.*, 2006; Kaartvedt *et al.*, 2007; Soetje *et al.*, 2007; Sørnes *et al.*, 2008). Like *P. periphylla* the genus *Atolla* is widely distributed in many of the world's oceans at mesopelagic and bathypelagic depths (e.g. Larson *et al.*, 1991; Lindsay *et al.*, 2004; Raskoff *et al.*, 2005; Donnelly *et al.*, 2006; Osborn *et al.*, 2007; Youngbluth *et al.*, 2008). However, compared with *Periphylla* much less is known about its biology and ecology beyond the early descriptions of Russell (1959, 1970).

Life cycles and reproductive biology in the Scyphozoa have been studied extensively in coastal species, primarily the semaeostomes (e.g. *Aurelia* sp., *Cyanea* sp., *Chrysaora* sp. and *Pelagia* sp.) and rhizostomes (e.g. *Cassiopea* sp., and *Rhizostoma* sp.) (Eckelbarger & Larson, 1988; Rottini-Sandrini & Avian, 1991; Arai, 1997; Pitt &

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Kingsford, 2000; Lucas, 2001). In the coronates, sexual reproduction has been described for the coastal species *Nausithoe aurea* (Morandini & Silveira, 2001), *Nausithoe atlantica* and *Linuche unguiculata* (Eckelbarger & Larson, 1992). However, in deep sea jellyfish (including coronates) reproduction is poorly described, primarily due to low sampling frequency typical of deep-sea research and the relatively low abundances encountered at mesopelagic and bathypelagic depths. Nevertheless, we know that adaptations to life in the deep-sea include holopelagic life histories that may involve reduced and/or parasitic polyps or direct development with a complete absence of the benthic polyp (Russell, 1953; Kramp, 1961; Osborn, 2000; Lucas & Reed, 2009). Recently the life cycle and development of *P. periphylla* has been described by Jarms *et al.* (1999, 2002). The species has a holopelagic life cycle with direct development from a large yolky egg into a medusa without either planula larva or ephyra stages, and based on preserved and fresh material, 14 developmental stages from egg to adult medusa have been identified (Jarms *et al.*, 2002).

The two studies by Jarms *et al.* (1999, 2002) have greatly advanced our understanding of the life history of deep-sea coronate medusae. However, ultrastructural descriptions of gonads and gametogenesis in coronates, and indeed other jellyfish, are extremely sparse. Apart from older texts (Haeckel, 1882; Claus, 1883; Maas, 1897; Vanhöffen, 1902; Widersten, 1965; Russell, 1970) descriptions of ovarian morphology and oogenesis in scyphozoans are limited to those of Eckelbarger & Larson (1988, 1992), Eckelbarger (1994), Lesh-Laurie & Suchy (1991) and Morandini & Silveira (2001). Apart from older texts (e.g. Haeckel, 1882; Claus, 1883; Maas, 1897; Vanhöffen, 1902), published accounts of gonad structure and gametogenesis in the coronates are limited to the shallow water species *L. unguiculata* (Eckelbarger & Larson, 1992) and *N. aurea* (Morandini & Silveira, 2001). This paper describes the structure of gonads and gametogenesis in the deep water coronates *Periphylla periphylla* and *Atolla wyvillei* (Haeckel, 1880) collected from mesopelagic depths in the Gulf of Mexico and Cape Hatteras region of the western North Atlantic.

MATERIALS AND METHODS

Study areas and sample collection

Specimens were identified according to the descriptions of Russell (1959, 1970). *Atolla wyvillei* and *Periphylla periphylla* medusae were collected from Cape Hatteras (33°10′N to 35°14′N, and 74°52′W to 75°47′W) in early–mid-September 1994, and from the eastern Gulf of Mexico (running along the 1000 m depth contour between 26°24′N 84°51′W and 27°04N 85°09′W) in mid-September 1995.

At both Cape Hatteras and the Gulf of Mexico, medusae were collected using the 'detritus sampler' on the 'Johnson-Sea-Link' submersible. At Cape Hatteras, 3 specimens of *P. periphylla* were collected from between 400 and 686 m depth and 5 specimens of *A. wyvillei* were collected from between 820 and 909 m depth. Water temperature at these depths ranged between 5.5 and 6.2°C. In the Gulf of Mexico, a total of 18 *P. periphylla* and 7 *A. wyvillei* medusae were collected from depths between 638 m and 831 m. The temperature recorded at these depths ranged between 5.45 and 6.8°C. Additional specimens of *P. periphylla* ($N = 26$) and *A. wyvillei* ($N = 7$) were collected using a Tucker Trawl on the Gulf of Mexico cruise. Trawling took place primarily at night time, at depths ranging between 130 and 850 m.

Within 2 hours of collection, the bell diameters (BD, mm) of all medusae were measured using a ruler and their sex and state of maturity noted where possible (i.e. immature with no gametes visible, male and female). Undamaged individuals were then either frozen at −20°C for biochemical analysis (see Lucas, 2009), or preserved in 2% gluteraldehyde for histological analysis.

Histology and image analysis

Whole male and female gonads were dehydrated in graded alcohol, cleared in Histo-Clear®, embedded into 20 × 20 mm paraffin wax blocks and serial sectioned at 7 μm. Tissue sections were mounted on slides and stained with Pasini's triple stain. Image analyses of gonads containing gametes were captured using SigmaScan Pro 4 software, with feret (average) diameter used to measure the size of developing and mature oocytes.

