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Reproductive investment, synchrony and recruitment success in marine broadcast spawners: Effects of mating system and habitat (exposed shore versus estuary)

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ABSTRACT

The timing and synchrony of gamete release in broadcast spawners have important implications for fertilization success, recruitment and to explain differences in reproductive success under distinct reproductive modes in sympatry. Our objective was to compare the reproductive timing and investment for sister species with contrasting mating systems; *Fucus guiryi* (selfing hermaphroditic) and *Fucus vesiculosus* (dioecious) in habitats with different wave exposures (exposed shore and estuary). Over two months, daily gamete release, recruitment and population structure were recorded. Our results show spawning synchrony between species and habitats, but release events in hermaphrodites occupied broader temporal windows in estuarine than exposed shore habitats. On the exposed shore both species increased the synchrony of release and amount of eggs. In the estuary, hermaphrodites relied on broader temporal spawning windows and a larger canopy, and the dioecious species had higher recruitment success, important factors determining persistence.

1. Introduction

The timing of reproduction plays a key role in the success, distribution and abundance of many marine organisms (Menge, 1991, 2000; Roberts, 1991). This is particularly important for broadcast spawners, for which environmental cues can regulate spawning synchrony and timing in ways that maximize reproductive success (Serrão and Havenhand, 2009). Furthermore, such effects might explain the divergence of reproductive modes in sympatric closely related species (Pearson and Serrão, 2006). Environmental cycles, such as daily, tidal, lunar and seasonal cyclic changes, are able to set the timing of reproduction in many marine organisms. The fucoid algae that structure ecosystems along cold and temperate shorelines worldwide use cues from tidal and/or lunar cycles to synchronise reproduction (reviewed in Pearson and Serrão, 2006; see also Monteiro et al., 2009, 2012). If the tidal cycle is the most important factor in timing reproduction, then periodicity of gamete release within a species would be expected to vary across the geographic range (spatial scale) according to different tidal patterns. Tidal patterns are also expected to cause variation at a range of temporal scales (Connell, 1985; Jenkins et al., 2000). Different habitats have different selective pressures and these might affect the timing of gamete release, increasing/decreasing the optimal windows of opportunity. On exposed shores (open coast), tidal cycles cause differences in hydrodynamic conditions and timing of tidal phases relative to the neighbouring sheltered estuarine habitats. Exposed rocky shore versus estuarine habitats can therefore provide useful case studies of natural populations under contrasting wave exposure regimes, allowing predictions derived from hypotheses of wave action effects on reproductive success to be tested.

Many marine organisms retain external fertilization as a means of reproduction; a process that depends crucially for its success on gamete encounters in the water column. The timing, as well as the synchrony of gamete release have important implications not only for fertilization success, but also for the success of recruitment and early survival in organisms with external fertilization. The divergence of reproductive strategies might contribute to reproductive

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isolation in sister species with similar geographical ranges (sympatric species) and has important ecological and evolutionary consequences. It also affects the distribution of genetic diversity and gene flow between and within populations. Different reproductive modes between closely related *taxa* also provide good models to understand the implications of spawning synchrony, hybridization and reproductive isolation in species with external fertilization (broadcast spawners).

Together with marine invertebrates and fish, the brown algal genus *Fucus* is one of the most well-studied groups of broadcast spawners (Pearson and Serrão, 2006). *Fucus* species occupy distinct, but often overlapping, niches on exposed shores, estuaries and lagoons. Several species of *Fucus* are sympatric throughout much of their ranges. Mating systems can vary between species from obligatory outcrossing to predominant self-fertilization (e.g., Engel et al., 2005; Perrin et al., 2007), potentially influencing evolutionary responses to habitat differences and reproductive isolation. Such variability in breeding systems is therefore interesting to assess the relationships between mating systems, reproductive ecology and reproductive isolation in sympatric closely related species with incomplete reproductive barriers (e.g., Billard et al., 2010).

The timing of spawning by *Fucus* species has been studied on several distinct Atlantic shorelines, with contrasting tidal regimes, along the European and American coasts (reviewed Pearson and Serrão, 2006). These include estuaries (Brawley, 1992), intertidal exposed rocky shores (Berndt et al., 2002; Ladah et al., 2003; Monteiro et al., 2012), tide pools (Pearson and Brawley, 1996), and the non-tidal Baltic Sea (Serrão et al., 1996). All these studies showed synchronous semilunar cycles of reproduction. Additionally, calm hydrodynamic conditions were required for gamete release (Serrão et al., 1996; Pearson et al., 1998). To date, most studies have focused on the reproductive periodicity of a single species and habitat, but have not addressed habitat-related variation within a species and/or the role of mating system on reproductive success. This study aims to fill this gap, by comparing reproductive timing, investment and success in sympatric species with divergent mating systems in different habitats, and assessing the hypothesis of stronger selection for synchronous spawning in obligate outcrossers relative to selfing species under similar environmental conditions (Pearson and Serrão, 2006).

