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HABITAT DIFFERENCES IN THE TIMING OF REPRODUCTION OF THE INVASIVE ALGA *SARGASSUM MUTICUM* (PHAEOPHYTA, SARGASSACEAE) OVER TIDAL AND LUNAR CYCLES[1]

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Sargassum muticum **(Yendo) Fensholt is an invasive species that is firmly established on intertidal and subtidal rocky shores of Europe and the Pacific coast of North America. Local success and spread of *S. muticum* is thought to rely on its reproductive potential that seems dependent on exogenous factors like tidal and lunar cycles. This study is the first to compare the reproductive patterns (periodicity of egg expulsion and embryo settlement) of this invader in two different habitats: the middle and low intertidal. The combination of monthly, daily, and tidal samples at triplicate sites within each habitat showed a semilunar periodicity of egg expulsion and embryo settlement coincident with increasing tidal amplitude just before full and new moons. In both habitats, duration of each egg expulsion event was ~1 week, and embryo settlement occurred during the first daily low tide and with the incoming high tide during spring tides. However, both expulsion and settlement started 1–2 d earlier, expulsion saturation was faster, and settlement was higher in the mid- compared to the low intertidal. Our results suggest that the exact timing of gamete expulsion and embryo release of *S. muticum* responds to local factors, including tidal cues, which result in differences between mid- and low-intertidal habitats.**

Key index words: **egg expulsion periodicity; embryo settlement periodicity; reproductive ecology; *Sargassum muticum*; tidal and lunar cycles**

Abbreviations: **PVC, polyvinyl chloride**

The intertidal zone of rocky shores presents large variations in physical conditions that occur over small distances, comparable in magnitude to those occurring in scales of kilometers in most terrestrial ecosystems. These extreme gradients make intertidal rocky shores a good model to study the role of environmental factors on the reproductive success of marine species. The combination of favorable pre- and postsettlement environmental conditions is crucial for the success, distribution, and abundance of marine populations and has been suggested to be a major factor regulating population structure on rocky shores (Menge 1991, 2000, Roberts 1991). In marine populations, settlement is highly variable at a range of temporal and spatial scales (Connell 1985, Jenkins et al. 2000). The timing of reproduction is affected by the interactions of several biological and physical factors, which vary along timescales, mostly with the light:dark (L:D), tidal, lunar, and seasonal cycles (Yamahira 2004). The influence of tidal and/or lunar cycles on reproductive synchrony has been reported for many marine organisms, the most famous being the coral spawning events on a few full-moon and last-quarter-moon nights per year (Harrison et al. 1984).

In several fucoid algae, the reproductive periodicity is correlated with lunar or tidal cycles, as has been reported for *Silvetia compressa* (previously named *Pelvetia*, Johnson and Brawley 1998), *Fucus ceranoides* (Brawley 1992), *Fucus distichus* (Pearson and Brawley 1996), *Fucus vesiculosus* (Andersson et al. 1994, Serrão et al. 1996, Berndt et al. 2002, Pearson and Serrão 2006), *Sargassum vestitum* (May and Clayton 1991), and *Sargassum muticum* (Fletcher 1980, Norton 1981, Okuda 1981). The reproductive periodicity might, however, vary across the geographic range within a species if tidal cycles are involved, because tidal cycles show geographic variations (Pearson and Serrão 2006). To date, studies focusing on patterns of gamete release and reproductive investment have not addressed small-scale habitat-related variation. Reproductive timing and synchronized reproduction itself may increase fertilization success and can be important for the survival of eggs and larvae and/or dispersal capacity and successful settlement, as well as predator avoidance (Yamahira 2004).

