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Spatial patterns of reproductive synchrony by four genera of tropical green seaweed across a latitudinal gradient in the Caribbean.

K. E. Clifton[1]

1) Lewis and Clark College, Department of Biology, 0165 SW Palatine Hill Rd., Portland OR 97219, USA

Abstract. Spatial and temporal patterns of reproductive effort are an especially significant feature of fertilization success for virtually all broadcast spawning organisms. While most research efforts on this topic have focused on varying temporal scales of reproductive synchrony (i.e., diel, lunar, and seasonal scales), patterns of reproductive synchrony on varying spatial scales (i.e. from meters to hundreds of kilometers) are less well studied. Simultaneous investigations of sexual reproduction by tropical green seaweeds (e.g., *Caulerpa, Halimeda, Penicillus, Udotea*) across a latitudinal gradient in the Caribbean (Panama, U.S. Virgin Islands, Florida) reveal patterns of reproductive synchrony on different spatial scales. Within a region, spatial synchrony often extends beyond local populations (meters to tens of meters) to at least scales of tens of kilometers, however, such synchrony is not maintained across larger (hundreds of kilometer) spatial scales. Relative synchrony within and between genera is maintained across this larger latitudinal gradient, however. Reproductive seasonality also shows an interaction with latitude for these seaweeds, with shorter, temporally delayed seasons of reproductive activity occurring at higher latitudes.

Key words: Broadcast spawning, Coral reef, Green algae, *Halimeda*, *Penicillus, Udotea*.

Introduction

Broadcast spawning, the release of gametes directly into the water column, is a common reproductive tactic for a diverse array of benthic marine organisms including stony corals (e.g., Harrison *et. al*. 1984; Baird et. al., 2001), soft corals (e.g., Lasker et al. 1996), echinoderms (e.g., Babcock and Mundy 1992; Levitan 1991, 1995), green algae (e.g., Clifton 1997, Clifton and Clifton 1998), sponges (e.g., Hoppe and Reichert 1987; Fell 1993; Ritson-Williams et al. 2005), and mollusks (e.g., Shelley and Southgate 1988; Lucas 1994; Kenchington et al. 2006). Synchrony of gamete release in both space and time is a consistent feature of these reproductive events, as organisms that match the timing of their gamete release with those of neighbors should enjoy increased fertilization success. Understanding the proximate cues that organize these reproductive events, as well as their ecological and evolutionary consequences remains a topic of interest to coral reef biologists.

Broadcast spawning can be examined at diel, lunar, and seasonal temporal scales. Patterns of reproductive timing are becoming increasingly better known, particularly for well-studied broadcast spawners like the stony corals (e.g., Tanner 1996, Guest 2004, Guest et al., 2005, Mangubhi and Harrison 2008). Studies of spatial patterns of reproduction have received less attention (although see: Oliver et al. 1988; Willis et al. 1985; Hughes et al. 2000; and Baird et al. 2002). As might be expected, even less is currently known about the degree to which temporal patterns of broadcast spawning behavior are preserved or altered at increasingly larger spatial scales.

This paper describes temporal and spatial patterns of broadcast spawning behavior for 4 genera of Caribbean seaweed (Bryopsidales) across a latitudinal gradient of 15°. Diel and seasonal patterns of gamete release for these algae at a single location (Caribbean Panama) are already described (Clifton and Clifton 1998). When compared with more northerly sites (St Croix, US Virgin Islands and Key Largo, Florida), changes in the diel timing of gamete release shifted with changes in the onset of sunrise. At the most northern site seasonal shifts in reproductive activity correlated with an annual change in water temperatures. Interspecific patterns of reproduction observed at local spatial scales were preserved over latitudinal gradients. This suggests that, at any one location, the relative contribution that various endogenous and environmental factors ultimately make to the timing of reproduction will vary, depending on the temporal scale being examined.

Material and Methods

Four genera of green macroalgae in the Order Bryopsidales (*Halimeda*, *Caulerpa*, *Penicillus*, and

Udotea) were observed for this study. All are common and abundant within shallow tropical marine communities across the Caribbean, including coral reef, seagrass bed, and mangrove habitat. Algae were identified to species using Littler and Littler (2000) and Littler *et. al.,* (1989).