Our objective was to test the hypothesis that the reproductive success of marine broadcast spawners is affected by interactions between habitat conditions (exposed rocky shore versus sheltered estuarine habitats) and reproductive modes (selfing hermaphrodites versus dioecious obligate outcrossers). We compared reproductive investment, spawning synchrony and recruitment success in hermaphroditic and dioecious species of the genus *Fucus*. The models were two co-occurring sister species that coexist as distinct entities despite potential hybridization (Billard et al., 2005; Engel et al., 2005; Zardi et al., 2011) in northern Portugal, *Fucus guiryi* (hermaphrodite) and *Fucus vesiculosus* (dioecious).

2. Materials and methods

2.1. Study habitats study habitats

The study was carried out at Viana do Castelo, northern Portugal, on estuarine (Lima estuary) and exposed shore (Praia Norte) habitats (41°41′47 N 8°51′10 W), which differed strongly in wave exposure. This region is the southernmost distribution limit where *F. guiryi* and *F. vesiculosus* co-occur in sympatry. Further south, *F. guiryi* inhabits only the open coast, while *F. vesiculosus* occurs exclusively in estuaries and sheltered coastal lagoons (Ladah et al., 2003). Where these species co-occur, *F. guiryi* is found predominantly higher in the intertidal zone than *F. vesiculosus*, despite overlapping at their vertical distributional edges (Billard et al., 2010; Zardi et al., 2011). Viana do Castelo has a cool temperate climate and a semidiurnal tidal regime. The west-facing shore (Praia Norte) contains rocky outcrops that reduce the predominant NW wave action (see Ladah et al., 2003; Araújo et al., 2012; Monteiro et al., 2009). The Lima river estuary is located ≈1 km south of Praia Norte. The study sites were located on the northern margin and ≈3 Km from the mouth of the estuary.

2.2. Model organisms

F. guiryi is a self-compatible hermaphrodite and *F. vesiculosus* is dioecious and therefore an obligatory outcrosser. In addition to different reproductive structures, these species are clearly distinguishable by the presence of air vesicles in *F. vesiculosus*. Both species were identified as described by Zardi et al. (2011). In the genus *Fucus* the reproductive structures (receptacles) develop apically. Each receptacle contains spherical conceptacles with numerous antheridia (each containing 64 sperm) and/or oogonia (each with 8 eggs). Sperm are biflagellate and reach ca. 5 μm in length whereas eggs are non motile and reach ca. 80 μm in diameter. In hermaphrodites all conceptacles contain both sperm and eggs, whereas in dioecious species the sperm and egg develop in separate conceptacles from different male and female individuals. Antheridia and oogonia are released through the ostiole from each conceptacle. Both are negatively buoyant (i.e., they sink), therefore settlement occurs immediately after release in the calm water conditions under which gamete release takes place (Serrão et al., 1996; Pearson et al., 1998). Shortly after release the antheridia and oogonia open, liberating the eggs and sperm and fertilization occurs externally, most likely at the bottom. Most eggs become fertilized (Brawley, 1992; Pearson and Brawley, 1996; Serrão et al., 1996; Berndt et al., 2002; Ladah et al., 2003; see also Pearson and Serrão, 2006 for a review of conditions influencing fertilization success), therefore a sample of settled eggs most likely consists almost entirely of zygotes. Egg tends to fall immediately below the releasing individual (Serrão et al., 1997). The highly restricted dispersal inferred in several studies (Serrão et al., 1997; Dudgeon and Petraitis, 2001; Coleman and Brawley, 2005; Engel et al., 2005; Perrin et al., 2007) might function as one ecological mechanism that prevents hybridization. Fertile hybrids do occur but are rare and are found mainly in the contact zone within the intertidal where the vertical species distributions overlap (Engel et al., 2005; Billard et al., 2005, 2010).

2.3. Daily spawning periodicity

The periodicity of egg settlement (which occurs immediately after spawning) was monitored daily from June 7 to August 5 2009, for *F. guiryi* and *F. vesiculosus* in two habitats (exposed shore and estuary). The eggs were collected on artificial substrates (5.96 cm^2, as described in Ladah et al., 2003) with a roughened surface to promote zygote settlement and adhesion. Two sites per habitat were haphazardly selected in the centre of the intertidal range of each species. Sites within species were ca. 15 m apart, and more than 5 m from the nearest individual of the other species. In *F. guiryi*, the study sites were at heights of 2.4 and 2.3 m on the exposed shore and in the estuary, respectively. In *F. vesiculosus* the sites were at 1.7 and 1.9 m on the exposed shore, and 1.7 and 1.8 m in the estuary. Five disks per site were fixed to the rocks with bolts, under different algae ca. 10 cm apart. Disks were collected and replaced daily during the diurnal low tide and the number of eggs was counted in the laboratory under a dissecting microscope (as in Monteiro et al., 2012).

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