The Asian brown seaweed *Sargassum muticum* is one of the most invasive algae in Europe and North America (Norton 1977), having rapidly spread and firmly established itself as a major colonizer of lower littoral and shallow sublittoral regions (Critchley 1983a,b). The success and fast spread of *S. muticum* along European coasts is at least partly attributed to its reproductive potential (Umezaki 1984), extensive fertile season, and large number of reproductive structures produced (Hales and Fletcher 1989). In

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addition, the capacity for self-fertilization (Fletcher 1980, Norton 1981) might increase fertilization success, as has been suggested for self-compatible hermaphroditic fucacean algae (Brawley and Johnson 1992, Pearson and Brawley 1996). This phenomenon is considered one of the main reasons for the success of introduced species (Norton 1976, Prud'homme van Reine and Nienhuis 1982). This species is an interesting system for studies of reproduction because (1) it has shown the capacity for rapid colonization along European and North American coasts (Norton 1977, 1981, Critchley 1983b); (2) it can inhabit different types of habitats; and (3) gametes are expelled from receptacles in a number of discrete pulses, but instead of being released immediately into the seawater, they are fertilized and retained outside the receptacle for one to several days after fertilization (Fletcher 1980, Norton 1981, Hales and Fletcher 1990). This last attribute facilitates observations of gamete release pulses.

Seasonal patterns of growth and reproduction have been reported for *S. muticum* in different latitudes (see Fletcher and Fletcher 1975, Okuda 1981, Critchley 1983a, De Wreede 1983, Deysher 1984, Espinoza 1990, Fernández et al. 1990, Arenas and Fernández 1998). In their native region, Japan, the liberation of eggs takes place during spring tides, probably with a semilunar release pattern (Okuda 1981). In invaded regions like England and Southern California, embryo release is synchronized and occurs on average every 13 d, just after spring tides (Fletcher 1980, Norton 1981). Laboratory studies showed that the release is influenced by temperature and lunar phase, but in the field, the lunar phase seems to have more influence than temperature (Fletcher 1980, Hales and Fletcher 1990). In Portugal, the fertile season occurs between January and September, depending on the location, and varies from year to year. The expulsion and embryo settlement in tidal pools occurs during spring tides but depends on local conditions, as differences between locations and pools have been observed (Engelen et al. 2008). Other studies reveal annual differences in fertility as well as differences between invaded and native regions (Deysher 1984, Arenas and Fernández 1998).

Reproductive patterns in *S. muticum* have been studied at regional scales, but never at a local scale, between different types of habitats. In this study, we describe natural egg release and embryo settlement in two different intertidal habitats. Our hypotheses are that (1) the reproductive periodicity of egg expulsion and embryo settlement is dependent on tidal and/or lunar cycles, and (2) the periodicity of egg expulsion and embryo settlement differs between habitats. To test these hypotheses, we quantified the daily variation of egg expulsion and embryo settlement along tidal cycles in both habitats.

MATERIALS AND METHODS

Study site. The Portuguese coastline is influenced by a semidiurnal tidal regime, in which two similar tidal cycles occur per day. The study was carried out at the intertidal zone of Praia Norte (Viana do Castelo, northern Portugal, 41°41′47 N 8°51′10 W) where the shoreline is protected from wave action by offshore rocky bluffs that greatly reduce the predominantly NW wave action. *S. muticum* inhabits mid-intertidal pools, lower intertidal channels, and subtidal zones; the lower intertidal channels are submersed during the neap tides and form large pools during the spring tides. For further description of the area, see Ladah et al. (2003).

Periodicity of egg expulsion. The egg expulsion of *S. muticum* was monitored from August 1 to September 17, 2005, and from May 8 to June 30, 2006, in three mid-intertidal pools and three sites in a tidal channel dominated by *S. muticum*. Eggs of *S. muticum* are fertilized on the surface of the receptacles and are retained until settlement takes place (Deysher and Norton 1982). As it is not possible to distinguish by eye eggs from zygotes or early embryos, we use the term ''egg'' as long as the egg and embryo are attached to the receptacle and the term ''embryo'' when settlement takes place. Egg expulsion was assessed by collecting two fertile secondary laterals from five haphazardly selected individuals within each of the three sites within each habitat. Daily sampling was done every hour during low tide, as soon as the algae were accessible, which usually included some time before and after the area was uncovered by the tide. Egg expulsion of each sampled individual was calculated as the percentage of laterals containing receptacles with extruded eggs.

