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REPORT

Contrasting reproductive strategies in three deep-sea octocorals from eastern Canada: *Primnoa resedaeformis*, *Keratoisis ornata*, and *Anthomastus grandiflorus*

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Abstract Various aspects of reproduction were studied in three deep-sea octocorals belonging to the order Alcyonacea that co-occur at bathyal depths on the continental edge and the slope of eastern Canada. The main goals were to expand knowledge of deep-water heterotrophic corals and ascertain whether reproductive strategies could explain the known patterns of occurrence. *Anthomastus grandiflorus* is a gonochoric species with a female-biased sex ratio that exhibits internal fertilization and brooding of planula larvae. Conversely, *Primnoa resedaeformis* and *Keratoisis ornata* rely on broadcast spawning and external fertilization; their sexuality remains undetermined as spermatocysts were not found. In *P. resedaeformis*, the presence of mixed size classes of oocytes in samples from all months, depths, and locations studied suggests continuous oogenesis or overlapping development of oocyte cohorts, indicative of a gametogenic cycle spanning more than a year. No evidence of periodicity was found in this species, although it could have been masked by the striking bathymetric variation in potential relative fecundity (oocytes polyp^{-1}). The two other octocorals displayed a clear annual breeding pattern. Spawning in *K. ornata* and larval release in *A. grandiflorus* occurred in late summer and fall, respectively, possibly in response to environmental factors, as supported by shifts in the reproductive peak of *A. grandiflorus* across latitudes. The three species are presumed to share a nonfeeding larval mode, and data on their reproductive potential do not present any striking disparities. Published data on bycatches and video surveys in Atlantic Canada indicate that the gonochoric brooder *A. grandiflorus* is more widely distributed than the two free spawners, *P. resedaeformis* and *K. ornata*, which is contrary to common dispersal potential paradigms.

Keywords Octocorals · Reproduction · Gametogenesis · Spawning · Deep-sea · Cold-water

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Introduction

Although the reproduction of deep-sea corals is a key element in determining the level of their vulnerability or resilience to disturbances, very little information exists on their sexual and asexual proliferation and almost nothing is known of the factors that can influence these processes temporally and spatially. Most of the limited information relates to scleractinian (stony) corals of the subclass Hexacorallia (Waller 2005), whereas the subclass Octocorallia is comparatively less studied in the deep ocean. Octocorals include approximately 3,000 extant species subdivided into three main orders (Daly et al. 2007): Pennatulacea (sea pens), Helioporacea (blue corals), and Alcyonacea, the latter representing a morphologically diverse and widespread group of soft corals and sea fans (gorgonians) with numerous representatives in deep ecosystems (Freiwald et al. 2004; Watling and Auster 2005; Wareham and Edinger 2007). Very few data are available on the sexual reproduction of cold-water and deep-water pennatulaceans (Rice et al. 1992; Tyler et al. 1995;

Eckelbarger et al. 1998) and alcyonaceans (Lawson 1991; Brito et al. 1995; Cordes et al. 2001; Orejas et al. 2002, 2007; Sun et al. 2009, 2010a, b) compared to tropical and temperate species (e.g., Benayahu 1991; Dahan and Benayahu 1997; Ben-David-Zaslow et al. 1999; Zeevi Ben-Yosef and Benayahu 1999; Santangelo et al. 2003; Excoffon et al. 2004; Torrents et al. 2005; Gori et al. 2007; Hwang and Song 2007; Ribes et al. 2007; Hellström et al. 2010).

Colonies of alcyonacean corals are either gonochoric or hermaphroditic and their sexual reproduction can be subdivided into two main types: (1) free spawning or broadcast spawning, where fertilization and development occur in the water column and (2) fertilization inside or on the parent colony and subsequent internal or external brooding of embryos and planula larvae. The frequency of brooding versus free spawning varies both taxonomically and geographically. The two modes of reproduction are common in tropical shallow-water alcyonaceans (Alino and Coll 1989; Brazeau and Lasker 1990; Coma et al. 1995), whereas cold-water gorgonians studied so far are predominantly gonochoric brooders (Ribes et al. 2007). In the deep ocean (below 200 m), several brooding soft corals have also been reported (Cordes et al. 2001; Orejas et al. 2007; Sun 2009; Sun et al. 2010a, b).

The large body of evidence gathered from shallow-water octocorals has shown that they may undergo seasonal or so-called continuous reproduction, synchronous or asynchronous spawning and that their patterns of sexual reproduction can be primarily correlated with temperature, depth, lunar, and solar cycles (e.g., Alino and Coll 1989; Brazeau and Lasker 1990; Benayahu 1991; Coma et al. 1995; Dahan and Benayahu 1997; Ben-David-Zaslow et al. 1999; Gori et al. 2007; Ribes et al. 2007). While investigations of reproductive patterns in the deep ocean remain limited, recent studies on deep-sea octocorals have documented seasonal patterns of reproduction in correlation with environmental factors such as temperature, sedimentation (e.g., phytodetritus), and lunar cycles (Mercier et al. in press).

Alcyonaceans are the dominant deep-sea corals found at bathyal depths on the continental slope of eastern Canada (Mortensen et al. 2006; Wareham and Edinger 2007). The latter surveys indicate that the gorgonians *Primnoa resedaeformis* and *Keratoisis ornata* and the alcyoniid soft coral *Anthomastus grandiflorus* are among the most common and conspicuous, exhibiting overlapping ranges but distinct levels of occurrence. To our knowledge, their reproduction has never been investigated. The present study was undertaken to close this gap and to test the hypothesis that differences in reproductive strategies might explain the distributional patterns. Life history traits (e.g., spawning mode, larval type) are perceived as important predictors of population structures in reef corals (Baird et al. 2009), although molecular evidence is not always supportive of this assumption (Miller and Ayre 2008), emphasizing the need to expand our understanding of coral reproduction, particularly in heterotrophic (azooxanthellate) species.

Various aspects of the reproduction were examined in three deep-sea corals collected over 4 years in an effort to: (1) determine the mode of reproduction of each species; (2) highlight annual/seasonal trends in gametogenesis and estimate peak spawning/planulation period; (3) make preliminary correlations with latitudinal factors, depth distribution, and environmental conditions; and (4) reconcile available data on the distribution and abundance of these species with their respective reproductive strategy.

Materials and methods

Sampling and field data

Specimens of *Primnoa resedaeformis*, *Keratoisis ornata*, and *Anthomastus grandiflorus* were collected during surveys conducted by the Department of Fisheries and Oceans Canada (DFO) with a Campelen shrimp trawl between 2004 and 2007 along the continental edge and slope off Newfoundland and Labrador and in the Arctic (Fig. 1). They were frozen at −20°C on board of the vessels. Samples of *P. resedaeformis* were collected between 176 and 1,179 m (Table 1), those of *K. ornata* from 302 to 876 m (Table 2), and those of *A. grandiflorus* from 346 to 1,404 m (Table 3). Information on local densities and small-scale distribution of the three species was obtained from images collected with the remotely operated vehicle (ROV) ROPOS aboard the vessel CCGS *Hudson* in July 2007.

Reproduction

For branching corals, only colonies that showed the presence of the main trunk and holdfast were used. A preliminary study of 11 colonies of *P. resedaeformis* and 8 colonies of *K. ornata* from various periods of the year revealed no difference in the number and size of sexual products in proximal, central, and distal branches (as per Orejas et al. 2002). No intra-colony heterogeneity was noted in 55 colonies of *A. grandiflorus*. Subsequent analyses were conducted on 3–6 haphazardly selected subsamples of each colony. In *P. resedaeformis* and *K. ornata*, these subsamples consisted of branch sections with 3–5 polyps. For *A. grandiflorus*, the subsamples consisted of slices of ~ 4 cm^2 cut from the surface of the capitulum toward the interior of the colony between the feeding polyps.