RESULTS

Atolla wyvillei Haeckel, 1880

GENERAL MORPHOLOGY OF GONADS

Observations on the general morphology of *Atolla wyvillei* gonads were based on 14 specimens from the Gulf of Mexico, 8–40 mm bell diameter (BD), and 5 specimens from Cape Hatteras, 40–145 mm BD, summarized in Table 1. Gonads were visible in specimens >17–22 mm BD, appearing as 8 oval or bean-shaped structures on the subumbrella wall of the gastrovascular sinus proximate to the coronal groove (Plate 1a). As the gonads matured, each one thickened along its periphery and in males the outer edge of the gonad was folded over. Together, mature male gonads formed an almost continuous ring around the stomach. Gonad colour varied from white-cream to tan, red or dark brown, and they appeared to be very organic-rich, as demonstrated by the very high percentage ash-free dry weights ranging from 67.6–96.5% of dry weight (Table 1). Gametes were clearly visible within the gonads (Plate 1b) even in medusae as small as 17 mm BD.

SPERMATOGENESIS

Histology was carried out on 1 or 2 gonads from each of 4 males of *Atolla wyvillei*. Spermatogenesis occurred within follicles arising from the gastrodermis. Many sperm follicles were present, evenly distributed throughout each gonad (Plate 2a). Each follicle was ovoid, but with some variability in shape and size; in a single male 80 mm BD where 27 follicles were measured, average (±SD) follicle size was 366 (±83.9) μm × 254 (±41.9) μm. Mature follicles, containing spermatogonia, spermatocytes, spermatids and spermatozoans (Plate 2b) were observed in individuals measuring 80 mm in Cape Hatteras and 30 mm in the Gulf of Mexico.

Table 1. Observations on the morphology of gonads of *Atolla wyvillei* medusae collected from the Gulf of Mexico (GoM) and Cape Hatteras (CH) regions. WW, wet weight; DW, dry weight; AFDW, ash free dry weight; F, female; M, male; i, immature—gonads or their contents not visible.

Medusa size (mm)	Location	Sex	Gonad colour	Individual gonad weight				
				WW (mg)	DW (mg)	AFDW (mg)	DW % WW	AFDW % DW
8	GoM	i	–	–	–	–	–	–
8	GoM	i	–	–	–	–	–	–
12	GoM	i	–	–	–	–	–	–
16	GoM	i	–	–	–	–	–	–
17	GoM	F	White and red	–	–	–	–	–
22	GoM	i	–	–	–	–	–	–
25	GoM	F	White–orange	5.08	1.22	1.17	23.89	96.53
27	GoM	F	White and red	3.45	0.64	0.62	18.67	95.50
28	GoM	F	White (v. small)	–	–	–	–	–
28	GoM	F	White	–	–	–	–	–
30	GoM	M	Yellow	1.59	0.30	0.21	18.92	67.57
30	GoM	M	White and red	2.80	0.64	0.57	22.58	90.50
32	GoM	F	Yellow	2.30	0.54	0.46	23.27	85.17
40	GoM	F	Red–brown	2.94	0.57	0.45	22.28	79.48
40	CH	F	White	1.50	–	–	–	–
60	CH	F	nd	4.50	–	–	–	–
80	CH	M	Brown–orange	45.00	–	–	–	–
80	CH	M	Brown	25.00	–	–	–	–
145	CH	F	Brown	–	–	–	–	–

OOGENESIS

Oocytes in different stages of development were observed in all the female medusae mature enough to have gonads. As described by Russell (1970) the smallest oocytes were visible around the periphery of the gonads, with the largest oocytes located in the central mesoglea region (Plates 1b & 2c). Although there was no significant relation between state of maturity and medusa size, it was noted that the largest specimen from Cape Hatteras (BD = 145 mm) had the largest gonads, measuring 11 × 7 mm, and that these contained a greater number of oocytes. In each gonad, the oocytes developed from the gastrodermis. These small pre-vitellogenic oocytes, 20–40 μm, appeared to be held to the cell wall by a peduncle (Vanhöffen, 1902) (Plate 2d) before detaching and migrating into the mesoglea as unattached early–mid and late vitellogenic oocytes without nutritive trophocytes (Plate 2e). As the oocytes developed and grew to ~70 μm and beyond, they appeared to gain increasing quantities of organic-rich yolk material and a large nucleus was present (Plate 2f).

OOCYTE SIZE—FREQUENCY DISTRIBUTIONS

The size–frequency distribution of oocytes was measured in 5 individuals of *Atolla wyvillei*; 3 from the Gulf of Mexico 25–40 mm BD, and 2 from Cape Hatteras, 80 and 145 mm BD (Figure 1). All of the medusae contained both developing and mature oocytes reflected in the wide range of oocyte diameters. In the medusae from the Gulf of Mexico the smallest oocytes measured between 43 and 71 μm, increasing to maximum diameters of between 331 and 543 μm. In the larger Cape Hatteras medusae, oocyte sizes ranged from minima of 24–53 μm to maxima of 226–263 μm.

Periphylla periphylla Péron & Lesueur, 1810

GENERAL STRUCTURE OF GONADS

The observations on general morphology of *Periphylla periphylla* gonads summarized in Table 2 were based on 44 specimens 15–80 mm bell diameter (BD) collected from the Gulf of Mexico. Gonads were visible in specimens >17 mm BD, although not all larger individuals had obvious gonads (see Table 2). In total, 13 medusae were identified as females (38.8 ± 10.0 mm BD), 11 as male (46.4 ± 12.6 mm BD),

