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Small-scale spatial distribution and oogenetic synchrony in brittlestars (Echinodermata: Ophiuroidea)

Gina M. Doyle [a], Jean-François Hamel [b], Annie Mercier [a,*]

[a] Department of Ocean Sciences (OSC), Memorial University, St John's, NL A1C 5S7, Canada
[b] Society for the Exploration and Valuing of the Environment (SEVE), St. Philips, NL A1M 2B7, Canada

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ABSTRACT

There is increasing evidence that spatial factors modulate reproductive processes over large (>150 km) and medium (10–100 km) scales in marine taxa, but few studies have explicitly determined the degree of inter-individual synchrony in gamete development at smaller scales within benthic populations. Using a ubiquitous broadcast-spawning species, the brittlestar *Ophiopholis aculeata*, we assessed variations in gametogenic activity over the annual reproductive cycle at various scales. Quantitative indices of oogenic maturity were compared in females collected: (1) in two substrata at a given site (distant ~200–300 m), (2) among clusters of individuals living in relatively close proximity (~10–50 m), and (3) within each cluster of individuals collected under/inside a given substratum (~2–20 cm). Gametogenic maturity was also examined in females collected from distant sites (~50–150 km). At the main study site, oogenic cohesion was greater within and among clusters of a given substratum than between substrata, and differences in reproductive output and spawning periods occurred between individuals from the two substrata studied. At the finest scale (within clusters of individuals) oogenic synchrony was maximal just before spawning. Comparing samples from distant geographic locations (>50 km) showed significant asynchrony outside the pre-spawning period. The present study shows that relatively high levels of asynchrony in gamete maturation may exist among conspecifics of a seemingly homogeneous population, except at the closest scale (within clusters) at the culmination of the reproductive cycle (near spawning). This emphasizes the likely interplay of inter-individual exchanges and small-scale distribution on the fine coordination of reproductive events.

1. Introduction

Variation in the timing of reproduction is a central topic of life-history studies, with implications in marine connectivity and conservation (Carson et al., 2010). Spatial variability in reproductive schedules has been investigated at various scales in a diversity of marine taxa (e.g. Bourgoin and Guillou, 1990; Guettaf et al., 2000; Contreras and Jaramillo, 2003; Lester et al., 2007; van Woesik, 2010; Sala-Bozano and Mariani, 2011; Santos et al., 2011). For many benthic invertebrates, particularly those that rely on broadcast-spawning, density and proximity of conspecifics within and between populations are important features that help maximize reproductive success (e.g. Pennington, 1985; Hamel and Mercier, 1996; Courchamp et al., 1999; Gascoigne and Lipcius, 2004; Mercier and Hamel, 2009). In contrast to how spatial factors (including density and proximity) may affect fertilization rates in broadcast spawners at the time of gamete release, the role of these factors on the synchronous development of gametes prior to spawning are poorly understood in most marine invertebrates. Fine-scale spatial factors (intra-habitat proximity) have mostly been studied in species that aggregate transiently at the time of reproduction (e.g. Hamel and Mercier, 1995; Selvakumaraswamy and Byrne, 2000; Mercier and Hamel, 2008), whereas large-scale spatial factors (inter-site synchrony), have mostly been investigated in species that do not display this behaviour (Lessios, 1981; Bourgoin and Guillou, 1990; King et al., 1994; Lefebvre et al., 1999; Guettaf et al., 2000; Kelly, 2000; Lamare et al., 2002; Lester et al., 2007).

Aggregation has been observed in many species of echinoderms, both throughout the reproductive cycle and just prior to spawning, and is generally thought to increase spawning coordination success and fertilization rates (reviewed by Giese et al., 1991; Mercier and Hamel, 2009). In holothuroid echinoderms, small-scale spatial distribution has been shown experimentally to affect reproductive synchrony, in that isolated individuals exhibited less synchronous gametogenic development than those in groups (Hamel and

* Corresponding author.
E-mail address: amercier@mun.ca (A. Mercier).

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Mercier, 1996, 1999). This supports the assumption that density and fine spatial arrangement of individuals can play a role in gamete maturation leading to spawning. Exchange of waterborne chemicals can mediate fine-tuning of gametogenesis, and ensure synchronous spawning (Hamel and Mercier, 1996, 1999). Specific hormones and steroidal products have been documented in echinoderms and are thought to function in inter-individual chemical signalling, allowing individuals to synch their reproductive cycles (Georgiades et al., 2006; reviewed by Soong et al., 2005; Wasson and Watts, 2007; Mercier and Hamel, 2009; Mercier and Hamel, 2013).

Because they are abundant in many benthic habitats and communities, brittlestars (Ophiuroidea: Echinodermata) are good candidates for studies of reproduction at various scales. Bowmer (1982) reviewed the ophiuroid *Amphiura filiformis* and noted that investigations conducted at different sites reported a wide range of reproductive periodicities. In reviewing the reproduction of *Ophioderma brevispinum*, Hendler and Tyler (1986) cited reports of spawning periods being shorter in northern locations than at sites closer to the equator. Lefebvre et al. (1999) found high spatial variability between populations of *Ophiothrix fragilis* in the English Channel, offshore populations having lower gonad indices, attributed to differences in temperature and food availability.