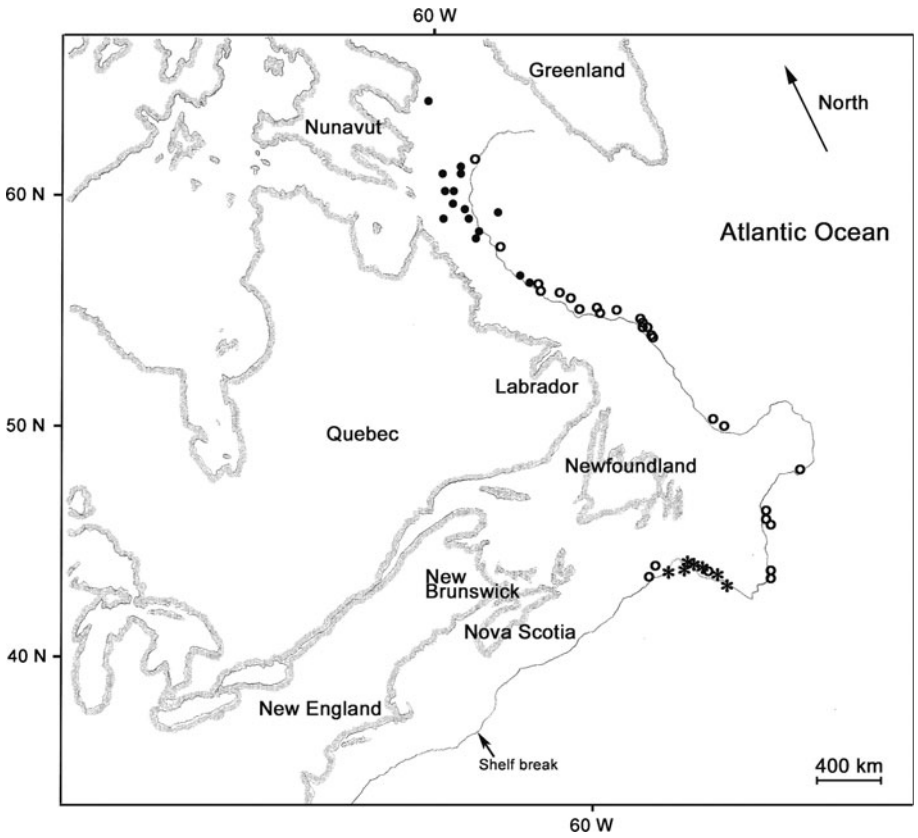

Fig. 1 Map of eastern Canada showing sampling sites for *Primnoa resedaeformis* (*closed circles*), *Keratoisis ornata* (*asterisks*), and *Anthomastus grandiflorus* (*open circles*) along the continental edge and slope. Sampling sizes, depths, and coordinates provided in Tables 1, 2, and 3

Table 1 *Primnoa resedaeformis*. Sampling coordinates, depths, and dates

Coordinates	Depth (m)	Date	*N*
60°06′40″N–61°26′02″W	254	5 Aug 05	5
60°07′58″N–64°13′01″W	376	4 Oct 05	5
60°32′06″N–62°14′56″W	398	5 Dec 05	4
65°28′39″N–62°09′27″W	176	6 May 06	4
55°42′36″N–57°04′44″W	466	7 July 06	3
59°36′03″N–60°53′06″W	670	4 Aug 05	4
59°26′02″N–61°04′01″W	854	5 Aug 05	2
60°28′01″N–58°46′58″W	867	2 Oct 05	3
60°29′52″N–61°23′42″W	914	3 Dec 05	3
60°45′57″N–62°05′38″W	963	4 May 06	4
60°50′31″N–62°22′48″W	830	5 Jul 06	3
61°38′02″N–61°20′31″W	870	6 Aug 06	5
61°40′44″N–61°09′36″W	759	8 Oct 06	3
61°46′08″N–62°18′14″W	962	13 Nov 06	2
56°00′00″N–57°18′50″W	1,179	17 Nov 06	2
			52

Table 2 *Keratoisis ornata*. Sampling coordinates, depths, and dates

Coordinates	Depth (m)	Date	*N*
44°34′01″N–53°46′01″W	876	18 Mar 05	7
44°29′52″N–54°17′25″W	664	9 May 05	8
43°52′01″N–52°31′01″W	302	8 Jul 05	6
44°26′02″N–54°10′04″W	578	7 Oct 05	7
44°46′01″N–55°34′01″W	958	2 Dec 05	8
44°07′58″N–52°55′58″W	713	13 Mar 06	6
44°34′01″N–53°46′01″W	876	18 Mar 06	5
			47

Microscopy

Unprocessed tissue samples were analyzed under a dissecting microscope Nikon SMZ1500 coupled to a Nikon DXM1200F digital camera. Size and abundance of gametes (in each polyp or slice) were established with the imaging software Simple PCI (v. 6.0) in all subsamples, which were also used to assess gametogenic development and reproductive potential (fecundity), as described later. Histology was used as a complementary tool to analyze the males of *A. grandiflorus* (to confirm the presence/absence of spermatozoa) and to assess stage of vitellogenesis of the oocytes in females of the three species. For this purpose, subsamples were placed in 4% formalin and processed using several variants of standard histological procedures to maximize the quality of the sections. Gorgonian samples were decalcified in 10% HCl at the onset. The smallest and most fragile samples were infiltrated with HistoGel^{TM} prior to

Table 3 *Anthomastus grandiflorus*. Sampling coordinates, depths, and dates

Coordinates	Depth (m)	Date	Sector	*N*	
				Females	Males
56°19′38″N–57°49′58″W	586	30 May 04	Labrador	5	2
55°15′45'N–56°01′57″W	1,237	8 Jul 04	Labrador	4	1
55°20′54″N–56°28′06″W	797	10 Sep 04	Labrador	5	1
56°30′46″N–57°04′51″W	1,320	27 Oct 04	Labrador	4	1
53°18′46″N–52°39′03″W	1,211	14 Nov 04	Labrador	4	1
53°14′49″N–52°13′44″W	416	15 Nov 04	Labrador	3	0
53°42′02″N–53°00′10″W	1,325	15 Nov 04	Labrador	4	0
54°41′02″N–53°43′22″W	1,308	16 Nov 04	Labrador	3	2
54°14′36″N–52°34′55″W	1,359	16 Nov 04	Labrador	4	1
54°21′30″N–52°31′15″W	1,365	16 Nov 04	Labrador	3	1
54°25′01″N–53°17′47″W	532	16 Nov 04	Labrador	2	1
55°00′00″N–53°34′59″W	1,211	17 Nov 04	Labrador	2	0
55°03′43″N–54°32′38″W	875	10 Jan 05	Labrador	4	1
55°23′20″N–56°16′58″W	304	11 May 05	Labrador	4	1
55°43′12″N–56°54′50″W	1,109	7 Oct 05	Labrador	3	1
56°19′12″N–57°21′54″W	1,432	3 Nov 05	Labrador	5	2
55°21′34″N–56°32′46″W	992	13 Nov 05	Labrador	4	1
57°38′52″N–59°14′56″W	1,045	3 Dec 05	Labrador	4	2
54°45′50″N–52°56′06″W	1,077	12 Dec 05	Labrador	4	1
46°10′44″N–47°18′36″W	672	19 Jun 05	Newfoundland	5	1
42°56′42″N–49°35′42″W	1,210	20 Oct 05	Newfoundland	3	2
43°38′20″N–49°02′09″W	753	21 Oct 05	Newfoundland	4	0
44°57′06″N–48°47′56″W	1,227	22 Oct 05	Newfoundland	3	1
45°00′10″N–48°40′37″W	1,302	22 Oct 05	Newfoundland	3	0
45°09′18″N–48°40′04″W	1,008	22 Oct 05	Newfoundland	3	1
49°11′49″N–49°58′01″W	706	1 Nov 05	Newfoundland	4	2
44°46′01″N–55°34′01″W	958	22 Nov 05	Newfoundland	4	2
44°13′01″N–52°58′01″W	868	14 Mar 06	Newfoundland	4	0
61°36′00″N–60°22′58″W	1,194	25 Apr 06	Arctic	4	1
62°04′58″N–60°37′58″W	871	18 Jul 07	Arctic	4	1
				112	31

embedding. All were dehydrated in a series of alcohol baths (80–100%), cleared, and embedded in paraffin. Sections (5–20 μm) were mounted and stained using hematoxylin and eosin. They were examined under a Nikon Eclipse 80i microscope attached to a Nikon DXM1200F digital camera.