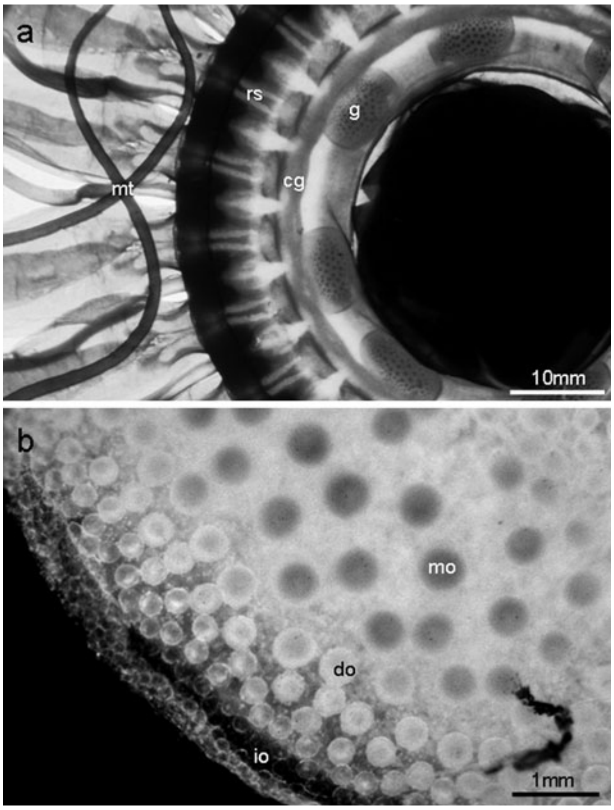

Plate 1. (a) Subumbrella view of 40 mm bell diameter (BD) female *Atolla wyvillei* from Cape Hatteras showing the position of the gonads (*g*) containing oocytes, coronal groove (*cg*), radial septum (*rs*) and marginal tentacle (*mt*); (b) gonad of female *Atolla wyvillei* (40 mm BD) containing oocytes in all stages of development from the immature oocytes (*io*) located at the gonad periphery to developing oocytes (*do*) and mature oocytes (*mo*) both unattached within the central mesoglea.