Reproductive activity was quantified from daily surveys of shallow marine habitats at one of three sites: Kuna Yala, Panama (9°33' N, 78°56'W); Tague Bay, St Croix, US Virgin Islands (17°45' N, 64°36'W; and Key Largo, Florida (25°05' N, 80°24'W). Observers snorkeled along proscribed routes for 30–60 minutes, examining a minimum of 500 thalli for macroscopic evidence of impending sexual reproduction. This occurs 12–24 hrs prior to gamete release for seaweeds in the genus *Halimeda* and *Caulerpa*, 36–48 hrs for *Penicillus* and *Rhypocephalus*, and 60-72 hrs for *Udotea* (Clifton and Clifton 1998). Time of gamete release was recorded during direct observations of undisturbed seaweeds during the early morning spawning period. Initial time and duration of gamete release was noted following the methods of Clifton and Clifton (1998). Seawater temperatures for Panama and St Croix were measured using "StowAway Tidbit" automated temperature loggers (Onset Computer Corp). Temperatures from Florida were downloaded from archived NOAA Data Buoy information (www.ndbc.noaa.gov).

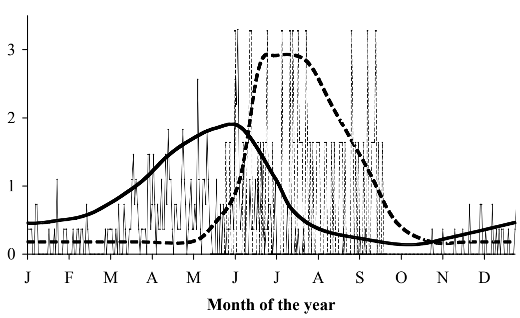

Figure 1: Seasonal patterns of sexual reproduction by green seaweeds at two sites: Panama (solid lines) and Florida (dashed lines).

Results

Seasonal patterns of reproduction

Populations of tropical green macroalgae across the Caribbean showed different seasonal patterns of reproductive activity. At 9° N latitude (Panama), reproduction occurred almost year-round, with a broadly seasonal peak from April to July that roughly corresponds to the onset of the region's annual wet season (Fig. 1). At 15° N latitude (Florida), reproductive activity occurred later in the year, between the months of June and September (Fig. 1). In general, a larger proportion of the population participated in a reproductive event on any given day at the more northern site (K. Clifton, *unpub data*), suggesting that, on an annual basis, total levels of reproduction between the two sites may not be that different. The seasonal peak of reproduction at the northern site correlated with the period of time when local water temperatures exceeded 27°C (Fig. 2).

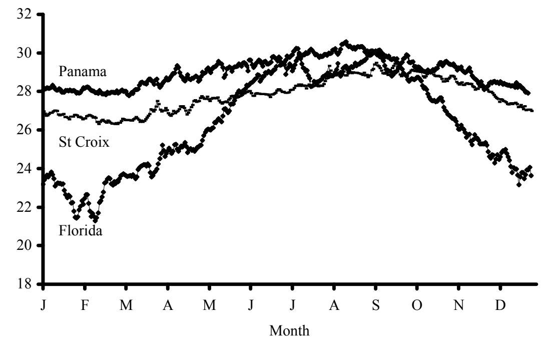

Figure 2: Seasonal variance in surface temperature at three Caribbean sites. The period of time when temperatures exceed 27°C is shorter and later in the year at higher latitudes. See text for details.

Sub-seasonal patterns of reproduction

The sub-seasonal scheduling of sexual reproduction by tropical green seaweeds does not show any obvious relationship to lunar or tidal cycles (Clifton 1997). There is, however, some regularity of spawning effort and this differs from one species to the next. For some species, a subset of the population reproduces every few days and this pattern is maintained across sites that differ in latitude. For example, the alga *Caulerpa cupressoides* reproduced roughly once every 7 days during the seasonal peak of reproduction in 1999 at all sites (Fig. 3).

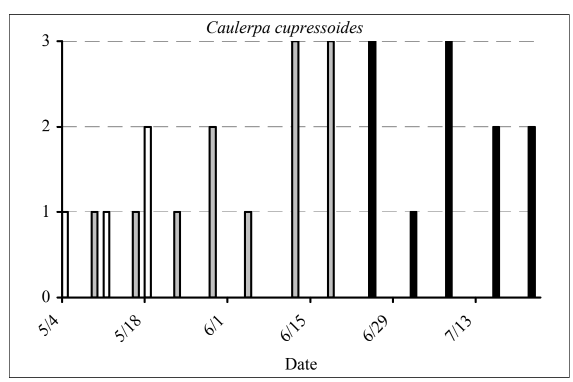

Figure 3: Patterns of sub-seasonal reproduction for *Caulerpa cupressoides* at three Caribbean sites. Color scheme as follows: open bars = Panama; shaded = St. Croix, USVI; black = Key Largo, Florida. "Extent of population" represents the percent of the population participating in the reproductive event as follows: 1: < 1% of the population; 2: 1% - 3%; 3: > 3% of the population.