Gametogenic development

Gametogenic stages of development were established using terminology adapted from Waller et al. (2005). Oogenic stages were defined in all species as follows: (1) early growth (Stage I), oogonia budding from the mesenteries; (2) growth (Stages II and III), dominant presence of pre-vitellogenic oocytes and some early vitellogenic oocytes, characterized by the rapid accumulation of yolk; (3) mature (Stage IV), dominant presence of the largest vitellogenic oocytes; and (4) post-spawning (spent), characterized by the virtual absence of oocytes. Spermatogenic stages were defined in *A. grandiflorus* as follows: (1) early growth (Stage I), first visible spermatocysts, empty lumen; (2) growth (Stage II), spermatocysts larger with the presence of few spermatozoa in the lumen; (3) mature (Stage III), spermatocysts packed with spermatozoa; and (4) post-spawning (Stage IV), virtual absence of spermatocysts.

Fecundity and size at sexual maturity

The number of oocytes per polyp was counted after surgical extraction from 3 to 5 polyps in *P. resedaeformis* and *K. ornata*. As per Mercier et al. (2011) adapted from McQuaid et al. (2009), potential relative fecundity (PRF) was defined as the total number of oocytes per polyp and effective relative fecundity (ERF) as the number of mature oocytes (Stage IV) per polyp. In *A. grandiflorus*, relative

fecundity could not be established; instead, the number of planulae per 4-cm^2 was measured as an indication of reproductive potential. Only samples of *A. grandiflorus* were suitable to establish size at sexual maturity (i.e., smallest size of colony found to exhibit mature gametes), as no small gorgonians were collected. Colonies of *A. grandiflorus* as small as 0.5 cm and up to 15 cm in diameter, collected in September and October 2004 ($n = 67$), were examined for the presence of planulae.

Data analysis

Relative fecundity (PRF and ERF) and proportion of mature oocytes were compared between two depth ranges and among dates using analyses of variance (ANOVA) after verifying assumptions of normality and homogeneity of variance. Where the latter were not met, a Kruskal–Wallis ANOVA on ranks was used. Post hoc pairwise analysis (Tukey test) was used to compare specific groups. Relationships with sampling depth and latitude were examined using Pearson's correlation. All data are provided as Mean ± SE.

Results

The three species studied colonize hard substrata, either bedrock, scattered boulders, or pebbles that occur randomly on the muddy substratum of the bathyal zone off the coast of eastern Canada (Fig. 2a, d, g). Images taken with the ROV suggest that clumps or aggregations of several colonies of *Anthomastus grandiflorus* occur on fairly small surface areas (up to 12 ind m^{-2}). In the same ROV footage, *Primnoa resedaeformis* reached densities of 7 ind m^{-2} and *Keratoisis ornata* of 5 ind m^{-2}.

Primnoa resedaeformis

A total of 52 colonies collected in 15 trawls between northern Labrador and the Arctic from August 2005 to November 2006 were examined (Table 1). The presence of spermatocysts was never detected. Conversely, oocytes occurred in all samples, including in polyps of the thinnest branches. Oocytes (maximum diameter ~1,000 μm) were located at the base of the polyps among the tissues surrounding the axial skeleton and the gastrovascular cavity

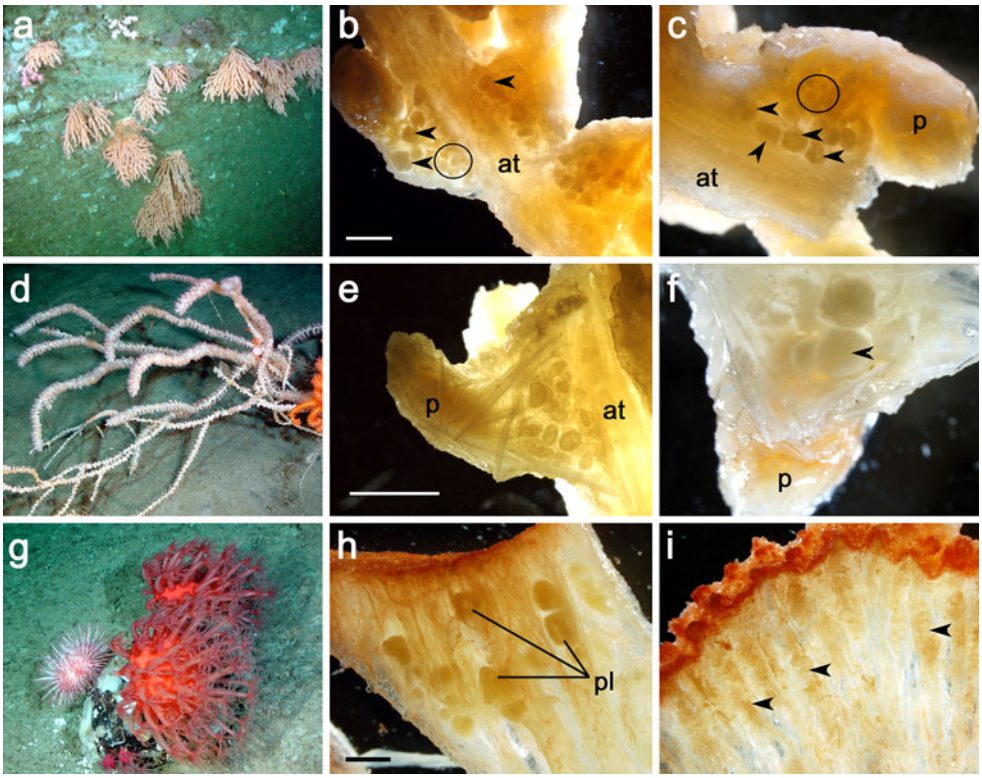

Fig. 2 **a** Colonies of *Primnoa resedaeformis* (~30 cm high). **b–c** *Primnoa resedaeformis.* Mature oocytes (*arrowheads*) and smaller size classes (*circled*) at the base of each polyp (p). **d** Colony of *Keratoisis ornata* (~80 cm high). **e** *Keratoisis ornata.* Polyp (p) with a growing number of oocytes of similar size (growth stage). **f** *Keratoisis ornata.* Fully mature stage with large vitellogenic oocytes (arrowhead). **g** Colonies of *Anthomastus grandiflorus* (~5 cm in diameter). **h** *Anthomastus grandiflorus.* Fully mature stage with planulae (pl). **i** *Anthomastus grandiflorus.* Male colony with spermatozoa (*arrowheads*). at: axial skeleton. Photographs in **a**, **d** and **g** were taken with the ROV ROPOS in July 2007 (© DFO 2007). *Scale bar* in **b** represents 5 mm in **b** and 3.3 mm in **c**. *Scale bar* in **e** represents 2.5 mm in **e** and 1.4 mm in **f**. *Scale bar* in **h** represents 2.1 mm in **h** and **i**