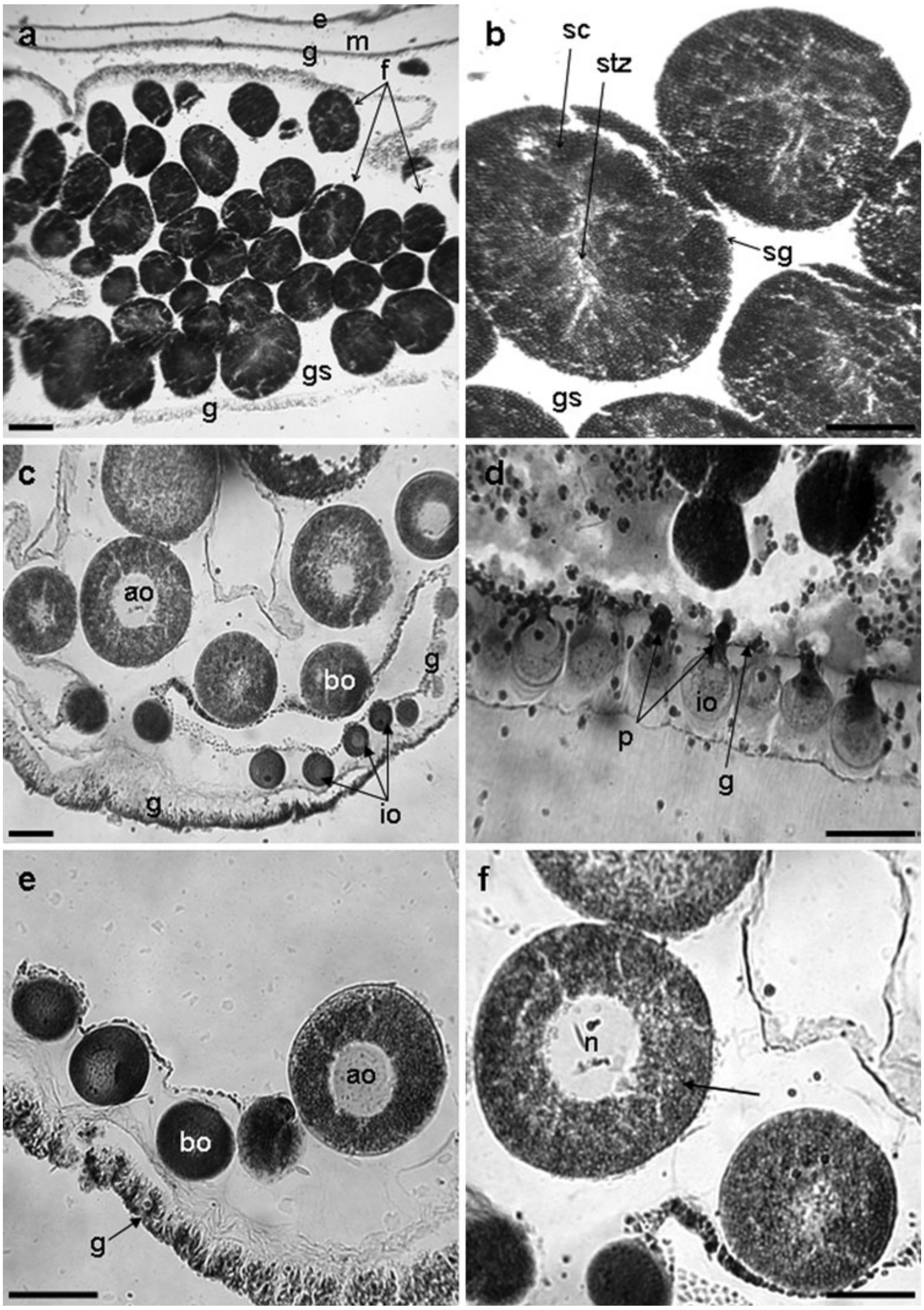

Plate 2. (a) Cross-section through a male gonad of a 40 mm bell diameter (BD) *Atolla wyvillei* from Cape Hatteras showing the evenly distributed sperm follicles (*f*). Also shown are the exumbrella surface (*e*), mesoglea (*m*), gastrodermis (*g*) and genital sinus of the gastrovascular cavity (*gs*); (b) close-up of sperm follicles from the same individual showing the spermatogonia (*sg*) located on the margin of the follicle. Spermatocytes (*sc*) mature into spermatids then spermatozoons (*stz*) as they move down the follicle. They are released into the genital sinus (*sg*); (c) cross-section through the female gonad of a 40 mm BD *A. wyvillei* from the Gulf of Mexico. Two areas of gastrodermis (*g*) are seen—thicker external and thinner internal. Small immature oocytes (*io*) are found at the periphery of the ovary, developing into densely-staining basophilic oocytes then lighter-staining acidophilic (mature) oocytes with a large nucleus (see Morandini & Silveira, 2001); (d) oocytes (*io*) arise from the gastrodermis, initially attached by a peduncle (*p*) (*A. wyvillei* 145 mm BD from Cape Hatteras); (e) basophilic (*bo*) and acidophilic oocytes (*ao*) continue their development unattached in a 40 mm BD *A. wyvillei* from the Gulf of Mexico; (f) mature oocytes can be identified by their large nucleus (*n*) and granular cytoplasm (*arrow*) (*A. wyvillei* 40 mm BD Gulf of Mexico). All scales = 100 μm.

with the remaining 20 unknown (29.11 ± 12.9 mm BD). Of these 20 individuals, 11 medusae did not have any gonads, while in the remainder the sex could not be determined because the gonads were too thin.

The eight gonads were located on the gastrovascular cavity attached to the subumbrella wall of the medusa. They initially appeared as thin straight structures in small medusae, 17–22 mm BD, becoming J-shaped in 24–30 mm BD medusae (Plate 3a). The distal end of the gonad was longer in medusae >35 mm BD, finally resulting in a convoluted (particularly males) U-shaped gonad with the inner margins of the adradial and interradial arms almost contiguous (Plate 3b). As with *Atolla wyvillei*, gametes were clearly visible in the gonads in medusae as small as 22 mm

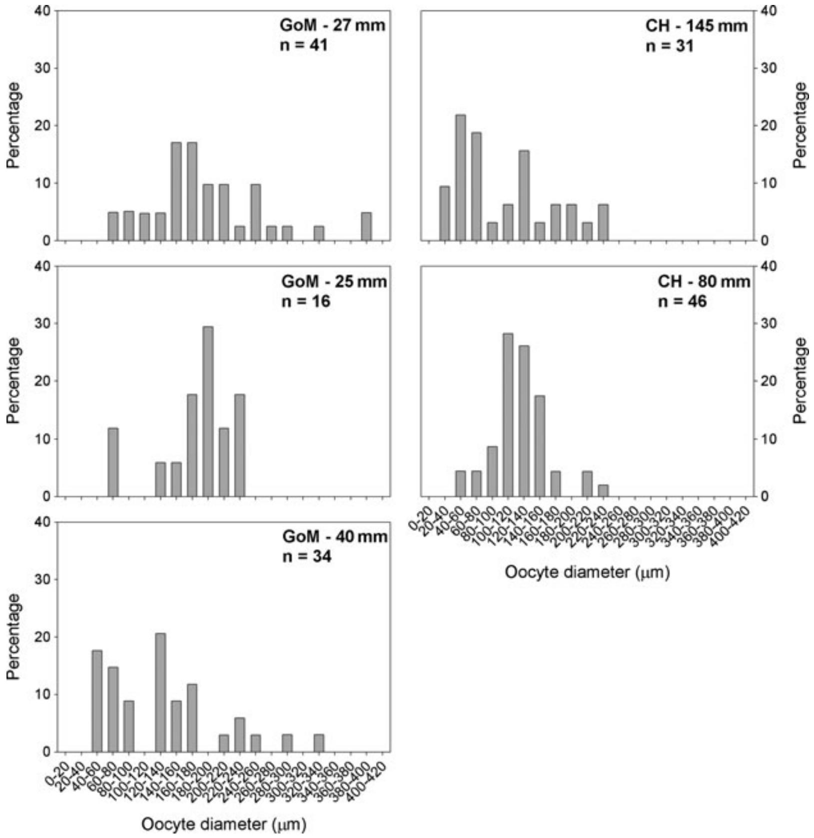

Fig. 1. Percentage size–frequency distributions of *Atolla wyvillei* oocytes from the Gulf of Mexico (GoM) and Cape Hatteras (CH). Medusa size given in mm, n is number of oocytes measured.

BD (Plate 3c). Gonad colour varied between cream, tan, orange and deep red, generally with darker colours in larger medusae.

SPERMATOGENESIS

Histology was carried out on 1–2 gonads from each of 4 males of *Periphylla periphylla*, 33–55 mm BD. The male gonads consisted of follicles containing spermatogonia, spermatocytes, spermatids and spermatozoans, consistent with other descriptions of coronate scyphomedusae (Russell, 1970). The sperm follicles were positioned in long convoluted rows normally one follicle thick (Plate 4a), with the follicle contents at similar stages of development. The smallest male with mature gonads had a bell diameter of 33 mm from Cape Hatteras and 40 mm from the Gulf of Mexico.

Table 2. The number of observations on the state of maturity of gonads in 10 mm size-groups of *Periphylla periphylla* collected from the Gulf of Mexico. No G, no gonads; unident, gonads present but sex not identifiable; M, male; F, female; nd, no data.

