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Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord, Norway

Sandra Brooke · Johanna Järnegren

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Abstract Between 2002 and 2008, samples of the cold-water scleractinian coral *Lophelia pertusa* were collected from the Trondheim Fjord in Norway to examine reproductive periodicity. Collections were made from three locations: Tautra, (63°35.36′N, 10°31.23′E at 40–70 m), Stokkbergneset (63°28.18′N, 09°54.73′E at 110–500 m), and Røberg (63°28.88′N, 09°59.50′E at 250 m). Populations of *L. pertusa* from the Trondheim Fjord initiated oogenesis in January and spawning occurred from late January to early March the following year. Gametogenic cycles of the female *L. pertusa* samples overlapped by approximately 2 months, with oogonia visible in January, but this was not evident in the males. This paper provides the most complete gametogenic cycle to date and spawning observations for this important structure-forming species. The results from fjord populations are compared with published and preliminary data from other regions and are discussed in the context of regional differences in physical and biological variables, particularly food supply. Differences in gametogenic cycles within a single species provide a rare opportunity (especially in deep-sea species) to examine potential drivers of reproduction.

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S. Brooke (✉)
Oregon Institute of Marine Biology,
63466 Boat Basin Road,
Charleston, OR 97420, USA
e-mail: sandra.brooke@marine-conservation.org

J. Järnegren
Norwegian Institute for Nature Research (NINA),
7485 Trondheim, Norway

Introduction

The most widespread and extensively studied of the cold-water, reef-building scleractinian corals is *Lophelia pertusa* (Linnaeus 1758). This branching stony coral colonizes hard substrata and can form large complex structures, generally at upper slope depths of 200–600 m. The highest known densities of *L. pertusa* ecosystems occur in the North Atlantic Ocean, along both eastern and western continental margins, and these have provided the basis for most of the current knowledge of the biology and ecology of cold-water corals (Rogers 1999; Freiwald and Roberts 2005; Ross and Nizinski 2007; Brooke and Schroeder 2007; Roberts et al. 2009). Some of the most extensive *L. pertusa* ecosystems occur along the mid-Norwegian shelf and slope at 200–400 m depths (Mortensen et al. 1995; Freiwald et al. 2002; Fosså et al. 2002; Hovland 2008). Norway is home to both the largest and the shallowest documented *L. pertusa* communities; the Røst Reef was discovered in 2002 and is over 40 km long (Thorsnes et al. 2004), whereas the shallowest documented (39 m) *L. pertusa* communities were discovered decades earlier in the Trondheim Fjord (Strømgren 1971).

Cold-water coral ecosystems are threatened globally by anthropogenic activities, such as bottom-fishing, energy industry activities, and the effects of climate change. Highly localized nutrient input from terrestrial discharge (Johannessen and Dahl 1996) and mariculture operations (Asche et al. 1999) may also damage Norway's shallow fjord coral ecosystems. These threats may result in direct physical damage as from bottom fishing (Koslow and Gowlett-Jones 1998; Rogers 1999; de Juan and Lleonart 2010; Clark and Tittensor 2010), mortality from sediment and toxins (Loya and Rinkevich 1979; Rinkevich and Loya 1979; Rogers 1999; Brooke et al. 2009; Larsson and Purser

2011), changes in calcification from reduced aragonite saturation state (de Putron et al. 2011) or proliferation of coral-encrusting organisms such as sponges (J. Jarnegren, pers. obs.). The tolerance of these deep-sea coral ecosystems to environmental variability is poorly understood (Pandolfi et al. 2011), nor is there adequate information on their ability to recover from natural or anthropogenic damage. Assuming availability of suitable substrate and appropriate environmental conditions, re-colonization of damaged *L. pertusa* reefs will be strongly influenced by the reproductive output (fecundity) of the adult coral and the dispersal, recruitment and post-settlement survival of the coral larvae (planulae). Understanding connectivity among these deep ecosystems is imperative for effective management, and yet with the exception of a few species (Brooke and Young 2003; Burgess and Babcock 2005; Waller and Tyler 2005), little is known of the reproductive and larval biology of cold-water reef-building species (Roberts et al. 2009; Morrison et al. 2011).

Colonial scleractinian corals grow via asexual replication of polyps, which in *L. pertusa* occurs by unequal intratentacular budding (Cairns 1979, 1995; Roberts et al. 2009). Uncommon modes of asexual reproduction, such as polyp bail-out and parthenogenesis, have been documented for shallow-water corals (Sammarco 1982; Krupp 1983; Stoddart 1983; McFadden et al. 2001; McFadden and Hutchinson 2004), but have not been reported for any cold-water scleractinian species. Many species of coral can also reproduce through fragmentation where pieces of the parent colony break off through mechanical stresses and continue to grow, thereby establishing new colonies that are genetically identical to the parent colonies (clones) (Highsmith 1982). Fragmentation, however, does not account for the establishment of new widely separated coral ecosystems, nor is it a mechanism for genetic exchange between established ecosystems; these require dispersive planktonic larvae produced through sexual reproduction (Harrison 2011). Most of the research on coral reproductive biology has focused on shallow tropical reef-dwelling corals (see reviews by Fadlallah 1983; Baird et al. 2009; Harrison 2011), whereas corals living in temperate, cold, and deep habitats have been neglected by comparison. Although scientific and conservation interests in cold-water corals have expanded rapidly, information on their basic life history patterns is still lacking, partly because obtaining samples throughout the year from cold-water coral ecosystems poses significant logistical challenges. Information on 444 species of scleractinians indicates that hermaphroditic broadcast spawning of gametes is the dominant fertilization mechanism (Harrison 2011). To date, all cold-water, structure-forming scleractinians are also broadcast spawners, but appear to be gonochoristic rather than hermaphroditic (Brooke and Young 2003; Burgess and Babcock 2005; Waller 2005; Waller and Tyler 2005). The duration of larval life is unknown for cold-water scleractinians, with one exception. Laboratory studies on *Oculina varicosa*, a shelf edge scleractinian species that forms large bioherms off the Florida Atlantic coast, documented a larval lifespan of approximately 14–21 days (Brooke and Young 2005).

Despite a proliferation of research in the last decade, information on the reproductive biology of *L. pertusa* was not published until quite recently. Using samples collected from the northeast (NE) Atlantic in March, July, August, September, and October, Waller and Tyler (2005) reported a seasonal reproductive cycle with one cohort per year, culminating in a spawning event, probably in February. They also reported equivocal information on gametogenic cycles of *M. oculata,* suggesting two cohorts per year. In contrast to structure-forming colonial species, which appear to be uniformly gonochoristic broadcast spawners, cold-water solitary scleractinians, such as *Flabellum* sp., (Waller and Tyler 2011; Mercier et al. 2011), *Caryophyllia* sp. (Waller et al. 2005), and *Fungiacyathus* sp. (Waller et al. 2002; Flint et al. 2007), have various reproductive strategies, including hermaphroditism, gonochorism, brooding, and broadcast spawning. The evolutionary significance of these differences is not clear, but larger eggs generally represent a larger maternal investment in the offspring and shorten the larval life and need for an exogenous food supply (Strathmann 1985; Havenhand 1993). *Lophelia pertusa* has a widespread distribution and can colonize hard substrata in many different habitat types (including oil rigs, shipwrecks, fjords, seamounts, and continental shelves and slopes), over a relatively large temperature range (4–14 °C). Recent genetic work on this species has shown that populations in the North Atlantic are relatively isolated, indicating some limit to dispersal potential (Morrison et al. 2011). More work is needed on larval dynamics and physical oceanography models to resolve the apparent contradictions between the widespread distribution of this species and the relatively limited dispersal rates derived from population structure.

