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Biology of a deep-water sea anemone (Anthozoa: Actiniidae) from eastern Canada: Spawning, development, and growth

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ABSTRACT

Knowledge of the general biology and reproductive ecology of deep-water species can help predict their resilience to environmental and anthropogenic disturbances. The present study centers on live specimens of a deep-water sea anemone which were collected at bathyal depths between 1100 and 1400 m and kept in a mesocosm for over 6 years. Morphology and DNA sequencing confirmed that the species belongs to the genus *Urticina*. Male and female (9–10 cm pedal disk diameter, 90 tentacles) spawned 4 years post collection, in early spring (March). Both sexes released gametes through the mouth. The negatively buoyant oocytes (550–600 μm in diameter) quickly settled on the rocks and soft sediments surrounding the female. Lecithotrophic embryonic and larval development occurred on the substratum. Fully developed planula larvae were detected after 17–21 days. Planulae started to crawl and swim around but remained demersal. Metamorphosis and settlement occurred after 30–35 days, exclusively on hard substrata and preferentially on undersurfaces. Offspring grew slowly, developing 8 tentacles after 5 months and 24 tentacles after 12 months (3–4 mm pedal disk diameter). After 2.6 years of growth, the captive-born sea anemones reached 12–16 mm in pedal disk diameter and possessed 48–54 tentacles.

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1. Introduction

Pelagic and benthic members of phylum Cnidaria have successfully colonized freshwater and saltwater environments all around the world (Rogers, 2009). They are particularly diversified and abundant in marine habitats, from coastal shores down to the deepest oceanic trenches. Studies of deep-sea cnidarians, including aspects of their distribution and biology, have largely focused on corals (Cairns, 1982, 2007; Watling et al., 2011; Young, 2003) due to the fact that they create complex tri-dimensional habitats and play major roles in ecosystem functioning (Baillon et al., 2012; Buhl-Mortensen and Mortensen, 2005; Cerrano et al., 2010; Roberts et al., 2006). This focal interest has deflected attention from other very abundant cnidarians of the deep, including members of order Actiniaria (sea anemones). Sea anemones are reportedly abundant on rocky bottoms of bathyal and abyssal zones, and around hydrothermal vents (Aldred et al., 1979; Rodríguez and Daly, 2010); as an example, Aldred et al. (1979)

indicated that the sea anemone *Actinoscyphia aurelia* could reach densities of up to 6 ind m⁻² at depths between 500 and 2000 m in the Northeast Atlantic.

Despite their abundance, deep-water sea anemones remain poorly studied, and the topic of a limited number of ecological or biological investigations (details below). From samples collected at bathyal depths in the Southern Ocean, the externally brooding *Epiactis georgiana* was determined to exhibit superfetation (several cohorts of offspring developing simultaneously) and seasonal release of embryos/larvae in the austral spring (Rodríguez et al., 2013). Van Praët and Duchateau (1984) and Van Praët (1990a, 1990b) revealed the existence of reproductive seasonality in correlation with the flux of organic matter at 2000 m in the sea anemone *Paracalliactis stephensoni* from the Bay of Biscay. Similarly, seasonal patterns of spawning in *Phelliactis hertwigi* and *Phelliactis robusta* from bathyal depths in the Porcupine Seabight (northeast Atlantic) were described by Van Praët et al. (1990a, 1990b), whereas Bronsdon et al. (1993) reported that *Amphianthus inornata* released gametes in the spring in the Porcupine Abyssal Plain (PAP). The sea anemone *Allantactis parasitica*, which lives on deep-sea gastropods in the Northwest Atlantic, spawned twice a year in the laboratory, during the spring and fall peaks of phyto-detritus abundance (Mercier and Hamel, 2009a). A few species

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were found not to display any detectable seasonal breeding, including the sea anemone *Kadosactis commensalis*, living as commensal on holothurians in the PAP (Bronson et al., 1993), and two carpet anemones (order Zoanthidae) associated with hermit crabs, *Epizoanthus paguriphilus* (770–1065 m) and *Epizoanthus abyssorum* (3749–4400 m) (Muirhead et al., 1986).

It is expected that most deep-water species will exhibit slow growth and great longevity (Gage and Tyler, 1991) compared with shallow-water counterparts, although data on growth rates of deep-sea cnidarians are scarce. Current knowledge is mostly centered on banding patterns and/or radiometric analysis of skeletal elements in corals (e.g. Andrews et al., 2002; Hamel et al., 2010; Mortensen and Rapp, 1998; Risk et al., 2002; Roark et al., 2009; Sherwood and Edinger, 2009). While these techniques cannot be used in sea anemones due to the absence of a hard skeleton, growth can also be estimated from the study of live specimens in the laboratory (Cordes et al., 2001; Hamel et al., 2010; Orejas et al., 2011) or in nature (Brooke and Young, 2009). To our knowledge, the only data available for deep-water actinarians were provided by Mercier and Hamel (2009a), who estimated that the sea anemone *A. parasitica* required 6–11 years to reach its maximum size, based on the growth of newly-settled juveniles to 15 months.