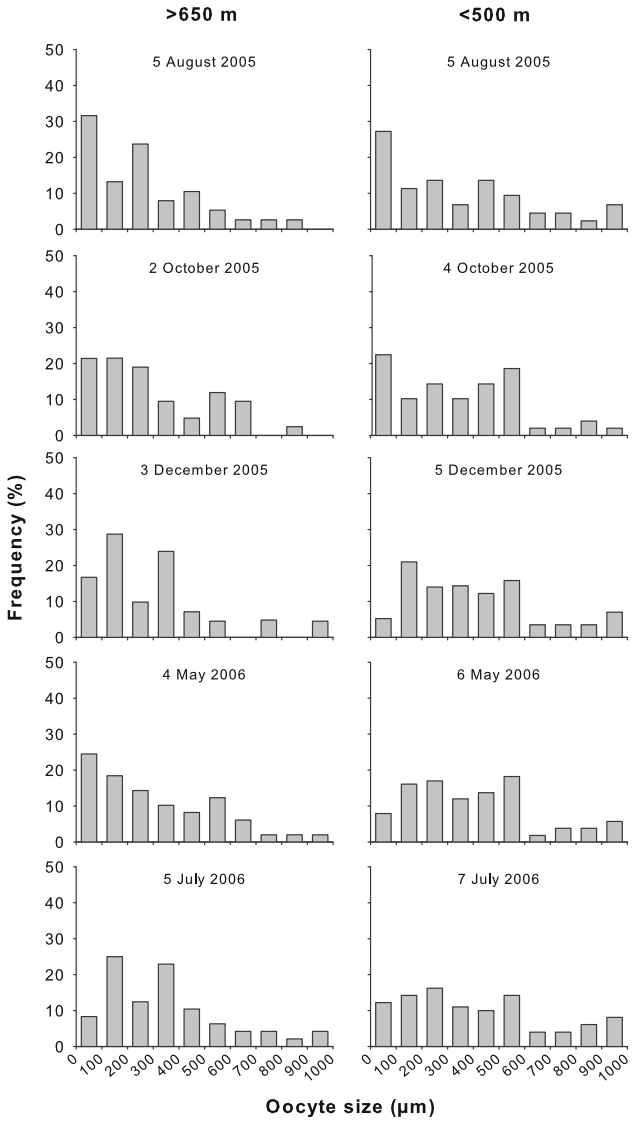

Fig. 3 Oocyte size frequency distribution in *Primnoa resedaeformis* collected at depths >650 m and <500 m between August 2005 and July 2006. Data compiled from 9 to 15 polyps in each colony. Sample size for each date and depth is provided in Table 1

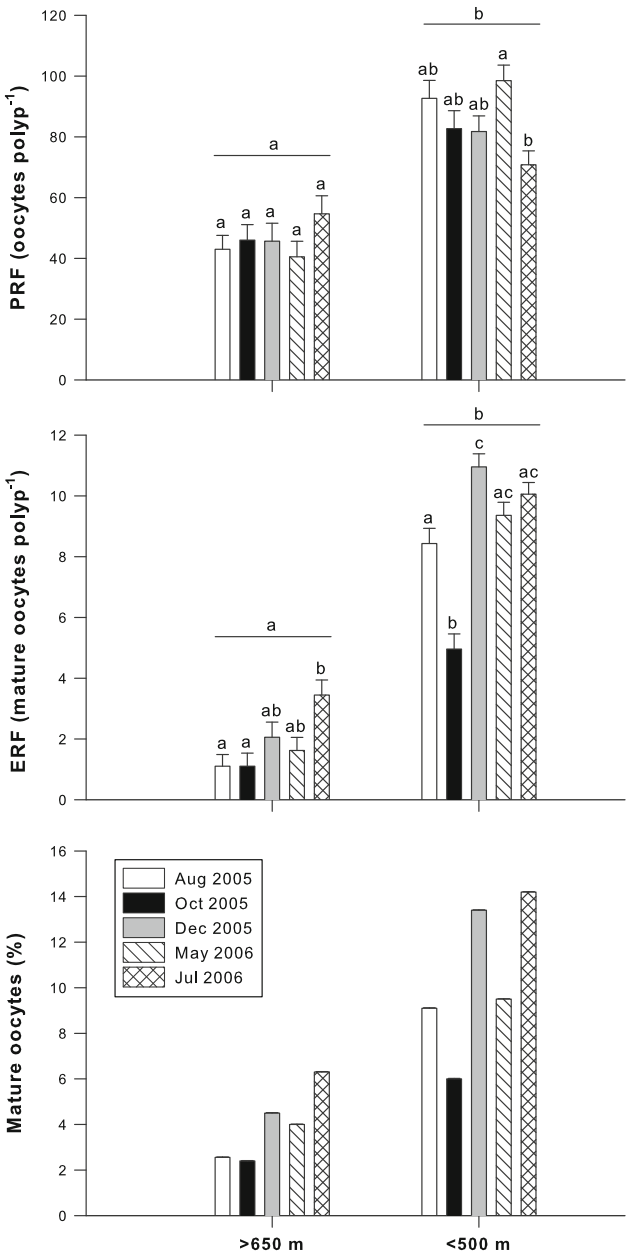

Fig. 4 *Primnoa resedaeformis*. Potential relative fecundity (oocytes polyp^{-1}; PRF), effective relative fecundity (mature oocytes polyp^{-1}; ERF), and overall proportion of mature oocytes in samples from two depth ranges collected at different times. Data for PRF and ERF are expressed as Mean ± SE. *Bars* in a group that exhibit different letters are statistically different

(Fig. 2b, c). They exhibited a yellow color that was especially pronounced in vitellogenic oocytes >500 µm. No larvae were observed.

All samples exhibited the full range of oocyte sizes with no predominant gametogenic stage established for any of the dates (Fig. 3). Dates for which deep and shallow trawls were available (Aug 2005, Oct 2005, Dec 2005, May 2006, and Jul 2006) showed an inverse correlation between proportion of mature oocytes and depth ($r = 0.73$, $P = 0.017$). Moreover, there was a clear inverse relationship between depth and fecundity, both as PRF ($r = 0.92$, $P < 0.001$) and ERF ($r = 0.78$, $P < 0.001$). Thus, further analysis was conducted using two groups for each date: shallow colonies from 176 to 466 m (i.e., <500 m) and deep colonies from 670 to 1,179 m (i.e., >650 m).

Overall, there was a positive relationship between PRF and ERF ($r = 0.84$, $P < 0.001$). A two-way ANOVA on PRF showed a significant interaction between depth range and date ($F = 4.62$, $df = 4$, $P = 0.005$; Fig. 4). Post hoc analysis indicated a significant difference between the two depth ranges ($P < 0.001$) and between May 2006 and July

2006 in samples <500 m ($P = 0.003$), although the latter samples were at either extremes of this depth range (176 and 466 m). An average of 84.3 ± 3.1 oocytes polyp^{-1} (with a maximum of 107) was observed in colonies collected <500 m compared to 45.5 ± 1.7 oocytes polyp^{-1} (maximum of 65) in colonies from greater depths (Fig. 4). For ERF, a two-way ANOVA also showed a significant interaction between depth range and date ($F = 8.30$, $df = 4$, $P < 0.001$). ERF was significantly greater in samples collected <500 m (9.0 ± 0.5 mature oocytes polyp^{-1}) than >650 m (2.5 ± 0.2) and varied among dates, especially for samples <500 m, but with no clear period (Fig. 4). There was a correlation between latitude and PRF but not ERF in shallow samples ($P < 0.001$ and 0.585, respectively), whereas the inverse was noted in deep samples ($P = 0.831$ and $P < 0.001$, respectively). Sample sizes were not sufficient to further investigate these trends. The proportion of mature oocytes showed variations among dates based on a one-way ANOVA on ranks, both in shallow ($H = 18.00$, $df = 4$, $P < 0.001$) and deep colonies ($H = 28.79$, $df = 7$, $P < 0.001$). An inter-annual trend was observed, with Aug–Oct 2005 samples at both depths exhibiting significantly lower values than either July 2006 samples (shallow colonies) or July–August–November 2006 samples (deep colonies). Figure 4 illustrates a portion of this annual trend (without Aug–Nov 2006 samples that were only collected from sites >650 m).