This manuscript presents new data on the reproductive periodicity of *L. pertusa* using samples from the Trondheim Fjord in Norway. The sheltered conditions and relatively shallow depths of the fjord permitted a more complete temporal sampling and description of gametogenesis than was previously possible. This data provide detailed information on initiation of gametogenesis, periods of maximum yolk deposition (vitellogenesis), and timing and duration of spawning for this important structure-forming species.

Materials and methods

Field sampling

Situated in the middle of Norway's west coast, the Trondheim Fjord is located between 63°30′–64°N and 09°30′–11°30′E, is 135 km long, and has a maximum depth of 617 m (Fig. 1). The fjord is fed by six large rivers (Smelror 2000) and is typically U-shaped in cross section, with steep walls and a flat base. The fjord is comprised of three basins separated by relatively shallow sills (100–195 m) (Jacobson 1983). The deeper water layers are a mixture of Atlantic Ocean water and the Norwegian Coastal Current, and during late winter and early spring, high salinity water penetrates the deeper parts of the fjord. Current speeds, which to a large extent are tidally driven, reach up to 1.0 m s^{-1} at the sills (Jacobson 1983).

Three different study sites were sampled within the fjord: Tautra (63°35.36′N, 10°31.23′E) at 40–70 m, Stokkbergneset (63°28.18′N, 09°54.73′E) at 110–500 m, and Røberg (63°28.88′N, 09°59.50′E) at ~250 m depth (Fig. 1). The Tautra reef is a shallow sill-reef consisting of large, abundant, and compact cauliflower-shaped *L. pertusa* colonies (Fig. 2a). At Stokkbergneset and Røberg, the coral colonies are attached to the steep rock walls and hang from the vertical faces or beneath overhangs, creating dense elongated structures (Fig. 2b). On these walls, live *L. pertusa* was found from 100 m to near the base of the wall at 500 m. Adjacent to the base of the wall are piles of predominantly dead coral colonies, molluscs, sponges, and other fauna that have fallen from the wall onto the soft sediment.

Collections were made using the R/V *Gunnerus* and the remotely operated vehicle (ROV) *Minerva*, owned by the Norwegian University of Science and Technology (NTNU). The ROV can operate to depths of 700 m and is equipped with four cameras and two manipulator arms (one 5 function hydraulic and one single function electric). The ROV navigation system is the Ultra-short Baseline system Kongsberg HiPAP 500, with EIVA NaviPac and CMAP maps. A total of 30 separate cruises were conducted between November 2002 and March 2008. Fragments of 76 different colonies from the three study sites were processed for histology. Most of the samples were collected from Tautra (16 site visits, 44 samples, depth range 44–120 m), followed by Stokkbergneset (6 site visits, 27 samples, depth range 119–500 m), Røberg (2 site visits, 5 samples, depth range 250–396 m) (Table 1). Samples were collected from every month, except July and September, at least once during the 2002–2008 study period, with more collections focused on the months when spawning was most likely (January, February, and March).

During each collection cruise, between one and eight (mean = 3.17, SD = 1.95), samples (each consisting of 10–20 branches) were taken from different colonies. Coral samples were collected using a landing net attached to the ROV, which could accommodate only one or two samples per dive. Both of the two *L. pertusa* colony colors (orange and white) were present at all of the study sites. In order to identify each individual colony after collection, either a single colony

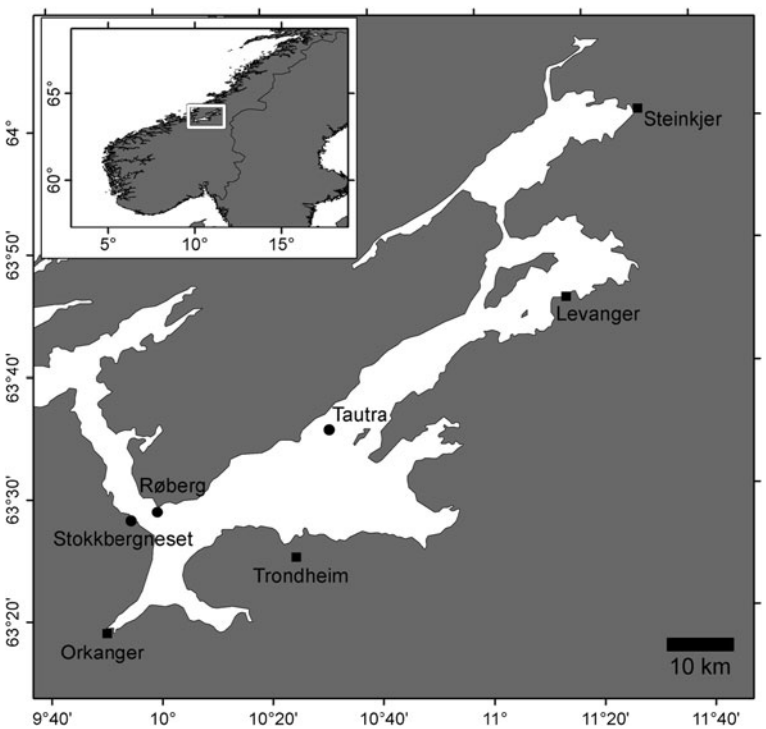


Fig. 1 Collection sites for *Lophelia pertusa* in Trondheim Fjord, Norway (indicated by *circles*): Tautra, Stokkbergneset and Røberg