Size-range (mm)	Total number	State of maturity				Comments
		No G	Unident	M	F	
<19	5	3	2	0	0	Very thin or no gonads
20–29	9	4	4	0	1	As above; 1 × J-shaped gonad
30–39	11	2	0	3	6	Oocytes visible
40–49	12	2	0	6	4	Range from thin straight gonad to gametes clearly visible
50–59	3	0	0	1	2	Large white oocytes clearly visible. Dense male gonad
60–69	1	1	0	0	0	No gonads obvious
70–79	0	–	–	–	–	nd
>80	1	0	0	1	0	Very large, long and convoluted

OOGENESIS

Histology was carried out on 1–2 gonads from each of 9 females, 30–80 mm BD. Oocytes in different stages of development (i.e. pre-vitellogenic to late-vitellogenic) were observed in each female medusa examined; even the gonads of a 30 mm BD medusa contained oocytes ranging between 49 and 288 μm diameter. The oocytes initially appeared near the distal end of the gonad (Plate 4b). A gradient of increasing oocyte size was apparent within each gonad with the largest oocytes located in the inner region of the gonad (Plate 4c). Mature, late-vitellogenic oocytes could be recognized from dense immature oocytes by their light granular acidophilic (eosin red staining) cytoplasm.

OOCYTE SIZE—FREQUENCY DISTRIBUTIONS

Oocyte diameters were measured in 9 individuals, 30–80 mm BD, collected from the Gulf of Mexico. As previously mentioned, 25% of medusae collected did not appear to have gonads, and in those that did have the larger J-shaped or U-shaped gonads, oocyte size–frequency distributions were variable (Figure 2), possibly biased by the small medusa and

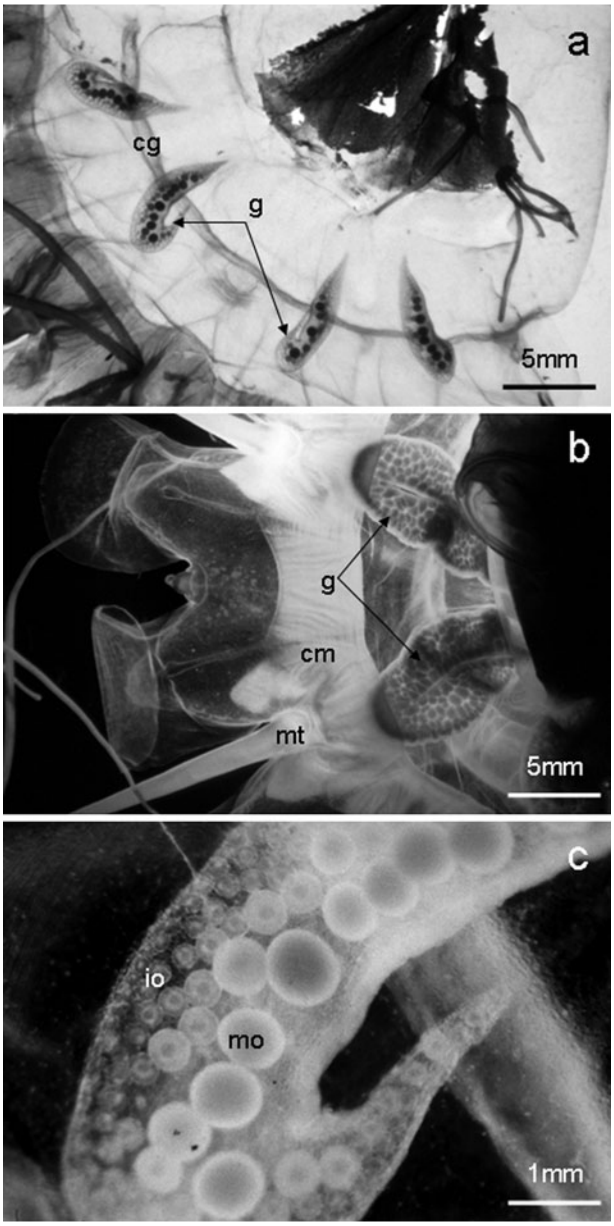

Plate 3. (a) Exumbrella view of a 30 mm bell diameter (BD) female *Periphylla periphylla* from the Gulf of Mexico showing the J-shaped gonads (*g*) lying under the coronal groove (*cg*); (b) a 35 mm BD male *Periphylla periphylla* from Cape Hatteras with densely-packed gonads (g). Also shown are the coronal muscle (*cm*) and a marginal tentacle (*mt*); (c) close-up of a female gonad from a 30 mm BD medusa highlighting the gradient from immature oocytes (*io*) at the periphery of the gonad to mature gonads (*mo*) towards the inner margins.

gonad sizes, and very low numbers of oocytes ($N = 7$ to 22) present in each gonad. For example, minimum oocyte sizes varied from between 44 and 168 μm in 30 mm and 58 mm BD medusae respectively, with no apparent trend with medusa size. The largest oocytes measured ranged between 252 μm in a 30 mm medusa and 777 μm in a 53 mm medusae (mean ± SD, 431.8 ± 164.9 μm, $N = 9$).