Periodicity of embryo settlement. The embryo settlement of *S. muticum* was monitored daily, from August 1 to September 17 of 2005 and from May 8 to June 30 of 2006, in three mid-intertidal pools and three sites in a tidal channel (in the same pools and sites used for the egg expulsion work). The periodicity of embryo settlement on the substratum was assessed with artificial substrates (5.96 cm^2) with rough surfaces to promote embryo adhesion (see Ladah et al. 2003). In each pool and site in the channel, a PVC holder containing three settlement disks was fixed at two haphazardly selected positions. The disks were collected daily during low tide, and the number of embryos on each disk was counted in the laboratory under a dissecting microscope (Zeiss, Stemi 2000-C).

Statistical analyses. To test whether there were significant differences ($P < 0.05$) between habitats and times (h) in the percentage of egg-bearing individuals ($n = 5$ in each site), a test for proportions using the normal approximation to the binomial was used (Zar 1999). The settlement experiment followed a spatial nested design to test the effect of habitat (middle-intertidal pools and low-intertidal channel—2 levels, fixed factor), site (3 levels, random factor and nested within habitat), and day (days with observed settlement, 13 in 2005 and 24 in 2006). Mean embryo settlement densities were analyzed using analysis of variance (ANOVA). Significant interactions between days and habitat were explored using one-way ANOVAs for each day. The variances were homogenous (Cochran's test), and thus no transformations were performed.

RESULTS

Egg expulsion. Egg expulsion in *S. muticum* occurred with a periodicity of 2 weeks (semilunar) coincident with full and new moons, and with spring tides in both the mid- and low intertidal (Figs. 1, 2). The first occurrence of egg expulsion was observed

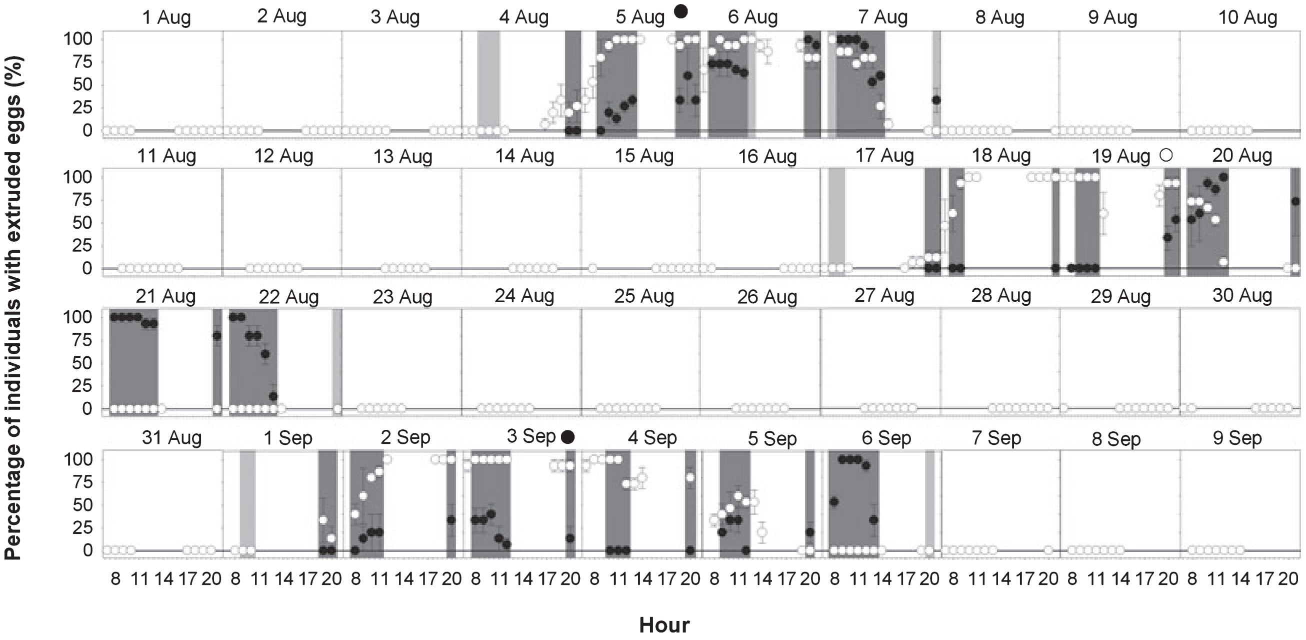

FIG. 1. Egg release by *Sargassum muticum* during diurnal low-tide periods in 2005. Percentage of branches (mean ± SE) with extruded eggs in mid-intertidal pools (open symbols) and low-intertidal channel (closed symbols). Dark grey backgrounds represent periods with significant differences between habitats, as opposed to light grey backgrounds. Open and closed circles above plots indicate full and new moon, respectively. Sampling was performed daily from August 1 to September 17, 2005.