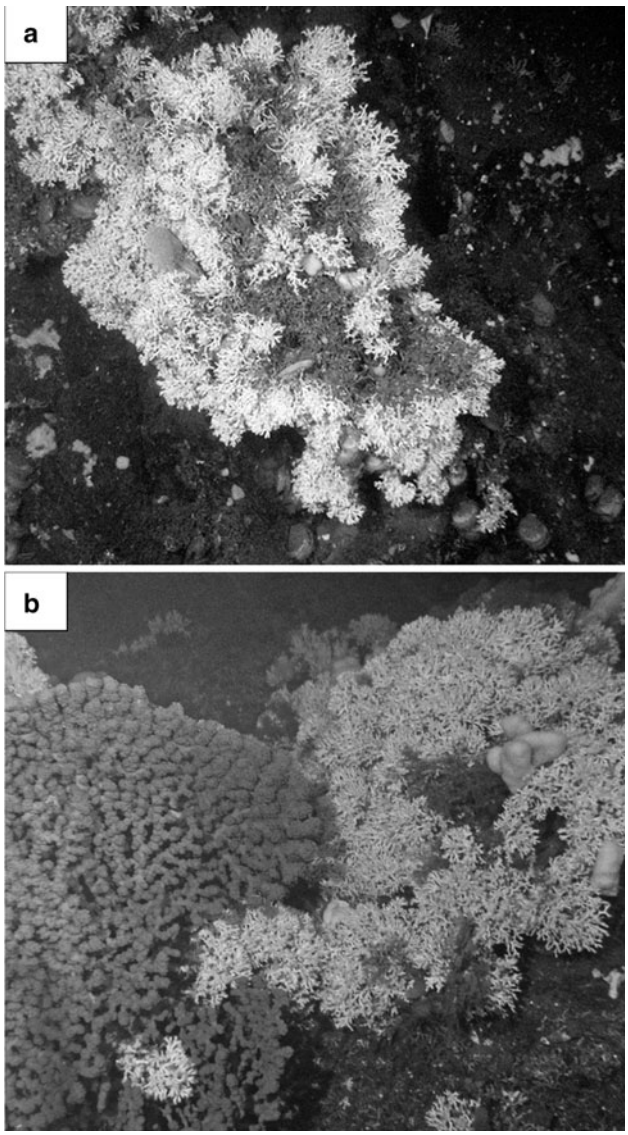


Fig. 2 **a** Colonies of *Lophelia pertusa* at the Stokkergneset study site are attached to the steep wall at ~250 m, **b** Colonies at the shallow Tautra site are clustered on the sill at <100 m

or one of each color was collected per dive. Sample colors were tracked throughout processing to assess whether there were significant differences in reproductive cycles between the two morphotypes. Gender cannot be determined in the field, but previous collections by the authors indicated that females were more prevalent than males in the fjord populations. Samples were maintained in cold (~6–7 °C) seawater until returned to NTNU, where small fragments (10–15 polyps) of each sample were preserved for histological analysis in 10 % buffered formalin solution.

Histology

Small polyps at the tips of each fragment were not used for histological examination, as they were potentially immature and non-reproductive (Rinkevich and Loya 1987). The remaining polyps (~8–10) were transferred to 5 % hydrochloric acid for 6–10 h to decalcify the skeleton, leaving the tissue intact for further processing. Polyps were rinsed briefly in distilled water and then dehydrated through a series of ethanol concentrations (70, 85, 95, 100 % × 2 changes) and transferred to a clearing agent (toluene or Histoclear©). The polyps were then embedded in paraffin wax (3–5 per block), serially sectioned into 8 µm slices, mounted on glass microscope slides, and stained using Mayer's Hematoxylin/Eosin B stains. Images of the microscope slides were taken using an Optronics digital camera attached to an Olympus BX50 compound microscope. These images were used for the description of gametogenic status for each individual coral fragment.

For each female fragment, 100 oocytes were measured from three to five polyps (occasionally more polyps were needed to meet the required number of oocytes). Only those oocytes with a visible nucleolus were measured. This ensured that the same egg was not measured more than once, as the nucleolus is small (approximately 9 µm diameter) that it only appears in one 8 µm slice. The area of each oocyte was measured and recorded using Image Tool (UTHSCSA) image analysis software. Oocyte 'feret' diameter was calculated, which uses the measured area of the oocyte and estimates the diameter is if it were a circle (Brooke and Young 2003; Waller and Tyler 2005). Feret diameters were used to generate means and standard deviations of oocyte diameters, and size–frequency distributions for each sampling date, which were then used to infer the timing of the female gametogenic cycle. The male reproductive periodicity was documented more qualitatively by developmental stage, as size of spermatocysts does not directly reflect their maturity. The male gametogenic cycle was documented by stages (after Waller and Tyler 2005) as follows: Stage I (early spermatogenesis), spermatocysts are lined with spermatocytes but lumens are empty; Stage II (maturation phase), thick layer of spermatocytes with some spermatozoa present, but with mostly empty lumens; Stage III (mature), spermatocyst lumens are filled with spermatozoa; Stage IV (post-spawn), spermatocysts are empty of spermatozoa, except occasional remnants of spawning.

Results

Gametogenesis

The samples were comprised of both males and females of each color; therefore, colony color was not an indicator of gender in *L. pertusa*. The gender ratio within the collections was unequal, with more females than males (f:m = 1.27);

Table 1 Collection data for *Lophelia pertusa* samples from the Trondheim Fjord over 6 years

Years	Date	Site	*N*	Depth (m)	Gender		
2002	November 7	Tautra	3	120	2F	1 M	
2003	June 20	Tautra	1	61		1 M	
2003	September 18	Roberg	2	365–396		2 M	
2003	October 23	Tautra	1	52	1F		
2003	November 25	Tautra	2	62–68		2 M	
2003	December 15	Tautra	1	59		1 M	
2004	January 14	Stokkbergneset	1	283	1F		
2004	January 15	Tautra	1	75	1F		
2004	February 9	Tautra	3	79–86	3F		
2004	February 17	Tautra	1	82	1F		
2004	April 30	Tautra	3	40–45	3F		
2004	May 25	Tautra	3	50–52		3 M	
2004	June 22	Tautra	3	56–70	1F	2 M	
2004	August 25	Stokkbergneset	4	250–500	2F	2 M	
2004	October 21	Stokkbergneset	3	250	2F	1 M	
2004	October 21	Roberg	3	250	1F	2 M	
2006	February 9	Tautra	5	44–46	4F	1 M	
2006	February 14	Tautra	5	44–47	5F[a]		
2006	February 22	Tautra	2	65–69	1F	1 M	
2006	March 5	Tautra	6	41–65	4F	2 M	
2008	January 31	Tautra	4	47	2F	1 M	1?
2008	February 12	Stokkbergneset	7	111–146	5F	2?	
2008	February 27	Stokkbergneset	8	119–160	2F	6?	
2008	March 10	Stokkbergneset	4	119–160	1F	3?	

Gender was derived from histological analysis

[a] Three of these females had spawned and had insufficient material to measure

however, a Chi-squared analysis showed no significant difference between the numbers of each gender ($\chi^2 = 19.76$, $p = 0.47$). Twelve of the samples were devoid of gametes, therefore their genders could not be established (Table 1).

There were insufficient samples from the same time, date, depth, and year to test for statistical differences in mean oocyte feret diameter among sites. Differences among years were tested using one-way ANOVA when sufficient data were available, and no significant differences were found. Table 2 presents a summary of comparisons and statistical outcomes. For this study, discussion of gametogenesis and reproductive periodicity apply to data pooled across color morphs, study sites, and years.

