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MINI REVIEW

From molecules to moonbeams: Spawning synchrony in coral reef organisms

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Summary

A mini-symposium at the 11th International Coral Reef Symposium highlighted significant advances towards understanding the factors controlling reproductive timing and spawning synchrony in coral reef organisms. Studies of the phenology of reef organisms are finally moving beyond the purely descriptive and researchers are starting to explore the molecular mechanisms underpinning spawning synchrony. An increasing geographical focus of research, in particular much novel work from the centre of coral reef diversity, is enabling rigorous examination of latitudinal gradients of spawning synchrony and the role of environmental factors such as sea temperature and insolation in regulating spawning timing.

Key words: Coral reefs, evolution, reproduction, spawning synchrony

Introduction

Sexual reproduction is one of the most important processes for the persistence of reefs, yet we know surprisingly little about the factors that regulate reproductive events for the majority of reef species. Worldwide, reef systems are being rapidly degraded and face a multitude of threats including global climate change, over-fishing and declining water quality. While we have a reasonable understanding of the effect of these threats with regard to mortality of reef organisms; sub-lethal effects, such as reproductive failure, are less well understood, yet these can have fundamental effects on population regulation and recovery following disturbance. A recent mini-symposium on the timing of sexual reproduction by coral reef organisms highlighted advances in this field of inquiry at the 11th International Coral Reef Symposium held in Fort Lauderdale, Florida in July 2008.

The mini-symposium asked delegates to present papers broadly based around four key questions:

- Are there sufficient data to make valid comparisons about reproductive patterns among geographical regions?

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- Which environmental factors control reproductive timing in coral reef invertebrates?
- How are these signals perceived and transduced by the organisms?
- Will changes in environmental cues associated with climate change affect reproductive success?

Almost two-thirds (64%) of the 36 talks focused on tropical scleractinian corals, further highlighting the important role that this taxonomic group plays in understanding patterns of reproduction on reefs. However, a number of papers describing patterns of reproduction in other groups, including soft corals (11%) deep sea corals (3%), reef invertebrates (11%), reef fish (8%) and algae (3%), were also presented. Given the similar physical processes associated with gamete release into an aqueous medium, there is considerable potential for studies of one taxonomic group to advance understanding in other groups. For example, the reproductive tactics of tropical green algae (Clifton, 1997; Clifton and Clifton, 1999) share many analogs with the broadcast spawning behaviour of stony corals, including conspecific synchrony of gamete release, temporal partitioning of gamete release across species, and the tendency for males to release gametes just prior to females (Levitan et al., 2004). Given the obvious potential for studies of non-coral species to improve our understanding of coral reproductive biology, studies of spatial and temporal pattern in broadcast spawning behaviour across a range of reef taxa should continue to be encouraged.

Evolution of Reproductive Traits

Studies on the reproductive phenology of reef flora and fauna from different regions of the globe add to our expanding knowledge of the diversity of reproductive tactics employed on coral reefs. The value of this growing body of work was demonstrated by Alex Kerr from the University of Guam. Kerr and co-workers scoured the literature for records on scleractinian reproductive traits, in particular, the mode of reproduction (brooding versus broadcast spawning) and sexuality (hermaphroditism versus gonochorism), accumulating information from over 350 species. This information was combined with a recent "super-tree" phylogeny (Kerr, 2005) — the first working hypothesis of evolutionary relationships of taxa within the scleractinian— to explore the evolutionary history of these traits. The dominant reproductive condition of the order, hermaphroditic broadcast spawning which is evident in nearly 65% of species examined to date, was found to be the result of dramatic differences in the rate of character evolution and highly correlated evolution between traits. Reproductive mode evolved at twice the rate of sexuality, while the evolution of sexuality was heavily biased. Gonochorism was over 100 times more likely to be lost than gained and then only among brooders, such that gonochoric spawners seldom evolve hermaphroditism. Gonochoric spawners preferentially shift to brooding and then, or jointly, become hermaphroditic before reacquiring spawning to attain the dominant scleractinian reproductive condition.