before new or full moons in mid-intertidal pools and 1 or 2 d later in the low-intertidal channel. The duration of the egg expulsion period varied between years. In 2005, when sampling took place between August 1 and September 17, expulsion periods of 4–5 and 3–5 d were observed, in the mid-intertidal and in low intertidal, respectively (Fig. 1). In 2006, when sampling took place between May 8 and June 30, expulsion was observed during longer periods, 7–9 d. The major events were observed from 20 to 28 June 2006 in the mid-intertidal and from 21 to 29 June 2006 in the low intertidal (Fig. 2).

In 2005, the egg expulsion at the mid-intertidal increased 1 or 2 d before the full and new moon days, whereas in the low intertidal, such an increase only took place a few days later, in general after full and new moon (Fig. 1). In 2006, the egg expulsion occurred earlier, 4–5 d before the full and new moon days and continued for longer than in 2005 (Fig. 2).

In general, we found significant differences between habitats in both years. In 2005, there were significant differences in egg expulsion between habitats in 80 out of 92 observations (87%) (dark grey boxes in Fig. 1). In 2006, 127 (64%) out of a total of 198 observations showed significant differences between habitats (Fig. 2). The total observations mentioned above for each year correspond to the days when egg expulsion was observed in at least one of the habitats. The percentage of individuals with extruded eggs reached a maximum of 100% in both years. The data from 2006 illustrate that in the first 2–4 d of each event, the percentages are normally near 100%. The standard errors of the percentage of individuals with extruded eggs were small, especially when the percentages were 100% or near 100%, in both habitats, indicating that egg expulsion was synchronized within each habitat.

Embryo settlement. Embryo settlement showed a clear semilunar pattern, coinciding with, or just after, the full and new moons (Fig. 3). The settlement period was 3 to 5 d in the late summer of 2005 and 4 to 7 d in the early summer of 2006. In both years, egg settlement started 1 to 2 d earlier in mid-intertidal pools than in the low-intertidal channel. Settlement densities differed between habitats and among sites depending on day (Table 1). During the first days of settlement, densities were higher in the pools, but toward the end of each event, the differences were either reversed (see all events in 2005 and the first in 2006; Fig. 3) or disappeared (May 29 and June 14 in 2006; Fig. 3). In 2005, the values for maximum embryo settlement in the tidal pools and in the tidal channel were 1.79 embryo · $cm^{-2} \cdot d^{-1}$ and 0.43 embryo · $cm^{-2} \cdot d^{-1}$, respectively, whereas the corresponding values in 2006 were 2.18 embryo · $cm^{-2} \cdot d^{-1}$ and 1.34 embryo · $cm^{-2} \cdot d^{-1}$.

DISCUSSION

S. muticum showed a semilunar pattern of egg expulsion and embryo settlement, coincident with full and new moons (spring tides) in both habitats