Female gametogenesis

During this project (2002–2008), female samples were collected at least once for each month except May, July, September, and December. Oocytes were found in samples from every collection, indicating continuous reproductive cycles with no intermission between spawning and onset of gametogenesis. Mature oocytes were present from January to March, with the peak in middle to late February. The samples kept alive in the laboratory were observed to spawn from January to March, with each sample releasing gametes multiple times. The smallest oogonia (<10 μm) and pre-vitellogenic oocytes (10–30 μm) were also observed in samples from January, February and March (see Fig. 3a, b for images of different stages of oogenesis), indicating the onset of the next gametogenic cycle. The gametogenic cycle, therefore, began at the end of January and terminated in February–March of the following year so the cycle was approximately 13–14 months in duration, with a one- to two-month overlap between cycles.

The oogonia developed within the mesenteries and in the early pre-vitellogenic stages were generally aligned along the mesenterial lamellae. As the oocytes grew, they migrated away from the mesenterial lamellae and increased in size, forming cohesive groups, generally toward the posterior end of the mesentery. There were fewer samples collected during the middle part (April–September) of the reproductive cycle than the onset and maturation periods, so oocyte growth rates could not be measured continuously. Average oocyte diameter data indicated little size increase between February and June ($\sim$4 μm month^{-1}), with rapid vitellogenesis from June to October ($\sim$14 μm month^{-1}) and slower growth toward the end of the cycle

Table 2 Statistical analysis of inter-annual variation in gametogenesis of *Lophelia pertusa*

Years	Date	Site	Depth	*N*	Oocyte diameter (μm)		*F*	*p* (α = 0.05)
					Mean	SD		
2003	October 23	Tautra	52	1	94.09	0	6.190	0.273*
2004	October 21	Stokkbergneset	250	2	72.68	4.969		
2004	October 21	Roberg	250	1	79.89	0		
2004	February 9th	Tautra	79–86	3	106.10	6.670	0.006	0.939*
2006	February 9th	Tautra	44–46	4	108.53	50.795		
2004	February 17	Tautra	82	1	92.53	0	0.484	0.642*
2006	February 14	Tautra	44–47	2	93.22	20.880		
2008	February 12	Stokkbergneset	111–146	5	82.16	13.238		
2006	February 22	Tautra	65–69	1	101.25	0	2.104	0.384*
2008	February 27	Stokkbergneset	119–160	2	54.14	26.518		
2006	March 5	Tautra	41–65	3	45.66	31.409	1.356	0.364*
2008	March 10	Stokkbergneset	119–160	1	87.90	0		

Analysis of variance was performed using mean oocyte diameters from the similar dates (within 2–5 days) across different years

* No significant difference in mean oocyte diameter was observed between sample dates

from October to February ($\sim$9 μm month^{-1}) (Fig. 4). The largest average oocyte diameter from a single colony was 133.7 μm (SD = 19.31) (February 9, 2006), and the largest oocyte found was 180 μm (February 14, 2006). Monthly size–frequency histograms (Fig. 5) provided a detailed presentation of the variability in oocyte development over time, particularly around the spawning period. March samples displayed the most variable oocyte size range as they contained a combination of mature oocytes from the current gametogenic cycle and developing oocytes from the next cohort. These frequency distributions indicate protracted spawning periods (both within each individual and for the population), rather than highly synchronous spawning where there would be a much smaller range of oocyte size classes, especially in the more mature stages.

Male gametogenesis

Between 2002 and 2008, male samples were collected for each month except April and July. Early spermatogenesis (stage I) was not observed in our samples; from May to November, the spermatocysts were in the maturation phase (stage II) with darkly stained spermatocytes and no spermatozoa present (Fig. 6a, b). Waller and Tyler (2005) reported Stage II as large open lumens; however, the spermatocysts from our samples were almost filled with spermatocytes, even in the earlier part of the cycle (May and June). From December to March, the spermatocysts were mature (Stage III) and filled with spermatozoa (Fig. 6c, d). As spermatogenesis progressed, the spermatocysts increased in size, often completely filling the mesoglea.

Twelve of the samples collected during the spawning period could not be assigned a gender since there were no visible gametes. Females examined during this period either had remnant mature oocytes or oogonia; therefore, these 12 samples may have been post-spawning males. If so, this indicates that, unlike the females, male *L. pertusa* colonies do not have overlapping gametogenic cycles.

Discussion

This study describes a more complete gametogenic cycle of *L. pertusa* than previous work, with samples that encompass both initial gamete production and the spawning period. These data clearly show that the Norwegian fjord populations have overlapping gametogenic cycles. In contrast, Waller and Tyler (2005) suggested that the NE Atlantic (785–980 m) populations had a resting phase after the spawning period, with initiation of gametogenesis in late summer to coincide with food influx to the benthos (late June–August) from the spring phytoplankton bloom. Our data show that oogenesis not only began earlier in the Trondheim Fjord than in the NE Atlantic populations, but that successive cycles overlapped by one to 2 months. Oocytes from NE Atlantic populations of *L. pertusa* (Waller and Tyler 2005) in August were smaller than those collected from the Trondheim Fjord (means = 41.3 vs. 57.8 μm, respectively), but by October the oocyte sizes were similar (88.7 vs. 79.8 μm, respectively) between areas. The rapid oocyte growth (vitellogenesis) that we measured between summer and late fall was therefore even more pronounced in the NE Atlantic populations.