Keratoisis ornata

A total of 47 colonies collected in 7 trawls from southern Newfoundland between March 2005 and July 2006 were examined (Table 2). No spermatocysts were found. Oocytes were located at the base of the polyps (Fig. 2e, f); they were greyish white or translucent, with a maximum diameter of ~700 µm. No larvae were observed.

Samples of *K. ornata* showed a striking variation in oocyte size frequency distribution across the monthly samples, with a clear succession of gametogenic stages, from post-spawning to maturity (Fig. 5). In 2005, gametogenesis started in March, with the first evidence of the early growth stage and an abundance of previtellogenic oocytes. The proportion of samples in the growth stage had increased in May, and the first mature colonies with the largest vitellogenic oocytes (600–700 µm) were observed in July. Between July and October, the mature stage disappeared, replaced by a mix of post-spawning, early growth, and growth stages. A similar combination was seen in December, with a slightly higher proportion of growth stage. The fewer 2006 samples followed a comparable trend with a dominance of early growth stage in March and a mix of growth and mature stages in July (Fig. 5).

The oocyte size frequency distribution showed a mode at 200 µm in March 2005 followed by a progressive increase toward a maximum recorded in July 2005 (mode at 650 µm; Fig. 6). Between July and October 2005, the mean oocyte size decreased to reach the minimum recorded during this study (~70 µm). The following months for which samples are available showed a progressive increase in oocyte sizes through July 2006 when oocytes measuring ~650–700 µm in diameter were found (Fig. 6).

A weak inverse correlation with depth was found in PRF and ERF ($r = 0.47$–0.59, $P < 0.008$). This was attributable to samples collected at 302 m in July 2005, which were removed for further analysis, narrowing the depth range to 578–958 m. Samples showed a PRF of 10–60 oocytes polyp^{-1} and an ERF of 0–10 mature oocytes polyp^{-1} with a negative relationship between the two ($r = 0.81$, $P < 0.001$). Minima in PRF and maxima in ERF occurred in May 2005 and July 2006, the only two occasions when mature oocyte (≥500 µm) occurred (accounting for 18.5 and 60.5% of oocytes, respectively). A one-way ANOVA

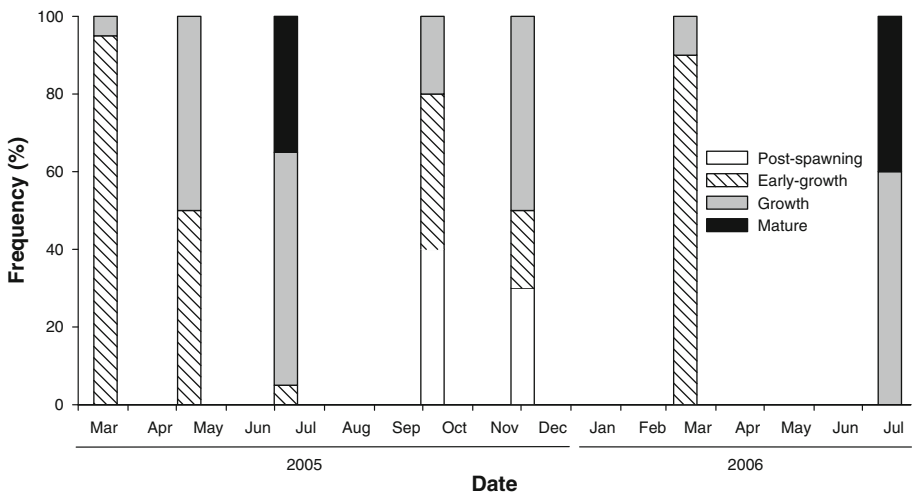

Fig. 5 *Keratoisis ornata.* Oogenic stages between March 2005 and July 2006

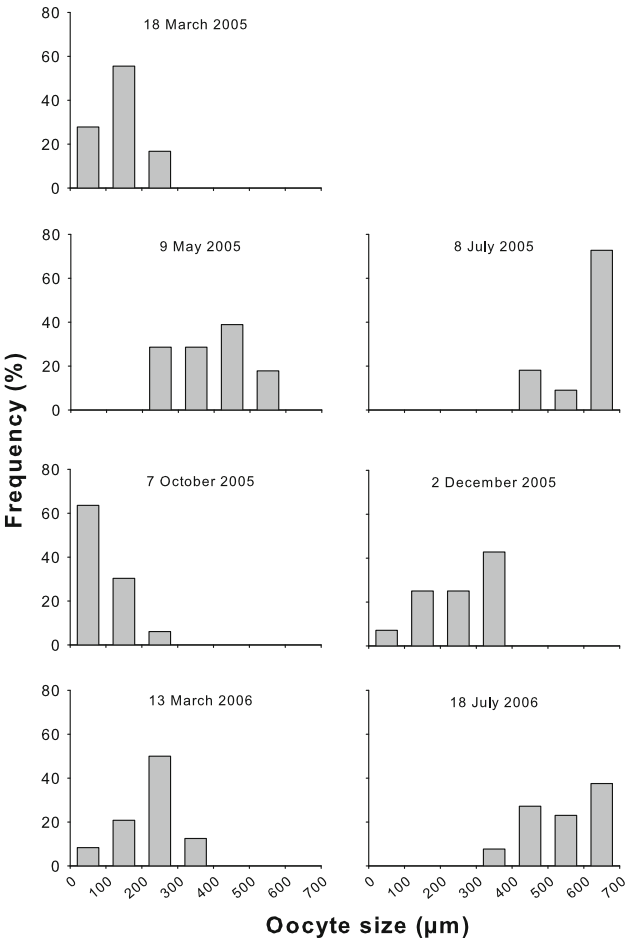

Fig. 6 Oocyte size frequency distribution in samples of *Keratoisis ornata* collected between March 2005 and July 2006. Data compiled from 9 to 15 polyps in each colony. Sample size for each date is provided in Table 2

confirmed that PRF varied significantly ($F = 48.80$, $df = 5$, $P < 0.001$); in May 2005, it was lower than for all other dates ($P < 0.005$) except December 2005 and July 2006, whereas July 2006 had the absolute lowest values ($P < 0.001$).

Anthomastus grandiflorus

A total of 112 female and 31 male colonies collected between the Arctic and southern Newfoundland from May 2004 to December 2005 were investigated (Table 3). Males and females (Fig. 2h, i) were identified, with a sex ratio of ~1:4 in favor of females. Both oocytes and brooded planulae occurred in the mesenteries of females (Fig. 2h). Oocytes were a translucent red. The largest vitellogenic oocytes and planulae had a maximum diameter of 1,000–1,100 µm. The smallest sexually mature colonies (composed of five polyps) weighed ~1.5 g wet weight in males and ~1.7 g in females. Due to the greater sample size obtained from Labrador, analyses were concentrated on this sector, unless otherwise indicated.

Gametogenic development followed a similar trend in males and females (Fig. 7). Spring and summer samples contained colonies mostly in the early growth and growth stages. In 2004, colonies in the mature stage (with late vitellogenic oocytes, or abundant spermatozoa in spermatocysts) appeared in June, became more abundant in September, and peaked at ~30–50% in October. In females, planulae were first detected in September and reached peak abundance (15.0 ± 1.0 larvae per 4 cm^2) in October (Fig. 7). May and October samples of 2005 were comparable to those of corresponding dates in 2004 in both sexes. Females from November 2004 and January 2005 and from November to December 2005 were empty of larvae and were characterized as post-spawning (Fig. 7). Spent males with residual gametes were found in November of 2004 and 2005 as well as in December 2005.