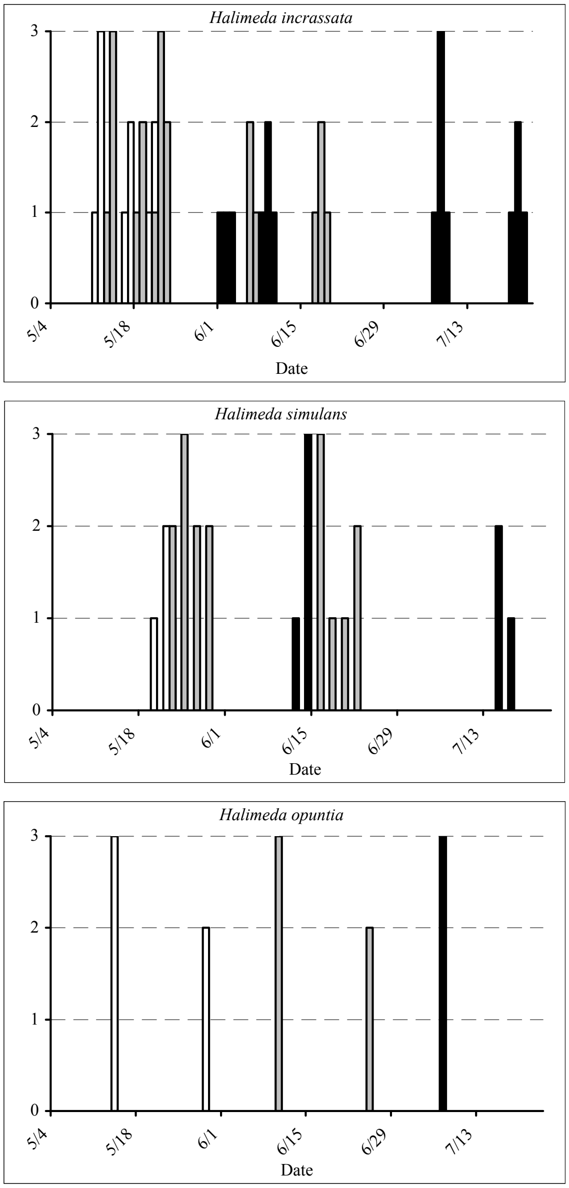

Figure 4: Patterns of sub-seasonal reproduction for three species of *Halimeda* observed during a three-month period in 1999 at three sites in the Caribbean. *H. incrassata* and *H. simulans* are closely related species that occupy similar soft bottom habitats. *H. opuntia* is a larger, sprawling species that occurs on reefs and in soft bottom habitats. Specific dates of observation: Panama: 5/4-6/29/99; St Croix, USVI: 5/4-6/28/99; Florida: 5/20-7/23/99. Shading and axes as in Fig. 3.

Other species showed quite different sub-seasonal patterns of reproductive activity. For example: *Halimeda incrassata* tended to reproduce in three day pulses, separated by gaps of 7 – 14 days; *Halimeda simulans* tended to reproduce every other day at somewhat varied levels of intensity for a several reproductive events, with less regular gaps between these pulses; and *Halimeda opuntia* tended to reproduce roughly every 14 days, with some variance around this tendency (Fig. 4). As with *Caulerpa cupressoides*, however, interspecific differences in the sub-seasonal timing of reproduction by different species of *Halimeda* were essentially preserved at all three sites, despite their differing latitude. Similar trends were found for four species of *Penicillus* (*P. capitatus*, *P. dumetosus, P. lamouroxii*, and *P. pyriformes*) as well as *Udotea flabellum*. *P. capitatus* and *P. lamorouxii* generally showed highly overlapping sub-seasonal patterns of reproduction (i.e., they showed a strong tendency to reproduce on the same day) as did the heterogeneric pair of *P. pyriformes* and *U. flabellum*. This latter pair tended to release gametes 2-3 days following bouts of reproduction by the former pair and, as with other species, this trend was preserved across a latitudinal gradient.