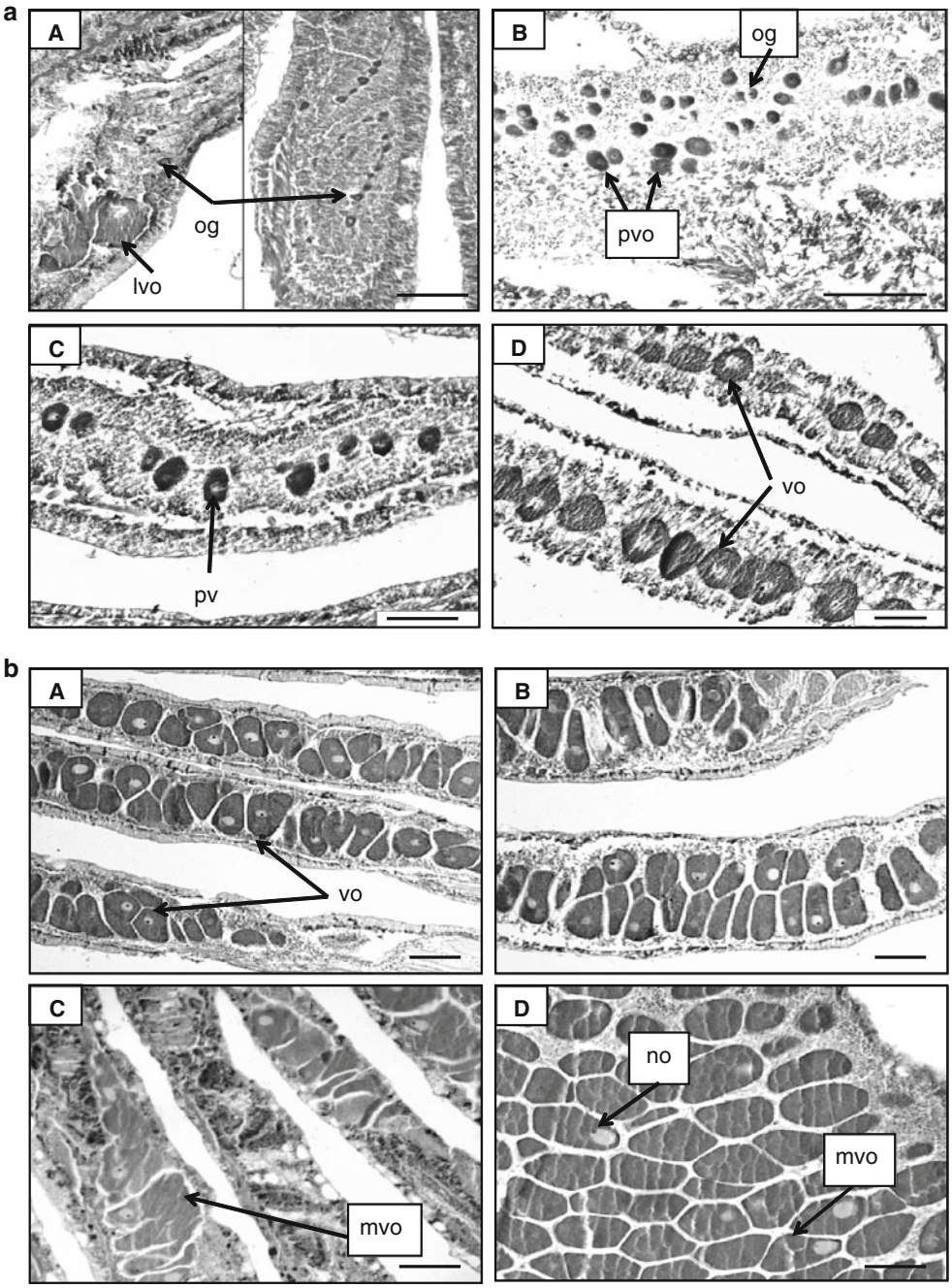


Fig. 3 **a** Early stages of *Lophelia pertusa* gametogenesis: **A** March: large oocytes in left image are remnants from spawning, and right image shows oogonia signaling the start of the next cycle, **B** April: oogonia and pre-vitellogenic oocytes, **C** June: pre-vitellogenic oocytes, **D** August: early vitellogenesis. *Lvo* late vitellogenic oocyte, *og* oogonia, *pvo* previtellogenic oocyte, *vo* vitellogenic oocyte. *Scale bars* **A**, **B** = 100 μm; **C**, **D** = 50 μm. **b** Late stages of *Lophelia pertusa* oogenesis **A** October: vitellogenic oocytes **B** November: vitellogenic oocytes become more mis-shapen as they fill the mesenteries **C** January: mature oocytes with nucleoli near periphery of nucleus **D** February: pre-spawning oocytes. *vo* vitellogenic oocyte, *mvo* mature vitellogenic oocyte, *no* nucleolus. *Scale bars* 100 μm

In summary, there are differences in female gametogenic cycles between the NE Atlantic offshore and the fjord populations of *L. pertusa*, including the presence/absence of a resting phase between cycles and the rate of vitellogenesis. Maximum oocyte diameter and the timing and duration of spawning cannot be compared as these data were not available for the offshore populations. The reasons for these differences are unclear, but could be linked to external environmental variables (temperature, food supply etc.) or differences in endogenous rhythms.

Male *L. pertusa* colonies, unlike the females, showed no indication of overlapping gametogenic cycles; however, it is not uncommon for anthozoan gametogenic stages to vary between males and females. Energetic investment in sperm is considerably less than for eggs, and sperm production and maturation is more rapid than egg development (Goffredo et al. 2002; Baillon et al. 2011).

There is ample evidence for exogenous control of reproduction in a variety of marine invertebrates, both in terms of both proximal cues (immediate) and ultimate drivers (evolutionary) (Giese and Pearse 1974, Tyler et al.