A slight shift in the reproductive cycle was apparent when comparing the oocyte size structure in samples from the different areas. In 2004–2005 off Labrador, full maturity (i.e., presence of the largest vitellogenic oocytes) was recorded between September and November, post-spawned (spent) colonies from mid-November to mid-January, and new cohorts of oocytes appeared between January and May (Fig. 8). Post-spawned colonies occurred earlier off Newfoundland (from October; Fig. 9). In that same area, new generations of oocytes appeared in March and mature oocytes in October (Fig. 9). Samples from the Arctic yielded empty colonies in April and showed the presence of new cohorts of small oocytes in July (Fig. 9), but finer investigation was hampered by low sample sizes.

Discussion

The findings presented here on the reproduction of *Primnoa resedaeformis, Keratoisis ornata*, and *Anthomastus grandiflorus* provide insights into the various reproductive strategies exhibited by sympatric deep-sea corals belonging to the same order (Table 4). The mix of brooding and free-spawning modes and the different gametogenic periodicities emphasize the absence of any universal latitudinal or bathymetric trend. Together with recent work (Waller 2005; Orejas et al. 2007), it further challenges the early prediction that aperiodic broadcast spawning would predominate in deep-sea invertebrates (Orton 1920). Conversely, this study supports the assumption made by Young (2003) that seasonal reproduction should be common in bathyal species that might rely on the downward flux of surface production. Interestingly, the brooding species was determined to occur twice as often as either of the

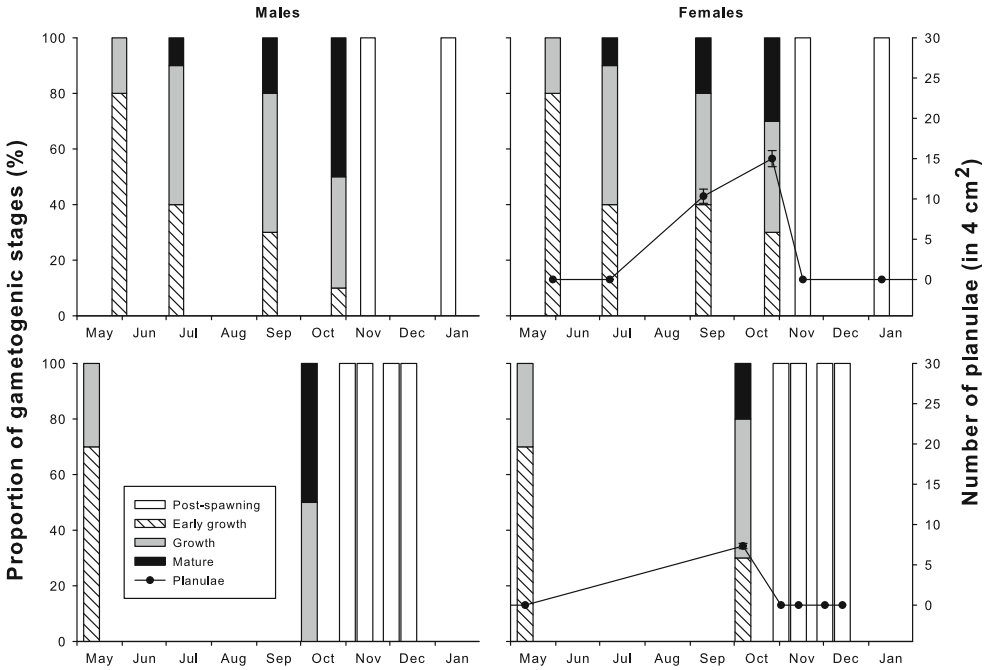

Fig. 7 *Anthomastus grandiflorus*. Proportion of gametogenic stages and number of planulae (Mean ± SE per 4 cm^2) in samples collected along the continental slope of Labrador. The *upper panel* shows data from May 2004 to January 2005 and the *lower panel* from May 2005 to January 2006. For the sake of clarity, samples collected between November 14 and November 17, 2004, were pooled together

free-spawning species in trawl samples from the same geographical area (Wareham and Edinger 2007).

It is clear from this study that *A. grandiflorus* is a gonochoric internal brooder, and almost certain that *P. resedaeformis* and *K. ornata* are broadcast spawners. The planulae observed in *A. grandiflorus* and the size of oocytes in the two other species are consistent with nonfeeding (lecithotrophic) larval development. Data available in the literature tend to show that octocorals exhibit continuous gametogenesis, internal fertilization, and brooding more frequently in temperate waters, whereas tropical representatives studied to date more often display short seasonal spawning periods with external fertilization (reviewed by Hellström et al. 2010). Although studies on cold-water octocorals from the deep sea remain scarce, current findings do not fully agree with this hypothesis. The gorgonian *Acanella arbusculata* from 2200 m in the northeast Atlantic displayed seasonal oogenesis and was proposed to brood based on large oocytes (730 μm) despite the absence of planulae (Lawson 1991). Cordes et al. (2001) determined that *Anthomastus ritteri* collected at 300–450 m depth in the northeast Pacific was a gonochoric brooder and did not find any evidence of periodic reproduction based on a limited number of histological sections and monitoring of 8 live colonies. Evidence of annual and monthly patterns of larval release was found in several brooding nephtheids of the genera *Drifa*, *Duva*, and *Gersemia* collected at ~100–1,250 m depth in the northwest Atlantic (Sun 2009; Sun et al. 2010a, b). This was based on the investigation of serial samples over 3 years and the long-term monitoring of planulation patterns in the laboratory. Studies of Antarctic gorgonians from 250 to 600 m depth using samples collected over a few weeks in two or three different years provided evidence of free spawning and brooding with no clear gametogenic patterns, although the occurrence of periodic, possibly annual, gamete, or larval release was suggested for some species (Orejas et al. 2002, 2007).

In the present study, one brooder (*A. grandiflorus*) and one broadcaster (*K. ornata*) showed evidence of seasonal reproduction. The third species (*P. resedaeformis*), also a broadcaster, showed a co-occurrence of all gametogenic stages in the available samples, providing no evidence of periodic reproduction. Conclusions for this species must be drawn cautiously as sampling intervals might have prevented the observation of a reproductive peak, which may be brief and/or restricted to a small portion of the population. While intra-colony variations in the reproductive status of the different polyps, as observed in an Antarctic gorgonian (Orejas et al. 2002), could mask a periodicity, evidence points to uniform oogenic development in the species studied here. Depth-dependent factors are most probably at play since major differences in relative fecundity were found across samples of *P. resedaeformis*: shallower colonies produced roughly twice more oocytes per polyp than deeper colonies, possibly because of limiting food sources at greater depths. Reduced allocation to reproduction with depth would fit the hypothesis of a depth-related shift along the *r*–*K* continuum, as suggested from studies on deep-sea molluscs (Scheltema 1972; Rex 1979) and asteroids (Mercier and Hamel 2008).