The main objective of the present study was to quantitatively compare inter-individual oogenic maturity at scales varying from a few cm to >50 km, over the annual reproductive cycle, to assess the level of cohesion in gametogenic development over time within and among populations. *Ophiopholis aculeata* (Linnaeus 1767) was selected for this study because of its abundance and prevalence in the Northwest Atlantic and its worldwide distribution in cold-temperate regions. Based on the knowledge that *O. aculeata* would exhibit an annual reproductive cycle (Doyle et al., 2012), and on research conducted previously on ophiuroids and other echinoderms (see review by Mercier and Hamel, 2009), it was hypothesized that individuals in closer proximity to one another (within natural clusters, such as grouped under a single rock) would be more gametogenetically synchronous than those further away from one another (in separate clusters, such as groups underneath different rocks). A corollary hypothesis was that oogenic cohesion would be strongest just before gamete release.

2. Materials and methods

2.1. Study sites and sampling methods

Collections of *O. aculeata* were primarily made in St. Philips, Newfoundland and Labrador, Canada (47° 35.5 N, 52° 53.5 W; Fig. 1) at 10–15 m depth in two adjacent substrata: (1) a low-grade rocky slope and (2) a rhodolith bed. Both the rocks and rhodoliths extended approximately 100–200 m across the field site, with an approximately 50 m wide boundary area between the two. Samples were collected during mid-monthly dives from June 2008 to June 2009, with an additional dive during the presumed spawning period (end of August 2008). Rocks were overturned and all individuals found underneath a given rock were bagged separately. Bags were also used to collect and isolate rhodoliths with their entire content (including brittlestars living inside). On each dive, 20–30 individuals were collected from each substratum, under 5–9 rocks (~15–30 cm diameter) and in 6–10 rhodoliths (~8 × 10 cm, 200 g).

The site in St. Philips is located in Conception Bay, a long (70–100 km) and narrow (~20–30 km at the mouth) bay with a salinity of 31–33 (negligible freshwater runoff), and semi-diurnal tides with an amplitude <1.5 m (de Young and Sanderson, 1995; Catto et al., 2003). There are three small islands of varying sizes located

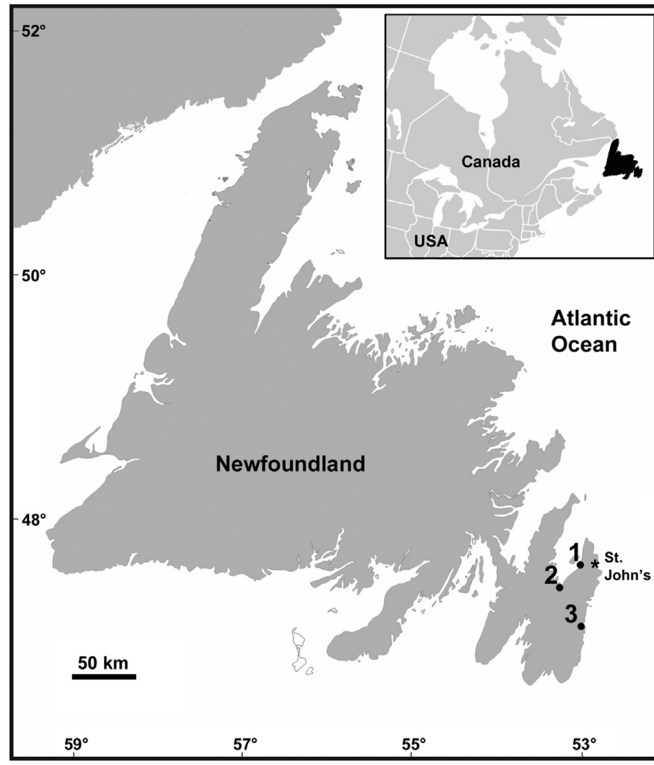

Fig. 1. Map of eastern Canada showing location of study sites on the Avalon Peninsula of Newfoundland (insert). 1. St. Philips; 2. Harbour Main; 3. Admiral's Cove.

on the southeast side of the bay. Two temperature/light logger HOBO® Pendants (UA-002-64) were cemented onto rocks at a depth of 10 m in the study site (set to record data every three hours). Monthly seawater samples (20 L) were collected to establish the abundance of phytoplankton (biweekly during the suspected spawning period in August–October). Plankton was isolated by filtering 1 L of seawater through Nitex® mesh (5 μm) and cells counted in four 10-μl subsamples using a Neubauer® brightline haemocytometer. The 2008–2009 data on photoperiod (day length) were obtained for nearby St. John's (www.timeanddate.com). Potential predators of *O. aculeata*, including sea stars *Asterias rubens*, *Leptasterias polaris*, crabs *Hyas* spp. and hermit crabs *Pagurus* spp. were evenly distributed in the study site.

Brittlestars were concurrently collected in Harbour Main (Fig. 1) at 10 m depth and Admiral's Cove (Fig. 1) at 12 m, within two days of the initial St. Philip's samples (July 10 and 12, 2008, respectively). Samples were again collected in Admiral's Cove in December 2008. Harbour Main (47°26.243 N, 53°09.311 W) is a relatively sheltered inlet located approximately 55 km southwest of St. Philip's, at the base of Conception Bay. Admiral's Cove (47°05.320 N, 52°54.364 W) is a much more exposed and dynamic environment located on the opposite side of the northeast Avalon Peninsula, approximately 166 km away along the coastline. Samples were collected from underneath 6–9 rocks in Admiral's Cove and from 7 rhodoliths in Harbour Main, using the previously described methods.

2.2. Processing

Live brittlestars were brought back to the laboratory within 1 h of collection and processed immediately. For each individual, two perpendicular measurements of disc diameter were recorded using the imaging software Simple PCI© (v. 6.0) from photographs taken under a Nikon SMZ1500® stereomicroscope attached to a Nikon DXM1200F® digital camera. Only sexually mature female