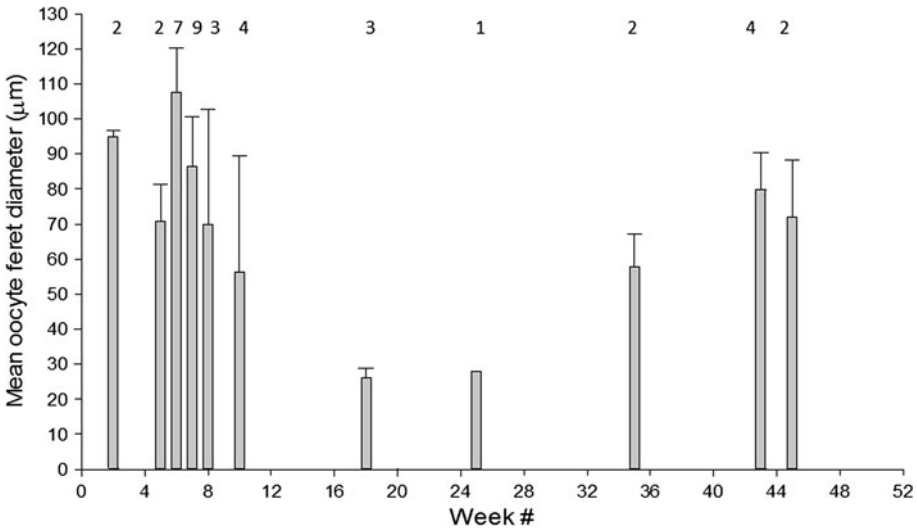


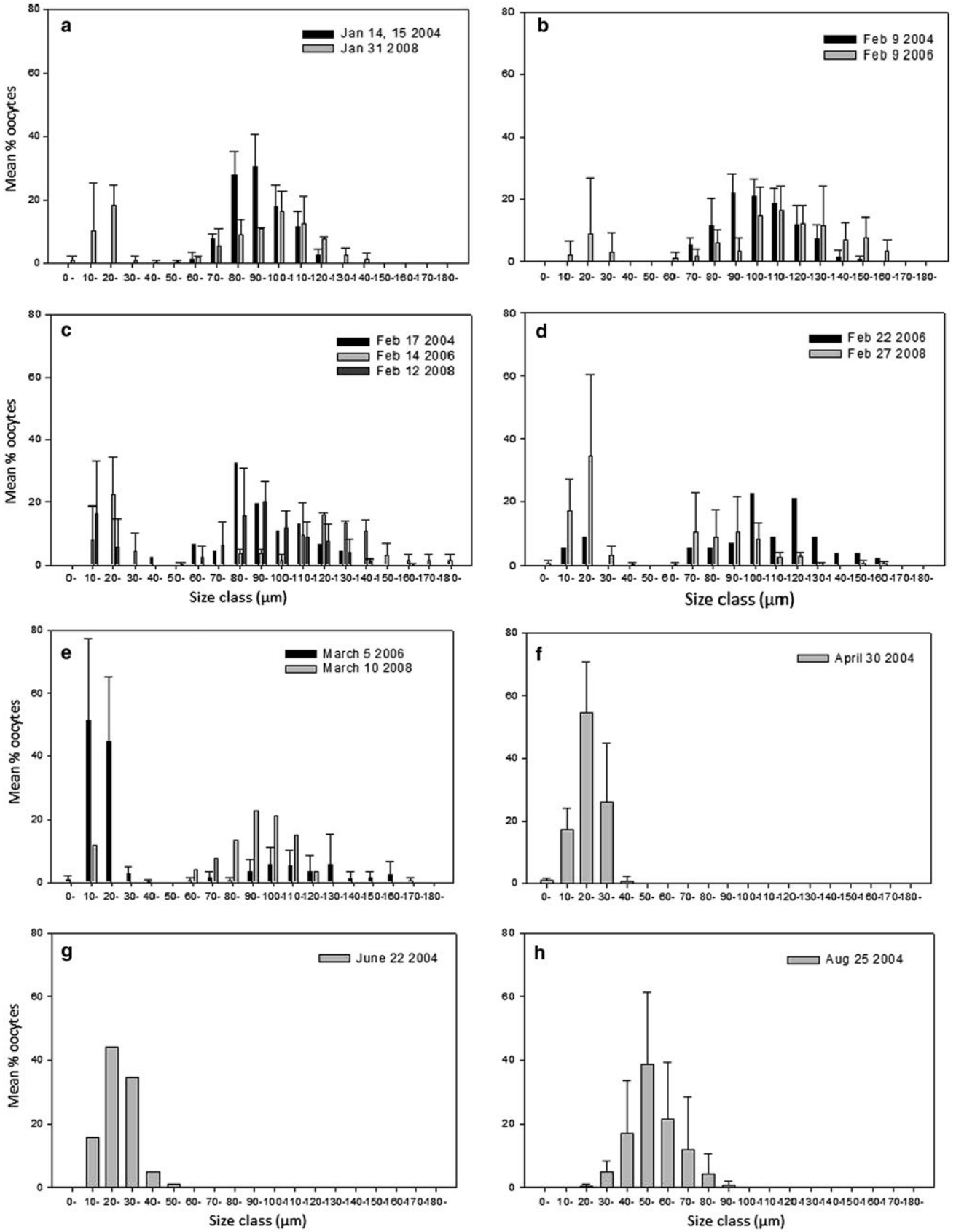
Fig. 4 Mean oocyte diameters of *Lophelia pertusa* from different sampling periods, with samples combined across years, showing the progression of the gametogenic cycle from oogonia (late Jan–early Mar) to pre-vitellogenic (Apr–Jun), vitellogenic (Aug–Dec) and mature vitellogenic (late Jan–early March) oocytes. Error bars represent one standard deviation from the mean. Numbers above the bars = number of females. Week # represents 7 day increments from January 1st

1994). These controlling factors include temperature, salinity, food supply, lunar phase, tidal cycles and daily light/dark cycles, solar insolation, rainfall patterns, and periods of calm that enhance fertilization (Himmelman 1980; Babcock et al. 1986; Yankson 1986; Sasaki and Shepherd 1995; Hardege and Bentley 1997; Mangubhai and Harrison 2008; Mercier et al. 2011, Harrison 2011). Seasonal change in sea temperature has been cited frequently as an important environmental factor that controls gametogenic cycles and planular release in shallow-water scleractinian corals (Szmant-Froelich et al. 1980; Kojis and Quinn 1981; Tranter et al. 1982; Fadlallah 1985; Stoddart and Black 1985; Babcock et al. 1986; Harrison and Wallace 1990). However, how environmental factors affect reproduction in marine organisms is still poorly understood and relies on correlations derived from field observations. Controlled experiments are needed to determine the extent to which environmental factors control scleractinian reproduction (Harrison 2011). This body of research has also focused primarily on shallow water, most likely for logistical reasons, rather than deep-sea ecosystems, so information on the latter is lacking.

The factors that drive reproductive periodicity in the deep sea are even less clear than for shallower depths. Synchronized seasonal or periodic reproductive cycles are quite common among invertebrate species that live shallower than 3,000 m (these species have a high degree of synchrony within species with short spawning periods), whereas those that live deeper tend to reproduce continuously (Gooday 2002). Temperatures are much less variable than in shallow waters, and potential reproductive cues linked to lunar, tidal, or diurnal cycles also attenuate with depth. Only one study has systematically investigated the relationships between lunar cycles and reproduction in deep-sea benthic invertebrates, observing that spawning and larval release in six species of echinoderms (living between 100 and 1,400 m) showed significant increase in activity around the new and full moons (Mercier et al. 2011). The authors suggested the lunar phase was a proxy for some other environmental factor such as cyclic currents or deposition of particulate matter (food) to the seafloor. Environmental data for deep-sea coral ecosystems are limited, and these topographic features often show dynamic environmental conditions on various temporal and spatial scales (Duineveld et al. 2007; White 2007; Davies et al. 2009; Roberts et al. 2009). It is possible that cold-water corals are exposed to environmental fluctuations of predictable timing, duration, and intensity, and one or more of these may influence various aspects of their reproduction.

In the deep sea, long-term environmental data are limited to a few locations where instruments have been deployed, and studies on reproductive cycles are also rare, limiting our ability to generate strong correlations. In the NE Atlantic from Norway to the Porcupine Seabight, temperatures at cold-water coral depths ranged from 6.5 to 9.9 °C (Dullo et al. 2008), but with no information on temporal variability. Measurements over a 1-year period near *L. pertusa* banks on the Rockall Trough (NE Atlantic) revealed an average bottom temperature of 8–9 °C, with maximum daily fluctuations of 2.6 °C (Mienis et al. 2007).

Fig. 5 **a**–**e** Size–frequency distributions of *Lophelia pertusa* oocytes ▶ by sample period: **a** Mature vitellogenic oocytes of *Lophelia pertusa* and the following cohort of oogonia and early pre-vitellogenic oocytes occurred simultaneously, indicating overlapping gametogenic cycles; (**f**, **g**) April and June samples consisted primarily of pre-vitellogenic oocytes; (**h**–**j**) Between June and August, oocytes transitioned from pre-vitellogenic to vitellogenic and increased in size steadily as they matured. *Error bars* represent one standard deviation from the mean percent number of oocytes in each size category


a
Jan 14, 15 2004
Jan 31 2008
b
Feb 9 2004
Feb 9 2006
c
Feb 17 2004
Feb 14 2006
Feb 12 2008
d
Feb 22 2006
Feb 27 2008
e
March 5 2006
March 10 2008
f
April 30 2004
g
June 22 2004
h
Aug 25 2004
Mean % oocytes
Size class (μm)
0- 10- 20- 30- 40- 50- 60- 70- 80- 90- 100- 110- 120- 130- 140- 150- 160- 170- 180-