DISCUSSION

The findings presented in this paper contribute to our understanding of gonad morphology and gametogenesis in *Atolla wyvillei* beyond the early texts (Haeckel, 1882; Claus, 1883; Maas, 1897; Vanhöffen, 1902; Russell, 1959, 1970), and to our increased understanding of the life history and breeding of *Periphylla periphylla* (Mauchline & Harvey, 1983; Jarms *et al.*, 1999, 2002). The relatively low sample numbers, particularly for Cape Hatteras, reflect the sampling methodology (i.e. individually collected *intact* specimens using a submersible) as well as the relative contribution of the study species to overall jellyfish diversity at the two sites. Cape Hatteras had a high diversity of mesopelagic jellyfish comprising coronate scyphomedusae (*A. wyvillei* and *P. periphylla*), the ulmarid scyphomedusa *Poralia rufescens*, narcomedusae and trachymedusae (*Aeginura grimaldii*, *Colobonema* sp., *Cunina peregrina*, *Eumedusa* sp. and *Halitrephes* sp.), as well as a variety of mainly unidentified ctenophores. *Atolla wyvillei* and *P. periphylla* accounted for less than a quarter of all gelatinous zooplankton collected. In contrast, submersible and trawl samples from the Gulf of Mexico were dominated by *P. periphylla* (40% of catch), with siphonophores (*Apolemia* sp. and *Halistemma* sp.), ctenophores (*Llyria* sp. and *Beroe* sp.) and *A. wyvillei* also abundant (21%, 15% and 8% of catch respectively).

The bell diameters of *P. periphylla* sampled (16–80 mm from the Gulf of Mexico, 33–60 mm from Cape Hatteras) fall within the range of those reported in other ecosystems, e.g. the Rockall Trough (Mauchline & Harvey, 1983) and Australia (Gershwin & Zeidler, 2008), although the biggest jellyfish sampled in this study are much smaller than those in the Lurefjord, Norway (145–170 mm) (Youngbluth & Båmstedt, 2001; Jarms *et al.*, 2002), Japan (150 mm) and the Antarctic (~230 mm) (Lindsay, personal communication). Indeed, Larson (1986) has reported that *P. periphylla* medusae were up to 350 mm in the Southern Ocean. Regarding *A. wyvillei* Russell (1959) reported that *Atolla* spp. from the Bay of Biscay reached a size of 130 mm, although it was suggested that two species were present: smaller *A. parva* and larger *A. wyvillei*. Similarly, in the Rockall Trough, north-eastern Atlantic, Mauchline & Harvey (1983) reported that *A. wyvillei* ranged from 9.3–79.7 mm, *A. vanhoeffeni* was 4.8–31.6 mm and *A. parva* was 5.0–46.3 mm. The largest specimens captured in this study were from Cape Hatteras (40–145 mm), whereas those from the Gulf of Mexico were between 8 and 40 mm BD. It is unclear whether variation in sizes represents sampling bias, geographical differences in food availability or breeding period (see Mauchline & Harvey, 1983). Similarly, although only one species of *Periphylla* is reported in the literature at present, Jarms *et al.* (2002) have commented that several species may exist in different regions, which may have different morphologies, sizes and developmental characteristics, as has been discovered with the common shallow water scyphozoan *Aurelia* (e.g. Dawson & Jacobs, 2001).

The wide range of medusa sizes and stages of maturity observed for both species in this study have been documented elsewhere. Several studies have published size–frequency distributions and stages of maturity in both *Periphylla* and *Atolla* species that indicate ongoing breeding throughout the year (Russell, 1959; Mauchline & Harvey, 1983; Jarms *et al.*, 2002), possibly with a primary breeding period in the summer months in more northerly latitudes in open waters (Russell, 1959; Mauchline & Harvey, 1983). Although Jarms *et al.* (2002) state that 'mature medusae with ripe gonads are present (in Lurefjord) throughout the year, and a distinct spawning period does not exist' the strong dominance of