Free-spawning corals often participate in synchronized mass-spawning events that possibly serve to reduce predation pressure on newly spawned gametes in the reef environment (Alino and Coll 1989). Synchronous

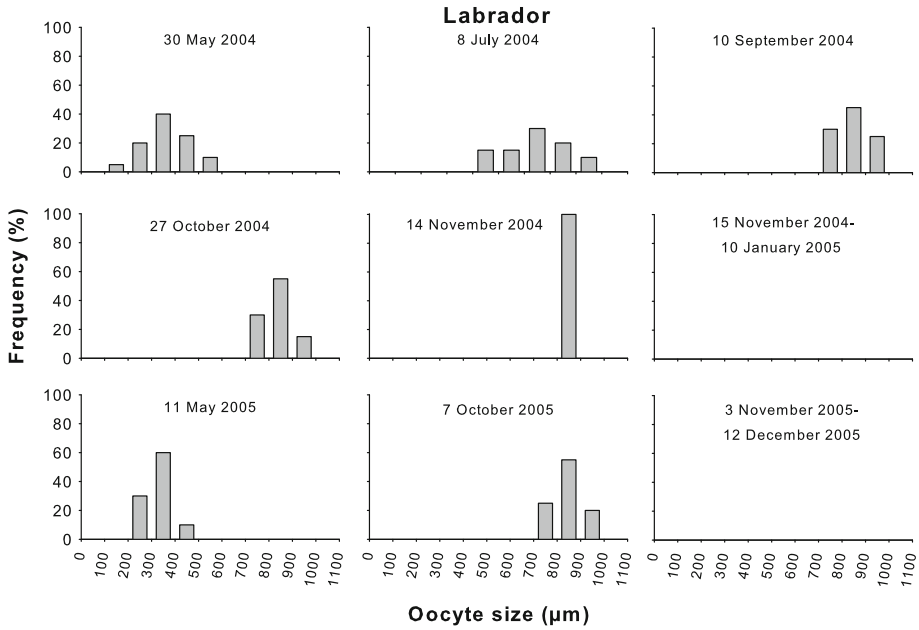

Fig. 8 *Anthomastus grandiflorus*. Oocyte size frequency distribution in samples collected along the continental slope of Labrador between May 2004 and December 2005. Data compiled from 3 subsamples of each colony. Sample size for each date is provided in Table 3. An empty graph denotes the absence of oocytes (i.e., post-spawning) in samples from the indicated interval. Note that oocytes in samples of November 14, 2004, were very rare (residual)

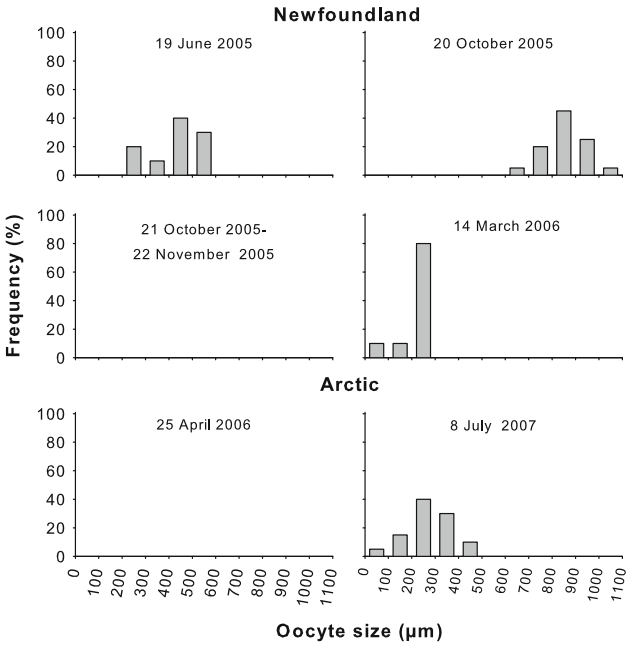

Fig. 9 *Anthomastus grandiflorus*. Oocyte size frequency distribution in samples collected off Newfoundland between June 2005 and March 2006 and in the Arctic in April 2006 and July 2007. Data compiled from 3 subsamples of each colony. Sample size for each date is provided in Table 3. An empty graph denotes the absence of oocytes (i.e., post-spawning) in samples from the indicated interval

spawning episodes are also likely to enhance reproductive output by favoring fertilization success (Coma and Lasker 1997). In this context, it may be argued that synchronous breeding is not as important among brooders, in which gametes are retained inside or on the colony until fertilization occurs. Nevertheless, synchronously breeding brooders do occur as presented in this and other studies (Alino and Coll 1989; Coma et al. 1995). Babcock (1990) proposed that brooding may help offset low fecundity by providing a refuge from predation and thus favoring the survival of larvae. Although it remains unclear how reproductive strategies in octocorals may be influenced by selective pressures or dictated by phylogenetic constraints, it is probable that both brooding and free spawning confer certain advantages, especially in different environments.

In the present study, *A. grandiflorus* exhibited a sex ratio that was significantly biased toward females (~4:1). Reports of similarly biased sex ratios exist for temperate octocorals (Ben-David-Zaslow et al. 1999; Gori et al. 2007), although the opposite is also observed (Gori et al. 2007; Hwang and Song 2007). The fact that males were not detected in *P. resedaeformis* and *K. ornata* may suggest that spermatogenesis in these species is localized or transient. The absence or episodic presence of male colonies has been documented in deep-sea scleractinians (Waller and Tyler 2005). Alternatively, *P. resedaeformis* and *K. ornata* may exhibit a sex ratio strongly biased toward females, as shown here in *A. grandiflorus* and in other deep-sea alcyonaceans from Newfoundland (Sun et al. 2009, 2010a, b). Antarctic alcyonaceans were also reported to be gonochoric, but with roughly equal proportions of male and female colonies (Orejas et al. 2002, 2007). The available literature confirms that free-spawning alcyonaceans are primarily gonochoric (Hwang and Song 2007; Ribes et al. 2007). Strongly biased sex ratios such as that of *A. grandiflorus* (and possibly *P. resedaeformis* and *K. ornata*) may have a great incidence on reproductive

Table 4 Summary table of reproductive traits and occurrence patterns in the three sympatric octocorals

Species (family)	Sex ratio	Reproductive mode	Reproductive periodicity	Larval type	Reproductive potential[a]	Maximum density	Level of occurrence[b]
Primnoa resedaeformis (Primnoidea)	No males found	Broadcast spawning	No evidence	Nonfeeding (inferred)	PRF = 30–107 (varies with depth)	7 ind m^{-2}	28
Keratoisis ornata (Isididae)	No males found	Broadcast spawning	Annual	Nonfeeding (inferred)	PRF = 10–60	5 ind m^{-2}	30
Anthomastus grandiflorus (Alcyoniidae)	Female biased (~4:1)	Brooding	Annual	Nonfeeding	Max. ~15 larvae per 4-cm^2 section	12 ind m^{-2}	65

[a] PRF refers to potential relative fecundity (oocytes $polyp^{-1}$)

[b] Number of bycatch samples showing the presence of the species in the study of Wareham and Edinger (2007)

success, especially in species with low densities. Typically aggregated distributions were observed with the ROV for the three species studied. Such clumps may be the product of larval strategies and are likely to favor fertilization success, especially when combined with high fecundity. In the two free-spawning species, average potential and effective fecundities (per polyp) were 39 oocytes and 3 mature oocytes in *K. ornata*, and 84 oocytes and 9 mature oocytes in *P. resedaeformis*. Potential colony fecundity in *P. resedaeformis* based on polyp density (Mortensen and Buhl-Mortensen 2005) for a colony of ~30 cm thus ranged between 100,000 and 250,000 oocytes, depending on depth. While large variations in polyp size and slight discrepancies in measurements may obscure comparisons, this is at the high end of gorgonian fecundity (Zeevi Ben-Yosef and Benayahu 1999; Orejas et al. 2002; Santangelo et al. 2003).

Environmental factors have been shown to mediate the synchronization and coordination of gametogenesis and spawning in several marine invertebrates, including corals. Reproductive periodicities influenced by environmental cues are well known in scleractinians (e.g., Fadlallah 1983; Fan et al. 2002, 2006; Heltzel and Babcock 2002; Zakai et al. 2006). In tropical and temperate octocorals, reproductive activity has been correlated with temperature, lunar cycles, and resource availability (Ben-David-Zaslow et al. 1999; Gori et al. 2007; Hwang and Song 2007; Ribes et al. 2007). Evidence of the influence of primary productivity and lunar phases on peak planulation events also exists for brooding alcyonaceans from the deep (Mercier et al. in press; Sun et al. 2010a).