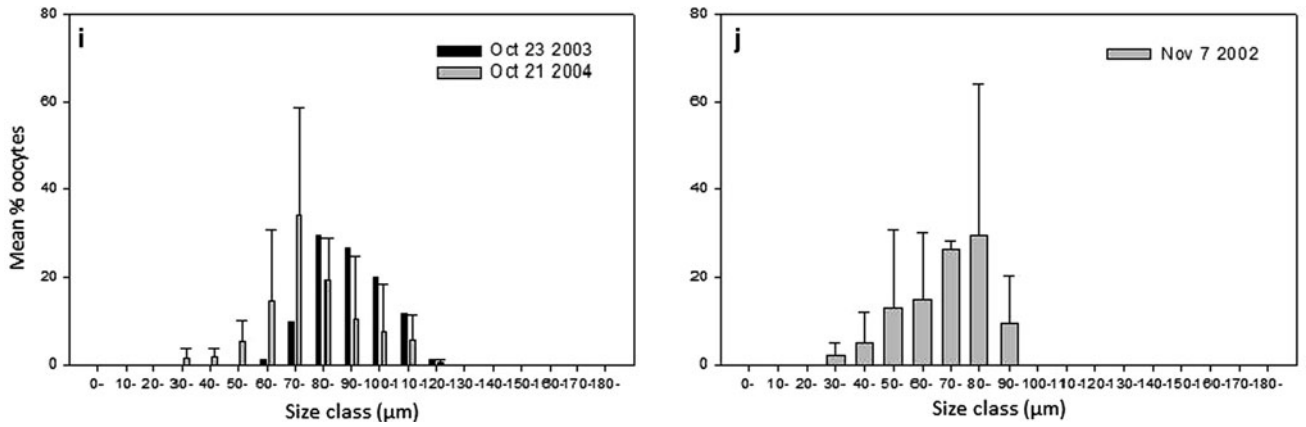


Fig. 5 continued

These temperature fluctuations correlated with tidal cycles, but there were no consistent seasonal signals that might drive reproductive cycles. Water temperatures in the Trondheim Fjord (near our sample sites) showed virtually no temporal variation (7.5–8 °C) at 100 m depth (Børsheim et al. 1999). In the western north Atlantic, extensive *L. pertusa* reefs occur off the southeastern USA (Ross and Nizinski 2007) and Gulf of Mexico (Brooke and Schroeder 2007). Limited environmental data from these sites (Brooks and Bane 1983; Bane et al. 2001; Continental Shelf Associates 2007; Mienis et al. 2012) show no clear connection between temperature and the timing of *L. pertusa* reproductive cycles.

The timing of food supply may influence various aspects of deep-sea invertebrate reproduction (Gage and Tyler 1991; Tyler et al. 1992, 1993; Campos-Creasey et al. 1994; Eckelbarger and Watling 1995; Gooday 2002; Young 2003), including initiation and timing of gametogenesis and vitellogenesis, timing of spawning or larval release, and timing of larval recruitment. Surface productivity blooms occur on a predictable seasonal schedule in many locations (Deuser 1986), with some inter-annual variation in timing and intensity. Delivery of labile carbon from the surface to the seafloor can occur in a few days at depths above 1,000 m in the NE Atlantic (Gage and Tyler 1991), creating seasonal food pulses to the benthos (Billett et al. 1983; Lampitt 1985; Rice et al. 1986; Thiel et al. 1989; Gooday 2002) that may also vary in timing, quantity, and composition (Deuser 1986; Newton et al. 1994; Wong et al. 1999; Takahashi et al. 2000, Lampitt et al. 2001). Vitellogenesis is energetically expensive as oocytes have high lipid (20–50 % of the egg composition) and protein content (Hoegh-Guldberg and Emlet 1997; Sewell and Manahan 2001, Moran and Manahan 2004; Byrne et al. 2008). Deep-sea species (especially those with large eggs or high fecundity) may therefore coordinate vitellogenesis with periods of high food delivery to the benthos (Eckelbarger and Watling 1995). For example, seasonal influx of organic material to the bottom was implicated in the initiation of gametogenesis or vitellogeneis in some cold-water scleractinians (Waller and Tyler 2005; Mercier et al. 2011) and octocorals (Sun et al. 2010; Mercier and Hamel 2011).

Food supply may influence different aspects of reproduction, including timing of spawning and larval release. Marine invertebrate species that produce large lipid-rich eggs generally produce lecithotrophic larvae, which do not need an exogenous food supply. Species that produce small eggs have a lower energy reserve and usually produce small planktotrophic larvae (Jaeckle 1995; Sewell and Manahan 2001; Prowse et al. 2008). Larval development mode has not yet been determined for *L. pertusa,* but this species produces small eggs (maximum = 140 μm) (Waller and Tyler 2005). To facilitate larval growth and development, species with planktotrophic larvae may therefore time their spawning to coincide with high food levels in the water column (Tyler et al. 1982). However, timing of larval recruitment with seasonal food pulses has only been observed in opportunistic macrofaunal species that have rapid reproductive cycles (Blake and Watling 1994; Gooday et al. 1996; Snelgrove et al. 1996). There are no documented examples of this response in megafauna, which produce eggs more slowly than the smaller macrofauna. Slower egg production disconnects food influx and the presence of mature larvae that are ready to recruit (Eckelbarger and Watling 1995).

Information on influx of food to the deep sea is limited and is restricted to a few locations. In the temperate North Atlantic, the spring phytoplankton bloom is usually well defined and results in a strong flux of phytodetritus that accumulates on the seafloor at bathyal and abyssal depths in the late spring and early summer (Lampitt 1985; Rice et al. 1994; Lampitt and Antia 1997; Longhurst 1998; Lampitt et al. 2001, Duineveld et al. 2007). Norwegian fjords also exhibit a spring (March/April to May/June)