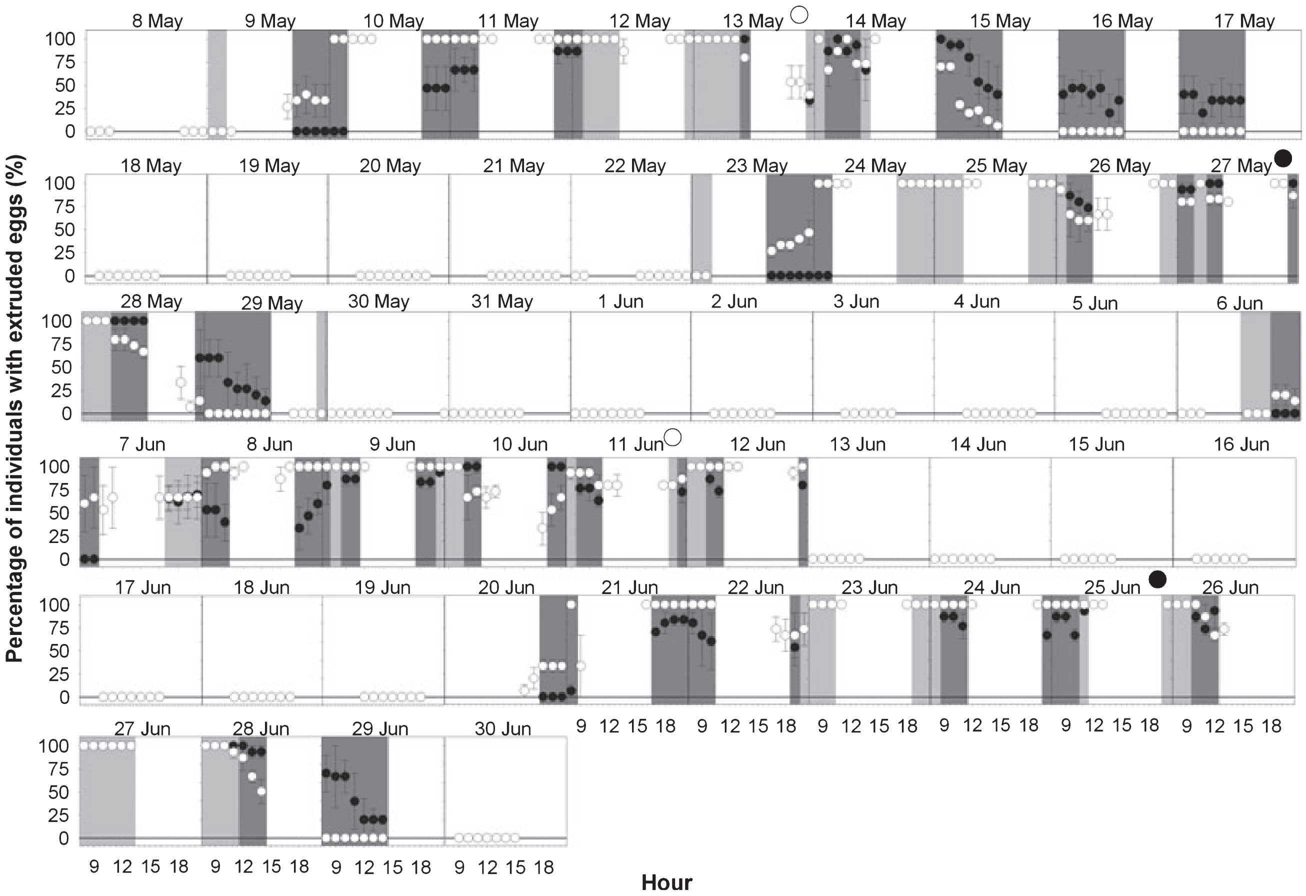

FIG. 2. Egg release by *Sargassum muticum* during diurnal low-tide periods in 2006. Percentage of laterals (mean ± SE) with extruded eggs in mid-intertidal pools (open symbols) and low-intertidal channel (closed symbols). Dark grey backgrounds represent periods with significant differences between habitats as opposed to light grey backgrounds. Open and closed circles above plots indicate full and new moon, respectively. Sampling was performed daily from May 8 to June 30, 2006.