Sea anemones are ubiquitous in deep waters of the Northwest Atlantic. In some locations of the rocky continental slope of Newfoundland and Labrador (eastern Canada), densities between 5 and 9 ind m⁻² have been recorded (DFO, unpublished data). Genera whose members are commonly collected as trawl bycatch include *Urticina*, *Bolocera*, *Hormathia*, and *Actinostola*. Among these, individuals of the genus *Urticina* are the most frequently encountered. A wide range of life styles and reproductive habits have been reported so far in shallow-water species of this genus, reflecting both significant diversity within the group and raising questions about its taxonomy (Fautin et al., 2005). Genetic studies (e.g. Solé-Cava et al., 1985, 1994) have failed to find differences among the North Atlantic species, but the circumscription of new species from within the previously global *Urticina crassicornis*, *Urticina eques*, and *Urticina felina* (Hand, 1955; Hauswaldt, 1999; Sanamyan and Sanamyan, 2006) have refined and limited the circumscription of the North Atlantic species.

Urticina (= *Tealia*) *crassicornis* was initially reported as a broadcast-spawner in Europe (Appellöf, 1900) and defined as a brooder on the west coast of the USA (Hand, 1955). Chia and Spaulding (1972) later confirmed that *U. crassicornis* in north-western USA fits the description of Appellöf (1900), whereas it is viviparous in the Barents Sea (Kaliszewicz et al., 2012). Most species described so far exhibit seasonal breeding. Individuals of *U. lofotensis* along the coast of California (USA) were shown to reach full maturity and spawn at the end of December (Wedi and Fautin Dunn, 1983). Studies of the reproduction of *U. felina* off the coast of Newfoundland (eastern Canada) revealed that planulation peaked in August and that internal brooding could lead to chimerism (Mercier et al., 2011b; Sun et al., 2012). Larson et al. (2012) reported seasonal external brooding in the similar-looking, co-occurring species *Urticina fecunda*.

Limited knowledge is currently available on deep-water sea anemones and, to our knowledge, nothing is known of the biology of *Urticina* species that are common at bathyal depths. The purpose of the present work was to gain a better understanding of spawning, gamete behavior, development, and growth of a deep-water sea anemone of the genus *Urticina* commonly collected along the continental slope of eastern Canada. Findings shed light on the traits and adaptations that make this species successful in heavily fished deep waters.

2. Materials and methods

2.1. Collection and maintenance

Animals were obtained as bycatch from routine research surveys conducted by Fisheries and Oceans Canada (DFO) in December 2009 with the CCGS *Teleost* along the continental slope off Labrador (56°26'N, 57°36'W), at depths ranging between 1100 and 1400 m. Surveys followed a stratified random sampling design with a Campellen 1800 trawl towed for 15 min on ~1.4 km of seafloor (gear opened and closed at depth). A total of 7 large sea anemones (9–10 cm pedal disk diameter, ~90 tentacles), assumed to be of the same species based on morphology, were collected and kept onboard the ship in a large flow-through tank (5000 L). Live specimens were brought back to the laboratory, where they were kept in a mesocosm, consisting of a 600-L tank supplied with running ambient seawater (~300 L h⁻¹) under darkened conditions. Temperature in the tank ranged annually between -1 and 8 °C, according to a temperature-light logger HOBO Pendant (UA-002-64). A chilling unit (Universal Marine Industries, 5 hp) was used for in-line cooling of seawater when ambient coastal temperatures were higher than those characteristic of the bathyal environment in eastern Canada (DFO, 2009). The bottom of the tank was filled with 15 cm of fine mud and scattered with a few boulders (15–20 cm in diameter) and deep-water coral skeletons to mimic the natural habitat. Sea anemones were fed periodically, generally once a month, either with complete live sea urchins (*Strongylocentrotus pallidus*), frozen deep-sea shrimps (*Eualus*, *Pandalus*, *Spirontocaris*) or shucked mussels (*Mytilus* sp.).

2.2. Taxonomic characterization, DNA extraction and sequencing

Small tissue samples were taken from the pedal disk of three of the seven specimens collected and preserved in 100% ethanol. Total genomic DNA was extracted from the samples with the DNeasy kit (QIAGEN). Using previously published primers (Supplemental Table 1), Template DNA, and illustra puReTaq Ready-To-Go PCR Beads the 12S, 16S, 18S, and partial 28S ribosomal genes were amplified following the thermalcycler profile: 4 min at 94 °C, 30 cycles of 15 s at 94 °C, 1 min at 52 °C, 1 min at 72 °C, and 10 min at 72 °C for the final extension step. PCR products were sequenced on the Applied Biosystems 3730xl DNA Analyzer by staff at Beckman Coulter Genomics (Danvers, MA). The forward and reverse sequences were assembled in the program Geneious version 7.1.7 (Kearse et al., 2012) and compared against the nucleotide database in GenBank (using BLAST searches) to determine whether the targeted loci were sequenced. The new sequences for *Urticina* sp. and *U. felina* have been deposited in Genbank (KT265262–KT265273). For our phylogenetic inference the newly acquired sequences of 12S, 16S, 18S, and 28S ribosomal genes were used in combination with previously characterized sequences (Daly et al., 2008; Rodríguez et al., 2014). For each ribosomal gene, the DNA sequences were aligned separately in MAFFT v7.017 (Katoh et al., 2002) using the search strategy L-INS-I and default parameters (scoring matrix: 200PAM/k=2; Gap opening penalty: 1.53; Offset value: 0.123). The concatenated alignments were then subjected to maximum likelihood analyses in RAxML v.7.2.8 (Stamatakis, 2006) using the GTR+ Γ option and allowing for the α parameter to be estimated for each marker independently. Clade support was determined using 1000 bootstrap replicates (Fig. 1).

A whole specimen of *Urticina* sp. was deposited at the Canadian Museum of Nature (Ottawa, Canada) under the reference number CMNI 2015-0012.

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