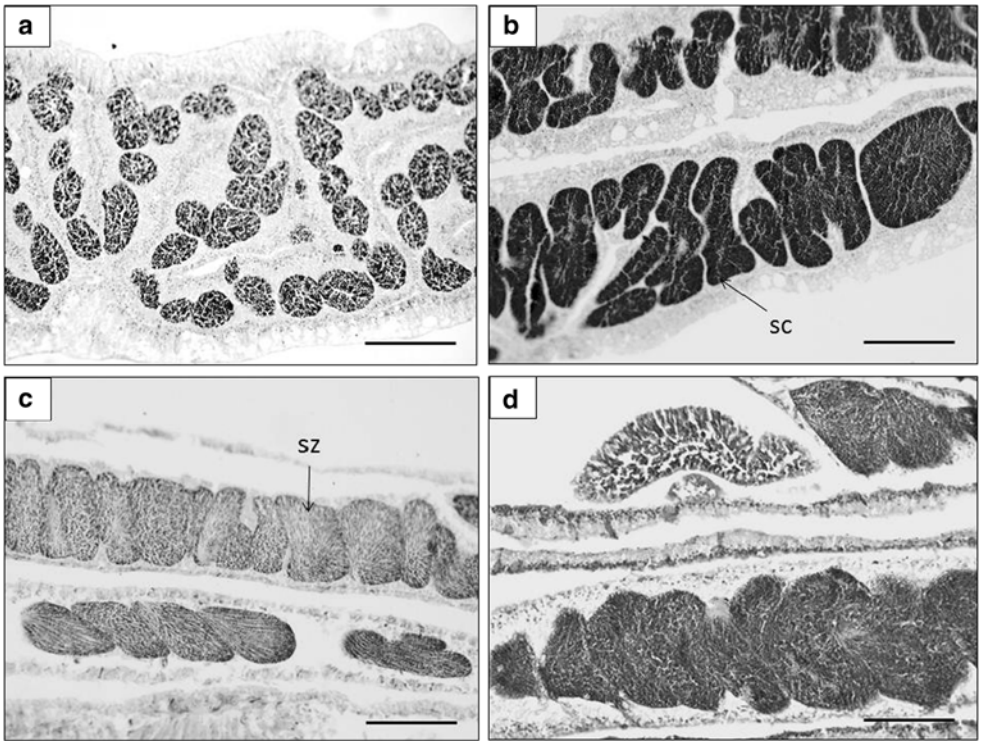


Fig. 6 a–d Spermatocysts in the mesenteries of male *Lophelia pertusa* colonies: **a** early Stage II spermatocysts mostly filled with spermatocytes from samples collected in June. **b** late Stage II spermatocysts, completely filled with dense spermatocytes from September samples. **c** Samples collected in December showing early Stage III spermatocysts with spermatocytes and some spermatozoa. **d** February samples with mature spermatocysts showing primarily spermatozoa with some spermatocytes. *Sc* spermatocyte, *sz* spermatozoa. *Scale bars* 100 μm

phytoplankton bloom, much of which sinks to the bottom (Burrell 1988; Wassmann et al. 1996), in a similar pattern to the offshore NE Atlantic. The Trondheim Fjord exhibits a variable seasonal pattern in dissolved organic carbon (DOC) between years, but in general DOC is highest at depth during the summer months (Børsheim et al. 1999). For more northerly Norwegian fjords, the deposition of particulate organic carbon (POC) peaked in April and May, coincident with the spring bloom; however, there were two additional pulses observed later in the year (June and September) in response to freshwater influx (Børsheim et al. 1999). These signatures are complicated by inter-annual variation in freshwater runoff, benthic re-suspension by currents and horizontal advection of water masses between the fjords and offshore areas. In fjord systems, the relationship between surface phytoplankton blooms and delivery of organic material to the benthos is more complex than for many open ocean or continental margin systems (Børsheim et al. 1999). These differences in food dynamics between open ocean and fjord systems may account for the observed differences in *L. pertusa* gametogenesis, but more data are needed before such correlations can be tested.

There is an apparent difference of several months in the onset of gametogenesis between our study in Norway (January) and that estimated by Waller and Tyler (2005) from the NE Atlantic ('late summer'). Endogenous or genetic factors cannot explain differences between conspecific populations that are in the same region and are genetically similar (Morrison et al. 2011). Exogenous factors seem more likely to account for the observed differences in the timing and duration of *L. pertusa* gametogenic cycles; however, there are not enough environmental data from the two study areas to draw conclusions on what these might be. Both studies showed a similar rapid increase in oocyte diameters from early summer through December, which coincides with the seasonal influx of particulate organic carbon from the spring and (smaller) fall phytoplankton blooms. The largest phytodetrital pulse disappears before the completion of the reproductive cycle (in both fjord and offshore locations), so either the corals have the capability of long-term energy storage or they may use a different food source to complete vitellogenesis. The large polyps of *L. pertusa* are well equipped with batteries of nematocysts that enable them to capture large, active planktonic food items (Freiwald 2002). Although there are few controlled feeding experiments or in situ observations of *L. pertusa* feeding, isotope studies indicate that this species has a mixed diet of zooplankton and

phytodetrital material (Duineveld et al. 2004; Kiriakoulakis et al. 2005) and in some cases phytoplankton material (Duineveld et al. 2012). Consideration of zooplankton dynamics at depth adds a layer of complexity to the role of food as a driver of reproductive activity. Zooplankton populations increase in response to phytoplankton blooms, and many zooplankton species undergo both diurnal as well as seasonal vertical migrations that reach the deep coral communities, especially in the shallow fjord habitats. Benthic zooplankton also exhibit diurnal vertical migrations in the vicinity of *L. pertusa* mounds, putting them within reach of the coral polyps (Davies et al. 2010; Mienis et al. 2012). In the Trondheim Fjord, the annual migration cycle of the abundant copepod *Calanus finnmarchicus* corresponds to the gametogenic cycle of *L. pertusa,* and it is possible that *C. finnmarchicus* constitutes an important food source for the corals at the onset of gametogenesis as well as throughout gonadal development. The dynamics of *C. finnmarchicus* in the north sea are very complex, and there may be differences in the amount and timing of the vertical migration of *C. finnmarchicus* in the offshore NE Atlantic (Heath et al. 2004) and the fjord systems that could account for the difference in reproductive timing between this study and Waller and Tyler (2005).

Reproductive cycles of *L. pertusa* from the southeastern US (S. Brooke, unpubl. data) and the Gulf of Mexico (Brooke et al. 2007) are offset by several months from those populations in the NE Atlantic. Spawning appears to occur in late September to early November in the southeastern US and Gulf of Mexico, rather than late January to early March in the NE Atlantic. The discussion above indicates that seasonal organic input may influence the reproductive cycles of *L. pertusa*; however, the exact mechanisms by which such environmental factors stimulate physiological responses are unknown (Roberts et al. 2009). In addition, while exogenous factors may influence invertebrate reproductive biology, there are also genetically constrained endogenous factors that may play a role in reproductive processes (Eckelbarger and Watling 1995). Large regional differences in reproductive timing within a single species, as occurs with *L. pertusa*, provide a rare opportunity to study exogenous factors that may influence the drivers of reproduction and identify which factors are constrained endogenously.

When corals are under stress, they may allocate energy away from reproduction into metabolic maintenance, tissue repair, or growth (Brown and Howard 1985; Richmond 1987; Ward 1995). Although this phenomenon has not been directly studied in cold-water corals, Waller and Tyler (2005) noted that samples of *L. pertusa* from their heavily trawled sites on the Darwin Mounds did not contain any reproductive material, whereas samples from the less impacted sites were packed with gametes. Population genetic analysis of *L. pertusa* from the heavily trawled Darwin Mounds also indicated very low levels of sexual reproduction (Le Goff-Vitry et al. 2004). Changes in reproductive output would not be immediately obvious, but could have a long-term influence on ecosystem resilience and possibly genetic diversity. This has important implications for deep coral reefs impacted by destructive human activities and future widespread changes in ocean conditions resulting from global climate change.

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