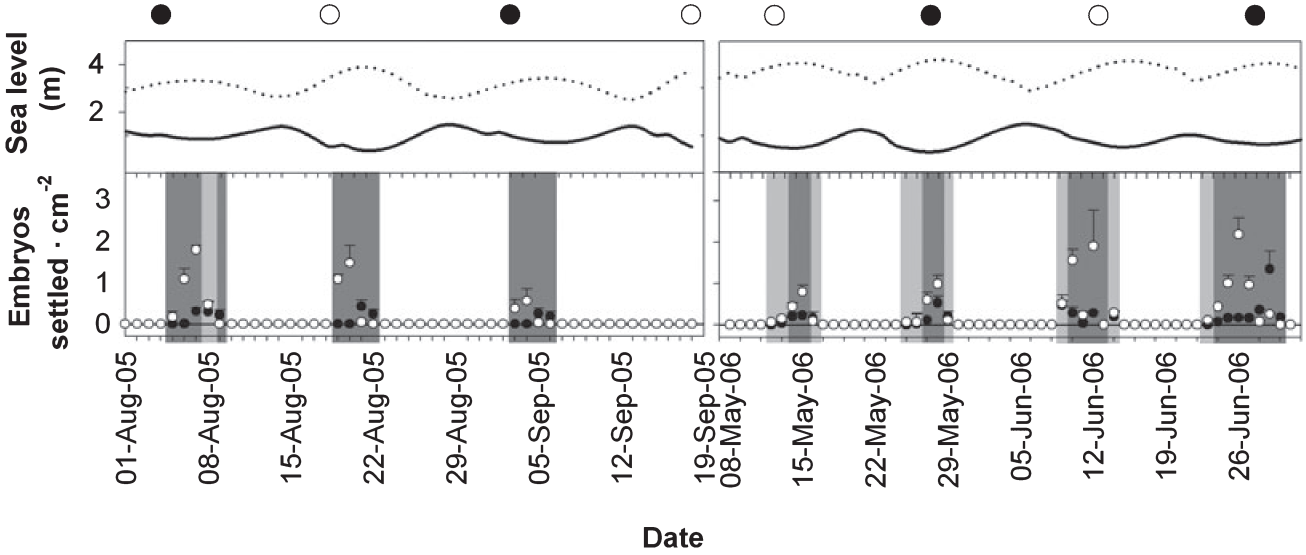

FIG. 3. Daily embryo settlement of *Sargassum muticum* in mid-intertidal pools (open symbols) and low-intertidal channel (closed symbols) in 2005 and 2006. Error bars show standard error ($n = 3$). Lunar phases (full and new moons) are shown above the graphs. The low-tide (black line) and high-tide (dotted line) levels are shown in the box above each plot. Dark grey backgrounds represent days with significant differences in settlement between habitats, as opposed to light grey backgrounds. Sampling was performed daily from August 1 to September 17 in 2005 and May 8 to June 30 in 2006.

TABLE 1. Analysis of variance of the effects of habitat and site within habitat on *Sargassum muticum* settlement density (embryo · cm^{-2}) in 2005 and 2006.

	2005				2006			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*
Habitat	1	16.982	12.372	0.245	1	18.731	12.014	0.257
Site (habitat)	4	1.373	10.078	0.001	4	1.559	12.508	0.001
Day	12	2.911	0.767	0.673	24	3.990	1.175	0.348
Day × habitat	12	3.794	13.241	0.001	24	3.396	6.768	0.001
Day × site (habitat)	48	0.287	2.104	0.001	96	0.502	4.026	0.001
Residual	390	0.136			750	0.125		

(mid-intertidal pools and low-intertidal channel) in Viana do Castelo (northern Portugal). This pattern is in agreement with natural reproduction in Japan (Okuda 1981), but not with patterns in England and Southern California where reproduction occurred after spring tides (Fletcher 1980, Norton 1981). The association of propagule release with lunar or tidal phases has been reported in many marine organisms, including fucoids, but phase shifts in the timing of release may occur across different geographic locations within the same species (Pearson and Serrão 2006). On a biogeographic scale, the occurrence of phase shifts associated with the lunar cycle within a species suggests that the differences in reproductive periodicity may be associated with geographic shifts in daily tidal patterns between sites. Smaller scale differences in propagule release patterns are, however, rarely documented and poorly understood (but see Pearson and Brawley 1996, Pearson et al. 1998).

In this study, we have documented local scale differences in the timing and rate of propagule expulsion and release between sites at two different levels of the intertidal zone. Both egg expulsion and embryo settlement started a few days earlier in the mid-intertidal pools than in the low-intertidal channel. Both types of events were asynchronous between habitats, suggesting that the trigger mechanism(s) may be associated with the amount of time that the habitat is disconnected from the sea, and thus to tidal amplitude. Many physical factors vary in tide pools as the tidal amplitude increases, particularly on sunny days, such as an increase in temperature, salinity, and pH and a decrease in CO_2 availability for photosynthesis. The lower intertidal environment would need more time to attain a certain threshold in any of these parameters. In other fucoid species that occur in tide pools, gamete release is triggered by limiting concentrations of inorganic carbon at low tide (Pearson et al. 1998). A similar type of mechanism could explain our observations that, higher in the intertidal, gamete expulsion starts a few days earlier than in the low intertidal, since a putative environmental threshold related to exposure time would be reached earlier in the higher intertidal.

