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The deep-sea neogastropod *Buccinum scalariforme*: Reproduction, development and growth

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ABSTRACT

Specimens of the neogastropod *Buccinum scalariforme* (60–70 mm shell height) collected between 700 and 1450 m depth along the continental slope of eastern Canada were kept for 4 years in mesocosm settings. Their mating, spawning and development were assessed, thereby generating the first complete life cycle account of a deep-sea gastropod. Egg laying occurred in March and September, with a total of 9 egg masses laid in 2013 and 2015, coinciding with periods of maximum deposition of particulate organic matter (phytodetritus). Oviposition lasted 2–3 days and the female protected the egg mass for ~3 more days until it had hardened. Typically, egg masses contained 50–75 egg capsules, each measuring 5–8 mm in diameter. A capsule contained between 100 and 150 spherical eggs (300–500 µm) of which ≤50 developed into embryos. Potential fecundity calculated from the entire egg mass at spawning was between 1500 and 2250 propagules; it drastically decreased over ~4–5 months of development to an effective fecundity of 30–50 juveniles emerging from the mass (0–2 juveniles per capsule). Development went through early embryonic stages in ~15 days and reached the trocophore in 15–21 days, followed by intracapsular veliger larva (480 µm) and intracapsular pediveliger (~1000 µm) after ~90 days. Completion of development relied on oophagy and adelphophagy. The juveniles hatched at a shell height of 1–2 mm and consumed the capsule membrane. Over 2.5 years, they reached a maximum size of ~8–10 mm shell height at an average of 9.8 µm day^{-1}. Estimations indicate that *B. scalariforme* could require between 20 and 50 years to reach maximum adult size. Large gastropods like *B. scalariforme* are among the most abundant motile benthic invertebrates of the bathyal zone of eastern Canada. Knowledge of their reproductive biology constitutes a first step in assessing their vulnerability and resilience to ever growing anthropogenic pressures, including fisheries, and oil/gas exploration and exploitation.

1. Introduction

The superfamily Buccinoidea is the most geographically widespread and ecologically diverse clade within the Neogastropoda (Harasewych and Kantor, 2004). These predatory and scavenging molluscs have radiated since the Early Cretaceous to occupy a breadth of benthic marine habitats, from tropical to polar regions and from intertidal to hadal depths (Clarke, 1962; Tracey et al., 1993). In the shallow coastal waters of eastern Canada, neogastropods form the vast majority of the large, active mollusc species, including members of the genera *Colus*, *Neptunea*, *Beringius*, *Plicifusus*, *Volutopsius*, and *Buccinum* (Brunel et al., 1998). Neogastropods remain the most abundant large mollusc species collected on sandy and muddy substrates in deep waters, especially in bathyal regions between 500 and 1500 m depth (MacDonald et al., 2010; Rowe et al., 1982). Despite the abundance of neogastropods in several regions of the deep sea, key features of their biology and reproductive strategies remain poorly studied.

It has been suggested that breeding occurs year-round in the abyssal gastropod *Benthonella tenella* in the Northwest Atlantic (Rex et al., 1979). Similar reproductive patterns were suspected to characterize the neogastropod *Colus jeffreysianus* and the trochid *Calliotropis ottoi* from the Northeast Atlantic. Gametogenesis appears to be a continuous process with oocytes in all stages found in the ovaries year round (Colman and Tyler, 1988a; Colman et al., 1986a). Olabarria and Ramirez-Llodra (2004) indicated that the shallow-water gastropods *Amphissa acutecostata* and *Gymnobela subaraneosa* from the Northeast Atlantic exhibited a quasi-continuous production of oocytes, suggesting release of a small number of oocytes all year long. Colman et al. (1986b) studied the larval shell morphology of several species of deep-sea neogastropods from the Northeast Atlantic to distinguish feeding and non-feeding development. Similar studies were conducted by Bouchet and Waren (1979) on bathyal and abyssal

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gastropods. Gustafson et al. (1991) analyzed the contents of gastropod capsules collected from hydrothermal vent fields and Gustafson and Lutz (1994) reviewed the life-history traits of molluscs from chemosynthetic environments. The review by Gage and Tyler (1991) indicated that planktotrophic development in gastropod snails became more prevalent with depth, from 25% of species at depths < 1 km to 50% at depths > 4 km. However, data on developmental patterns that would help understand the ecology, evolution, and distribution of deep-water gastropods were said to be scarce (Bouchet and Warén, 1994); a statement that still stands today.

Unlike the limited number of publications dedicated to deep-sea gastropods, literature on the reproductive biology of shallow-water gastropods, and Buccinidae in particular, has been gathering since the early 1900s (e.g. Gendron, 1992; Ilano et al., 2004; Kideys et al., 1993; Lamy, 1928; Martel et al., 1986a, 1986b; Portmann, 1925, 1930; Smith and Thatje, 2013). Neogastropods undergo a period of intracapsular development, after which propagules either hatch as free-swimming larvae or as crawling juveniles (Fretter and Graham, 1994; Miloslavich and Dufresne, 1994; Pechenik, 1979; Rivest, 1983). Forms of intracapsular food sources include nurse eggs (Gallardo and Garrido, 1987; Smith and Thatje, 2013) to be consumed by one or more larvae (Penchasziadeh, 1976; Smith and Thatje, 2013), yolk-filled oocytes (generally larger than 800 µm) (Borzone, 1995) and/or provision of nutrients in the intracapsular fluid (Miloslavich, 1996; Moran, 1999; Ojeda and Chaparro, 2004). Oogenesis, copulation and egg laying were documented by Staiger (1951) and Martel et al. (1986a) in *B. undatum* and by Ito (1978) in *B. kinukatsugi* and *B. miyauchii*. Miloslavich and Dufresne (1994) described the development of *B. cyaneum* from eastern Canada, whereas Ilano et al. (2003) examined the reproductive cycle, and size at sexual maturity of *Buccinum isaotakii*. Finally, Ilano et al. (2004) described copulation, development and fecundity in *B. isaotakii* from Japan.