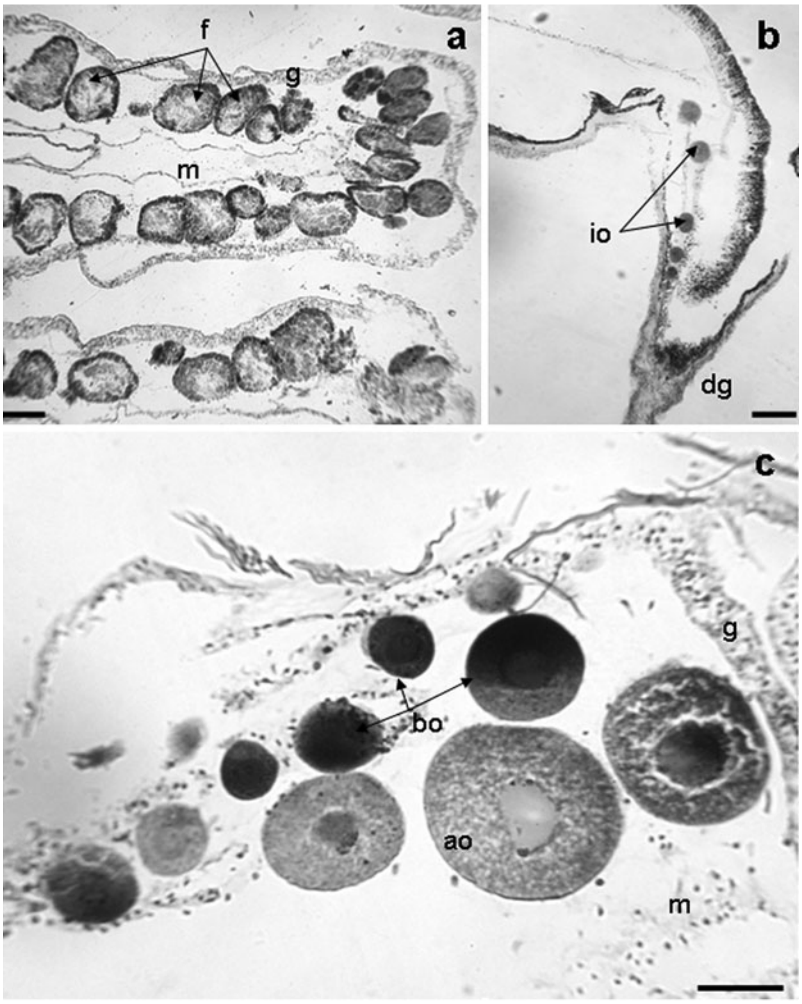

Plate 4. (a) Cross-section through the male gonad of a 55 mm bell diameter (BD) *Periphylla periphylla* from the Gulf of Mexico showing the long convoluted rows of sperm follicles (*f*) inside the gastrodermis (*g*). Also shown is the mesoglea (*m*); (b) immature oocytes (*io*) at the distal end of the gonad (*dg*) of a 53 mm BD *P. periphylla* from the Gulf of Mexico; (c) a clear gradient of increasing oocyte size and maturity in a 30 mm BD *P. periphylla* from the Gulf of Mexico, from basophilic oocytes (*bo*) nearer the gastrodermis (*g*) to mature acidophilic oocytes (*ao*) within the mesoglea (*m*) of the gonad. All scales = 100 μm.

individuals <10 mm in coronal diameter in October seem to indicate that periods of relatively high recruitment do occur in the summer (see Jarms *et al.*, 1999, p. 61), which has also been found in enclosed and tropical shallow water jellyfish populations (Lucas, 1996; Martin, 1999). Although sample numbers are rather low, female:male sex-ratios were 3.5 (N = 14) and 1.5 (N = 5) for *A. wyvillei* in the Gulf of Mexico and Cape Hatteras respectively, and 1.4 (N = 24) for *P. periphylla* in the Gulf of Mexico.

In both *A. wyvillei* and *P. periphylla* from the Gulf of Mexico gonads were distinguishable in medusae >17 mm. In their description of development stages of *P. periphylla* from the Lurefjord Jarms *et al.* (2002) noted that gonads were first evident in 'Stage 14B' medusae (coronal diameter, CD >25 mm; 37.0 ± 6.8 mm), with sexual dimorphism of gonads in 'Stage 14C' medusae (CD >40 mm; 57.3 ± 17.8 mm). Mature specimens, i.e. those containing eggs >1 mm, were >80 mm CD. In the Gulf of Mexico sexual dimorphism of gonads was evident at 22 mm. Using Jarms *et al.* (2002) criteria, maturity was not attained as oocytes did not reach 1 mm in size; indeed the maximum was 777 μm in a 53 mm medusa. However, based on histological examination we believe that the larger specimens in this study were mature, and this will be discussed further later. Russell (1959) identified 3 stages of maturity in *Atolla* spp.: I—gonads absent or just appearing, sex not distinguished; II—sexes determined but gonads not mature; and III—mature males and females, i.e. gonads full. In the Bay of Biscay mature (stage III) specimens of *A. wyvillei* were between 40 and 130 mm in size, while mature *A. parva* were 10–30 mm in size (Russell, 1959), with similar sizes reported by Mauchline & Harvey (1983) in the more northerly Rockall Trough.

The general structure of the gonads was very similar to previous descriptions of these and other coronate scyphomedusae (e.g. Russell, 1970; Morandini & Silveira, 2001). In *A. wyvillei* the gonad walls were many cells deep in places. In one individual the thickened gonad walls appeared to contain bunches of possible organic-rich granular material with small passages visible through them—similar to that reported by Morandini & Silveira (2001) for *Nausithoe aurea*.

The majority of descriptions of gametogenesis in shallow and deep water medusae have focused on oogenesis (e.g. Eckelbarger & Larson, 1988, 1992), with very few modern descriptions of male gonads (but see Kikinger, 1992; Pitt & Kingsford, 2000; Morandini & Silveira, 2001). Nevertheless,