Other factors, such as photoperiod and temperature, have been shown to regulate the physiological mechanism of reproduction in *S. muticum* and other species (Fletcher 1980, Norton 1981, Okuda 1981, Santelices 1990), but these processes have been reported to take place along larger temporal scales than the daily scales assessed in this study. Most available information on the effects of environmental factors on the reproductive success of *S. muticum* is related to the physiological limits for propagule survival rather than on their influence on the patterns of propagule release, so the information is scant and further studies are warranted.

The synchrony of egg expulsion and embryo settlement is an important factor that may contribute to the success of this species. Synchrony increases the concentration of eggs and sperm and consequently increases fertilization success and satiation for the herbivores (see Reed et al. 1997). *S. muticum* germlings are known to be susceptible to grazers, which can reduce their survival by 28%–86% (Sjøtun et al. 2007). The influence of synchrony on fertilization success may be less important for *S. muticum* because it is a monoecious seaweed capable of self-fertilization (Fletcher 1980, Norton 1981). Furthermore, eggs are retained outside the receptacle for several days during which fertilization can occur (Fletcher 1980, Norton 1981, Hales and Fletcher 1990), a process which tends to increase the success of fertilization by integrating the effects of variable sperm concentrations over a time period of a few days, as has been reported for marine invertebrates (Wahle and Gilbert 2002). In this study, it was observed that the *S. muticum* eggs were retained for 1 to 3 d. This egg retention at the surface of the receptacles is also expected to increase recruitment success by facilitating fast adhesion to the substrate, because when embryos settle they already possess developing rhizoids (Deysher and Norton 1982).

Our observations on marked branches showed intraindividual differences (i.e., differences within individual thalli) in the time of egg expulsion, that is, not all primarily laterals of a single individual expelled the eggs at the same time (unpublished results). This mechanism may allow cross-fertilizations, preventing potential inbreeding depression that could result from selfing. It is not known whether any mechanism exists in *S. muticum* that allows for selection of nonselfed sperm if multiple sperm are available during synchronous release periods. A significant amount of selfing is nevertheless expected, given the proximity of female and male conceptacles in the receptacle. Selfing does provide reproductive assurance, a very important characteristic for an invasive species such as *S. muticum,* which allows single individuals to start new populations.

The variable duration of egg expulsion events between 2005 (3–5 d) and 2006 (7–9 d), and in embryo settlement (2–4 d in 2005 and 4–7 d in 2006), may reflect the timing of the study. In 2005, the study was carried out in the last period of the reproductive season, whereas in 2006, the fieldwork was undertaken in the period of maximum reproductive biomass. Observations on *Fucus* spp. at the same site showed that expulsion events can be longer during the peak of reproduction compared to the rest of year (C. A. Monteiro, G. A. Pearson, E. A. Serrão).

Our results revealed much lower settlement densities of *S. muticum*, on the order of 2.18 embryos $\cdot$ cm^{-2} $\cdot$ d^{-1} (maximum average between pools), than observations in the southwest coast of Portugal, on the order of 50 embryos $\cdot$ cm^{-2} $\cdot$ d^{-1} (Engelen et al. 2008). This difference was not a methodological effect as the sampling procedure and disks used were the same in both studies, nor was it due to a difference in plant densities, but rather suggests a higher reproductive investment at the geographical distribution limit (southwestern Portugal populations) or environmental and biotic (herbivory) differences.

This study is the first to compare the reproductive patterns of the invasive species *S. muticum* in two different habitats in the middle and low intertidal. Our results show a strong relationship of both egg expulsion and embryo settlement with spring tides (during full and new moons) in both habitats. However, the consistent earlier start and faster egg expulsion and embryo settlement observed in higher intertidal levels suggest that tidal amplitude and consequent small-scale variations in local environmental cues play an important role in the exact timing of reproduction at different tide levels. This capacity for synchronous egg expulsion and embryo settlement during spring tides in response to very local cues may play an important role in the high reproductive success and invasiveness of this species.

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