Buccinum scalariforme Moller 1842 is currently recognized to occur from subtidal to bathyal depths in west Greenland, Iceland, the Arctic, eastern and western Canada, as well as Maine and Alaska (USA) (Gofas, 2004). To our knowledge, nothing is known about its biology. The present study explored the reproductive habits, including egg laying, development and growth, of *B. scalariforme* collected at bathyal depths off eastern Canada, from slope habitats that are under growing pressures from the fishing and petroleum industries.

2. Material and methods

2.1. Collection and maintenance

A variety of marine invertebrates were collected as by-catch during multispecies research surveys conducted by Fisheries and Oceans Canada (DFO) on the CCGS *Teleost* in Fall 2011 and 2013 off Newfoundland, eastern Canada (48°52'N: 45°51'W) between 700 and 1450 m depth. Collection of deep-sea species in the fall and early winter ensures that bottom temperature in the bathyal zone roughly matches surface temperature (~1 to 6 °C). 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). The density of *Buccinum scalariforme* was estimated from the trawls in which they were present (n=37) and for three depth ranges: 700–900 m, > 900–1100 and > 1100 m. All individuals collected were counted and measured. Some specimens were kept alive (n=12 in 2011 and n=37 in 2013) aboard the ship in 2000 L tanks supplied with running seawater pumped from the ocean, equivalent to ~75 water changes per day. Individuals from all depths adapted well to captive conditions.

The live gastropods (60–80 mm maximum shell height measured along the central axis) were held at the Ocean Sciences Centre (Memorial University) in flow-through tanks (350–800 L) for continuous monitoring. A minimum of 10 individuals were maintained together in each tank. All tanks were darkened and supplied with running unfiltered seawater at a rate ~50 L h^{-1}. They were filled with a thick layer of soft sediment (12–15 cm), boulders (~10 cm in diameter) and a few pebbles (< 2 cm diameter). An in-line chilling unit (Universal Marine Industries, 5 hp) was used to keep the running seawater suitably cold during warmer months, from July to October (< 7 °C). Overall, the laboratory conditions were set to mimic those found in the native habitat of *B. scalariforme* as closely as possible. The mesocosms in which *B. scalarifome* were kept also hosted numerous species collected simultaneously, i.e. the sea anemones *Hormatia* spp., *Urticina* sp. and *Bolecera* sp., the solitary cup coral *Flabellum alabastrum*, several sea stars (*Henricia lisa*, *Ceramaster granularis*, *Hippasteria phrygiana*, *Leptychaster*, *Poroniomorpha* spp.), basket stars, gastropods (*Stephanasterias albula*, *Boreotrophon clathratus*, *Neptunea* spp., *Colus* spp, *Apporhais* sp., *Beringius* spp. and other *Buccinum*) as well as polychaetes and small bivalves.

The temperature in the tanks was recorded with a temperature-light logger HOBO Pendant (UA-002-64), and was consistent with seasonal fluctuations in this area of the Canadian coast at depths down to 600–800 m (0–5 °C; DFO, 2009). The annual primary productivity (data from DFO Station 27) and load of suspended matter (monthly rate of detrital matter deposition) was obtained from concurrent and previous studies conducted in the same laboratory (Hamel et al., 2010; Mercier et al., 2011), and was consistent with observations during the study.

2.2. Behaviour and development

Monitoring of gastropods (behaviour and social interactions) occurred at regular intervals, generally 2 or 3 times a week (sometimes more often when more activities were noted). Individuals were scored either as pairing, mating, laying eggs or guarding their egg masses. Survival rates of adults over the whole study were noted.

The duration of egg laying, the time spent close to the egg mass after laying, the number and types of interactions with congeners and other species present in the tanks were also described. The size of the spawning individuals and of their egg masses, as well as the number of capsules per mass were recorded. We use the term egg mass here to describe the entire cluster of egg capsules (individual pouches filled with developing propagules) held together by a proteinaceous membrane. Predatory events on egg masses were scored when a predator remained static over the mass, and/or when its proboscis was inserted in the mass (gastropods) and/or its stomach was everted (sea stars). Predators where thereafter moved to a distant part of the mesocosm (1–2 m away), to preserve the egg mass. Recurrent attempts at predation (by the same individual) were also recorded.

Measurements of whole egg masses were done underwater (they were never removed from the holding tank). Groups of 5 capsules from each monitored egg mass were sampled at regular intervals, opened and examined under a microscope to take photos and measurements. For each of these capsules, the total number and development stage of all propagules were recorded and their Feret diameter or length (n=2–20 ind. per life stage) noted. The proportion of nurse cells and non-developing embryos was also established. The potential fecundity, i.e. the number of propagules at the onset of the development, was established from 3 capsules per mass, and the effective fecundity, i.e. the number of juveniles emerging from the egg mass, was documented from 3 egg masses.

Photographs and measurements were taken under a Nikon SMZ1500 stereomicroscope attached to a Nikon DXM1200F digital camera using the imaging software Simple PCI (v. 6.0), and with a Leica M205A stereomicroscope using the Leica Application Suite X (LASX) software.

2.3. Feeding

The diet of adults (60–80 mm shell height) and juveniles (free