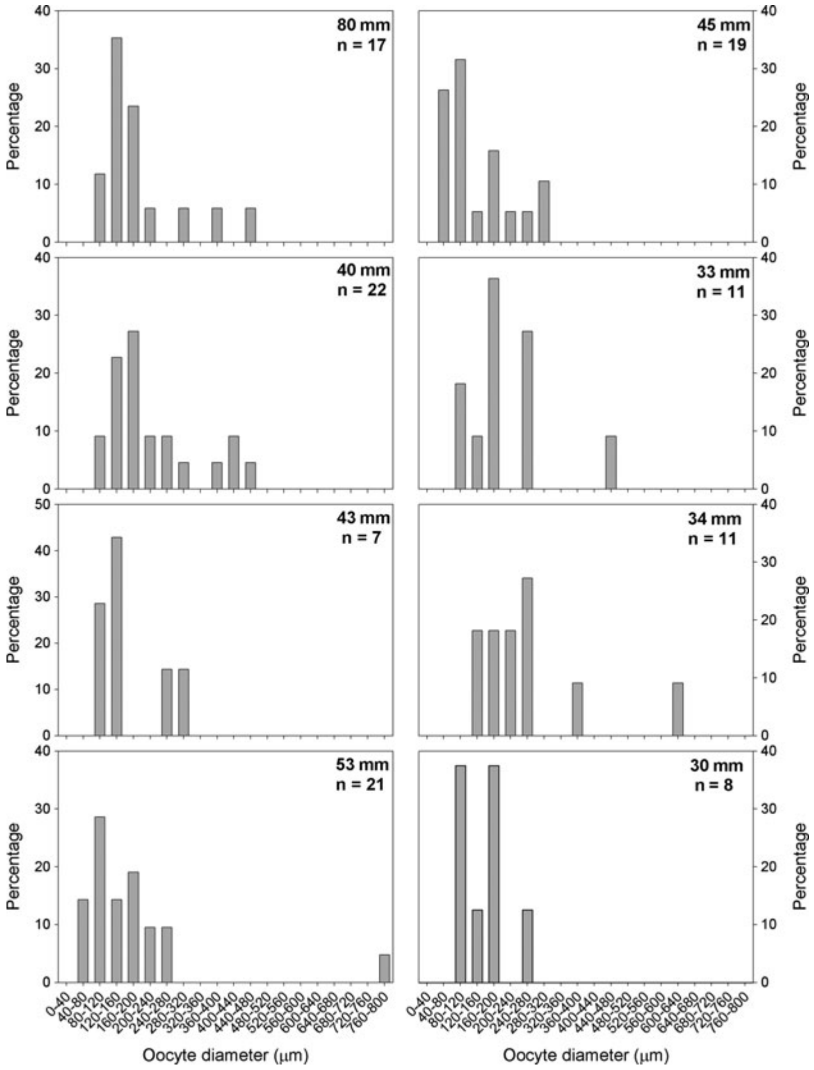

Fig. 2. Percentage size–frequency distributions of *Periphylla periphylla* oocytes from the Gulf of Mexico. Medusa size given in mm, n is number of oocytes measured.

the general structure of the testis of both study species resembled the descriptions of Widersten (1965), Campbell (1974) and Morandini & Silveira (2001). In coronates sperm follicles arise from invagination of the gastrodermis, and it is within these follicles that spermatogenesis occurs. In *A. wyvillei*, numerous ovoid sperm follicles were evenly distributed throughout the gonad (see Plate 2a), whereas in *P. periphylla* the gonads contained convoluted ribbons one follicle thick (see Plate 4a). According to Campbell (1974) release of spermatozoa occurs through the rupture of the testis wall.

In both *A. wyvillei* and *P. periphylla* oocytes in different stages of development were observed in all medusae possessing gonads mature enough for sexes to be distinguishable. In agreement with earlier descriptions of coronates (e.g. Russell, 1970) the gonads had very distinctive and characteristic distribution of oocytes, with small oocytes at the periphery and large oocytes in the centre. Unlike rhizostome (Pitt & Kingsford, 2000) and semaeostome (Eckelbarger & Larson, 1988) scyphozoans, early-mid vitellogenic oocytes break free from the gastrodermis, from where they arise, and continue their development freely in the mesoglea without the presence of nutritive trophocytes. In accordance with the conclusions of numerous authors (e.g. Russell, 1959; Mauchine & Harvey, 1983; Larson, 1986; Jarms *et al.*, 1999, 2002), the presence of oocytes in various stages of development in a wide variety of medusa sizes coupled with the apparent lack of spent gonads implies continuous and steady egg production over several years. There are no obvious relationships between oocyte size and medusa development.

Berrill (1949) was the first to suggest that large eggs were an indication of direct development, and indeed Jarms *et al.* (1999) described the holopelagic life cycle of *P. periphylla*, from large yolky egg to young medusa, without a polyp, planula larvae or ephyra. The eggs of *P. periphylla* are among the largest in the Cnidaria, being up to 10 times bigger than those for other scyphomedusae (see Jarms *et al.*, 1999). The organic-rich eggs produced by *P. periphylla* from the Gulf of Mexico were also large (maximum 777 μm) compared with shallow water scyphozoans, but did not attain the very large sizes, up to 1.28 mm, found in *P. periphylla* in the Lurefjord (Jarms *et al.*, 2002) (Figure 3). Jarms *et al.* (2002) suggested that oocytes were not mature until they were >1 mm diameter, although they provided no histological or quantitative criterion of how they defined oocyte maturity. Nevertheless, based on the large nucleus and light, granular acidophilic staining (see Morandini & Silveira, 2001) we

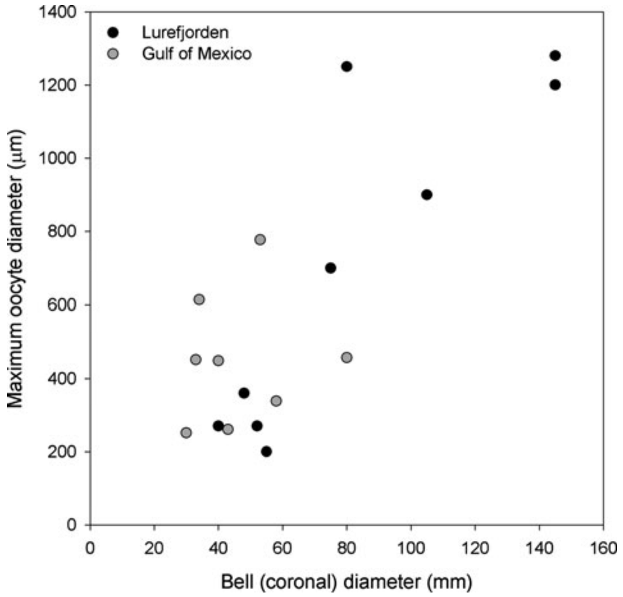

Fig. 3. Relationship between maximum oocyte diameter (µm) and medusa size (mm) in *Periphylla periphylla* (bell diameter for the Gulf of Mexico, coronal diameter for the Lurefjorden). Lurefjorden data taken from Jarms *et al.* (2002).

believe that some of the oocytes were mature. *Atolla wyvillei* oocytes were measured in specimens from both the Gulf of Mexico and Cape Hatteras, with maximum diameters of mature eggs ranging between 331–543 µm and 226–263 µm respectively. Given the very small sample sizes it is unclear whether the larger mature oocytes found in the smaller Cape Hatteras medusae reflects a genuine inverse relationship between maximum oocyte size and size/age of medusa, a site-specific relationship influenced by productivity of the two regions, or even molecular differences in medusae from the two regions. These ambiguities may be clarified if and when comparisons with other populations of *Periphylla* and *Atolla* occur in a global setting, but until more detailed ecological and molecular analyses are carried out on specimens, this area will remain poorly understood.

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