Protracted oogenesis and annual reproductive periodicity in the deep-sea pennatulacean Halipteris finmarchica (Anthozoa, Octocorallia)

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Abstract
Halipteris finmarchica is one of the most common species of deep-sea pennatulacean corals in the Northwest Atlantic; it was recently determined to act as a biogenic substrate for other species and as a nursery for fish larvae. Its reproductive cycle was investigated in colonies sampled in 2006 and 2007 along the continental slope of Newfoundland and Labrador (Canada). Halipteris finmarchica exhibits large oocytes (maximum diameter of 1000 μm), which are consistent with lecithotrophic larval development. Female potential fecundity based on mature oocytes just before spawning was ~6 oocytes·polyp⁻¹ (500–6300 oocytes·colony⁻¹); male potential fecundity was 16 spermatocysts·polyp⁻¹ (5500–57,400 spermatocysts·colony⁻¹). Based on statistical analysis of size-probability frequency distributions, males harboured one cohort of spermatocysts that matured inside 8–11 months, whereas females harboured two distinct cohorts of oocytes; a persistent pool of small ones (≤400 μm) and a small number (~20%) of larger ones that grew from ~400 to >800 μm over a year. Despite this difference in the tempo of oogenesis and spermatogenesis, a synchronic annual spawning was detected. A latitudinal shift in the spawning period occurred from south (April in the Laurentian Channel) to north (May in Grand Banks and July–August in Labrador/Lower Arctic), following the development of the phytoplankton bloom (i.e. sinking of phytodetritus). Prolonged oogenesis with the simultaneous presence of different oocyte classes in a given polyp is likely not uncommon in deep-sea octocorals and could hamper the detection of annual/seasonal reproduction when sample sizes are low and/or time series discontinued or brief.

Introduction
Pennatulaceans (Octocorallia: Pennatulacea), commonly called sea pens, are colonial corals that anchor themselves into soft sediment (mud, sand), allowing them to colonize large areas of the sea floor from the inter-tidal zone down to the abyssal plain (Williams 2011). Sea pens can occur sparsely or form large aggregations [e.g. large fields of deep-sea Pennatula spp.; (Baker et al. 2012)], suggesting that they may provide an important structural habitat to other organisms (Tissot et al. 2006; Baillon et al. 2012; Baker et al. 2012) by increasing the complexity of the soft-bottom sea floor. Despite this potentially important role and the existence of ~200 species (Williams 2011), sea pens are still poorly known, rendering their management and protection problematic. Sea pens have already been identified as vulnerable species (NAFO 2008; Murillo et al. 2011) due to their sensitivity to human disturbances such as trawl fisheries (Brodeur 2001).

Understanding the reproduction of a species is important to determining its resilience to disturbance. Despite the fact that sea pens are more abundant in the deep sea