Diel patterns of reproduction

Tropical green seaweeds release their gametes just prior to sunrise and the precise timing of this release is both highly predictable and species-specific (Clifton 1997, Clifton and Clifton 1998). For all species the timing of gamete release, relative to sunrise, was observed to shift to an earlier time with increasing latitude.

For example, the timing of gamete release for *Halimeda tuna* at the three Caribbean sites shifted approximately 30 seconds earlier for every degree of change in latitude across the 15 degree change in latitude across the region (Fig. 5). This trend was further supported by a single observation of gamete release by *H. tuna* from the more northerly, Adriatic Sea. A quadratic curve fitted to the mean time of release at each location ($y = -0.011x^2 - 0.107x - 11.37$) provided an excellent fit to these points (Fig. 5; $R^2 = 1.00$; n = 4; $p = 0.01$).

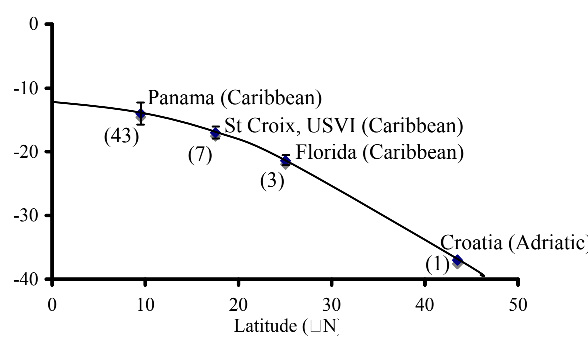

Figure 5: Quadratic curve fit to the mean time of gamete release for *Halimeda tuna*, relative to sunrise and as a function of latitude. Data from Panama are cumulative from observations in 1996-1998. Observations at the other three sites were made in 1998-1999. The single observation of gamete release in the Adriatic (43°9' N, 16°11'E) was provided by Ante Zuljevic. Sample sizes are in parentheses and error bars are ± 2 standard errors.

Discussion

As a general result, diel and seasonal patterns of broadcast spawning by tropical green seaweeds were found to shift with latitude, while sub-seasonal patterns of reproductive behavior were relatively unchanged, irrespective of distance from the equator. These results provide clues as to the proximate mechanisms structuring patterns of temporal synchrony in these broadcast spawning organisms.

Changes in the seasonal peak of reproduction by tropical green seaweeds to a later time of year in higher latitudes follows the trend seen in some stony corals, although simultaneous observations at several sites spanning large latitudinal distances are not common (see Baird et al. 2002; Wilson and Harrison, 2003; Nozawa, et al. 2006). For tropical green algae, the strong correspondence of the onset and cessation of seasonal reproductive activity at higher latitudes with the presence of water temperatures greater than 27°C strongly implicates a role for temperature as an important determinant of the timing of seasonal patterns of reproduction.

Unlike many other broadcast spawning organisms, tropical green seaweeds do not show lunar or tidal patterns of sub-seasonal reproduction (Clifton 1997, Clifton and Clifton 1998), yet the data presented here suggest there is some temporal structure to their patterns of reproduction from day to day. Although these are quite variable from species to species, the relative duration of inter-spawn intervals does show some within species specificity, as well as some intriguing patterns of correlation between species pairs such as *Penicillus capitatus* and *P. lamouroxii* or *P. pyriformes* and *Udotea flabellum*. While the proximate cues that help organize sub-seasonal bouts of reproduction for these seaweeds is not revealed from the results here, the consistency of pattern that was retained, even across a latitudinal gradient of 15° suggests that such organizing cues do exist and the results described here should encourage further study of this topic.

On a diel temporal scale, the shift to an earlier time of gamete release with an increase in latitude supports the idea that changing levels of pre-dawn light are an important component of what structures the exact timing of gamete release on a given morning. The curvilinear aspect of the relationship between time of release and latitude, as shown for *Halimeda tuna* in Fig 5, suggests that the trigger for gamete release may be more a function of cumulative light exposure rather than an absolute threshold of light level.

While much work remains to be done on the proximate mechanisms that organize and promote bouts of gamete release by broadcast spawning organisms, the results presented here suggest that there is utility in the study of gamete release that is done on a variety of temporal and spatial scales. As such, future studies in this arena should be encouraged.

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