In *Keratoisis ornata* studied here, the progressive increment in the size of oocytes over time strongly supports the assumption that gametogenesis is mediated by environmental factors. The onset of gametogenesis seemed to occur early in the year, no later than March, when day length and seawater temperature start to increase. The putative spawning in late summer and fall coincided with the warmest seawater temperature of the cycle (June-November) and with high rates of detritic matter deposition (September–October) (Sun et al. 2010a). Interestingly, the number of oocytes at the onset of gametogenesis was greater than the effective number of vitellogenic oocytes found along the mesenteries at maturity. In other words, potential relative fecundity was inversely related to effective relative fecundity, inferring that 'supernumerary' gametes (i.e., that do not mature) may provide nutrients to few developing oocytes.

Slightly shifted breeding periods across latitudes similarly suggest that the reproductive cycle of *A. grandiflorus* could be influenced by environmental factors. Off Newfoundland and along Labrador, oogenesis started in the spring; the colonies were determined to release larvae from early October in the southernmost locations and from November in northern areas. A correlation with peak seawater temperatures and the fall primary and secondary production can be made as peaks in those parameters spread from southern to northern regions (see DFO site: http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html). In the Arctic, evidence of early oogenesis in July suggests that it is triggered by the summer productivity peak; planulation cannot be accurately determined but the April samples were spent.

The reproductive cycle of *A. grandiflorus* can be broken down into clear periods of gametogenic development, full maturity, and spent stage. All mesenteries examined displayed a synchronous development, whereby the gametes present at a given time were roughly of the same size. Gametogenic stages, oocyte size frequency distributions, and abundances of planulae suggest a seasonal maturation of gametes starting in early winter and leading to planulation in summer and/or fall. The virtually empty mesenteries post-spawning infer that the vast majority of gametes matured and were fertilized, and that all larvae were released at the culmination of the reproductive cycle. Colonies reached maturity (i.e., presence of late vitellogenic oocytes and spermatozoa) a few months before planulae appeared in females, consistent with internal fertilization preceding brooding. Planulation appears to occur when seawater temperature reaches its annual maximum

and/or as it starts to drop again in mid-fall (Sun et al. 2010a). The fall and/or summer breeding could also be related to the delayed downflux of primary and secondary production to deeper waters. The fact that abundance of planulae did not match that of oocytes at the peak of maturity in *A. grandiflorus* suggests that only part of the latter are ultimately fertilized. The surplus may serve as an energy reserve to sustain gamete growth and other metabolic needs, or it may indicate dual brooding and broadcasting, as reported in some corals (Fautin 2002).

The presence of all size classes of oocytes of *P. resedaeformis* in a given colony from all depths, locations, and months studied could suggest the occurrence of continuous gametogenesis. Conversely, it might be due to overlapping cycles of oogenesis, similar to what has been observed in two Antarctic species from the same family, i.e., Primnoidea (Orejas et al. 2007) and in other aclyonaceans from the Mediterranean Sea (Ribes et al. 2007) and South Africa (Kruger et al. 1998). Data presented here on the proportion of mature oocytes are consistent with partial spawning and tend to show a build up toward major events at intervals greater than a year. Alternatively, it is not impossible that spawning occurs on an opportunistic basis when proper conditions align.

An analysis of bycatch samples from Newfoundland and Labrador (Wareham and Edinger 2007) yielded the following order of occurrence for the three species studied here: *Anthomastus grandiflorus* ($n = 65$) > *Keratoisis ornata* ($n = 30$) ~ *Primnoa resedaeformis* ($n = 28$). The most widely occurring was *A. grandiflorus* with records from the shelf edge and slope of the southern Labrador Shelf, northeast Newfoundland Shelf, and the Grand Banks at depths of 171–1,404 m. Small colonies of *A. grandiflorus* ($n = 541$) were also documented on the northeast side of the Flemish Cap (data in Wareham and Edinger 2007). *Keratoisis ornata* occurred on the southwest Grand Bank at 195–1,262 m depth, whereas *P. resedaeformis* was found at 162–1,157 m depth, mostly off Saglek Bank, with occurrences on the Labrador Shelf. The latter species dominated in certain gorgonian clusters, e.g., off Cape Chidley (Wareham and Edinger 2007), consistent with previous reports in the same location (MacIsaac et al. 2001; Gass and Willison 2005). Video transects off Nova Scotia also showed higher occurrences of *A. grandiflorus* than *P. resedaeformis* and *K. ornata* at the Stone Fence (twofold to threefold difference), whereas comparable occurrences were noted at The Gully (Mortensen et al. 2006). Average densities from the same video records ranged from 0.1 to 1.0 colonies per 100 m^2 for the three species (Mortensen et al. 2006). Peak density measured by Mortensen and Buhl-Mortensen (2004) for *P. resedaeformis* was 104 colonies per 100 m^2, whereas ROV images in the present study showed up to ~5 ind m^{-2}. Fragmentary data from the northeast coast of the United States indicate that *P. resedaefromis* is well distributed from shelf waters to the upper continental slope, the genus *Anthomastus* is mostly distributed in deep waters >500 m, and *K. ornata* is also present (Watling and Auster 2005). In the Aleutian Islands, species of the genus *Anthomastus* were found in 36% of 25 transects surveyed by a submersible over 26,597 m^2 of seafloor at depths of ~100–350 m (Stone 2006). They were also found in dense patches of >10 colonies m^{-2} at shallower sites to 30 m. The same study reported that a species of *Primnoa* (*P. wingi*) was observed at only three locations at 304–334 m depth.

Based on the available data (Wareham and Edinger 2007), the most widely distributed species studied here is *A. grandiflorus*, which is a gonochoric annual brooder (Table 4). This is somewhat contrary to the general belief that brooding species disperse less effectively than free-spawning species, although it is becoming apparent that the relationship between reproductive mode and dispersal is far from straightforward (Ayre and Hughes 2000; Miller and Ayre 2008; Jones et al. 2009). A recent review of tropical scleractinian corals found abundant brooders in the Atlantic and hypothesized that this was due to brooded larvae being typically autotrophic and having greater capacity for dispersal than lecithotrophic larvae (Baird et al. 2009). This assumption does not hold in deep-sea corals, which do not possess autotrophic larvae. Other factors that may affect dispersal and recruitment include larval behavior, habitat type, and adult distribution. Observed patterns of recruitment in given species may therefore be difficult to interpret. For instance, abundant new colonies of *P. resedaeformis* were observed on the northeast coast of the United States (Watling and Auster 2005), whereas in the Gulf of Alaska no recruits were found 7 years after colonies were removed by trawling and six recruits were found 1 year after trawling in another site (Krieger 2001). Small recruits of *P. resedaeformis* and *K. ornata* were never observed during the present study, but minute *A. grandiflorus* were found. It is important to note that measures of occurrence in sea fans (*P. resedaeformis* and *K. ornata*) may be biased by their sensitivity to bottom trawls. Hence, data from fished areas, such as in the work of Wareham and Edinger (2007) might not reflect their natural abundance as well as that of morphologically compact species like *A. grandiflorus*, which are presumably less impacted by trawls. Given the difficulties associated with accurately measuring both distribution and reproductive patterns in deep-sea corals, reconciliation between these two variables remains difficult to achieve.

What is clear is that deep-sea corals are submitted to a growing number of pressures, including fisheries and oil prospection (Roberts 2002; Roberts and Hirshfield 2004; Rogers 2005), emphasizing the need to further investigate

the level of their vulnerability and resilience to natural and anthropogenic disturbances. Better knowledge of reproductive strategies and periodicities in deep-sea corals will hopefully help strengthen and expand the overall understanding of these keystone habitats, providing a framework for future studies and conservation programs.

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