Molecular Control of Reproductive Synchrony

Several other papers in the session showed that the science is moving away from purely descriptive accounts of reproductive phenology to investigations of the physiological and environmental mechanisms that govern the timing and degree of synchrony of reproductive events. Spawning synchrony is critical to achieve high fertilisation in marine broadcast spawners and environmental cues such as sea temperature, moonlight and photoperiod are thought to play a role in regulating synchrony. One important advance is that researchers are now exploring at the molecular level how corals respond to these cues to synchronise reproductive timing. For example, a team led by Oren Levy of the Weizmann Institute of Science in Israel reported on the presence of blue light sensing 'cryptochromes' in the coral *Acropora millepora* and hinted at their potential role in spawning (Levy et al., 2007). Corals are capable of sensing the blue portion of lunar irradiance (Gorbunov and Falkowski, 2002), but they lack specialised light sensing organs and the molecular mechanisms involved in light detection are not yet understood. Cryptochromes are photoreceptor proteins that have been found to play varied roles in entraining the circadian clocks of mammals and insects (Cashmore et al., 1999). The work by Levy and his co-workers shows that cryptochromes are also present in one of the earliest of the multi-cellular phyla, the Cnidaria. It is not yet clear what role, if any, cryptochromes play in spawning synchronisation in corals; however, in their experiments with *A. millepora*, the cryptochrome genes *cry1* and *cry2* were expressed preferentially in light and *cry2* expression increased on full moon nights compared to new moon nights, hinting at a potential role in regulating rhythmic behaviour such as spawning synchronisation (Levy et al., 2007).

Peter Vize of the University of Calgary has also been examining the perception of light by corals and how the lunar cycle and the time of sunset might determine respectively the date and the time of spawning (Vize et al., 2008). For more than a decade Vize and colleagues have been examining the reproductive patterns of seven broadcasting coral species that spawn on the same night each year at the Flower Garden Banks in the Gulf of Mexico. A notable feature of these corals is that they are remarkably consistent in terms of their spawning times from year to year. The start and finish time of spawning for each species is usually predictable to within two to seven minutes. Surprisingly, although species spawn on the same night, there is very little overlap in terms of timing among species, so in most cases species spawn during a narrow and distinct temporal window (Vize et al., 2005). The consistency in spawning is likely to be regulated by interactions between endogenous rhythms and environmental cues such as sea temperature, moonlight and daylight. Cues may either entrain the biological rhythm, i.e., the timing of spawning remains the same for some time after the cue changes; or they may cause a direct response, i.e., spawning time will change if the cue changes. Current evidence suggests that circalunar cycles are entrained while responses to the day/night cycle are direct (Jokiel et al., 1985; Levitan et al., 2004). At the molecular level Vize et al. (2008) propose that spawning behaviour is modulated by a complex series of cellular changes involving G-protein coupled photoreceptors, cytoplasmic second messengers and changes in protein abundance or protein phosphorylation patterns. Preliminary studies show light dependent differences in the proteome of *Montastrea cavernosa* (Vize et al., 2008). These papers show that molecular studies are currently focused on light sensing. Further studies might examine how other environmental factors such as temperature or tidal rhythms are perceived at the cellular level.

Environmental Influences on Reproductive Timing

A wide range of environmental factors may influence the timing of reproduction in marine organisms at both an ultimate and proximate level. The most common paradigm for corals states that environmental cues work at progressively finer scales to regulate the time of year, night and time of spawning. Traditionally sea temperature has been considered the major seasonal cue as broadcast spawning often occurs as waters are warming or close to the annual maxima. However, recent provocative work by Rob van Woesik of the Florida Institute of Technology argues that insolation (the amount of solar radiation incident on the Earth's surface), not sea temperature, is the factor controlling the time of year for spawning. In Western Atlantic broadcast spawning corals it was found that the rate of change in sea temperature correlated poorly with the timing of spawning but average temperature at the time of spawning was significant, with most corals spawning when temperatures are between 28 and 30 °C. The opposite was true for insolation. Rate of change of insolation at the time of spawning was a good predictor whereas average insolation was not (van Woesik et al., 2006). Together these results suggest that Atlantic corals are responding to insolation changes to synchronise spawning but that timing is regulated to occur when water temperatures are optimal. In other words, responding to insolation may have allowed corals to synchronise spawning during periods when water is warm and calm weather prevails, which in turn could improve fertilization success.

Tracking Reproduction of Individuals

Following individual animals over time can lead to important new insights. Sex allocation theory is concerned with the allocation of resources in animals or plants into male or female function and includes hypotheses about the evolutionary consequences of sex change in animals or plants. By directly observing spawning in dozens of individual mushroom corals over three years, Yossi Loya of Tel Aviv University documented bi-directional sex change in a stony coral for the first time. The results of this work, when framed within sex allocation theory, suggest that sex change increases fitness in these species (Loya and Sakai, 2008). Similarly, Don Levitan of Florida State University has painstakingly documented spawning timing over 6 years in 350 tagged and genotyped individual corals in the Caribbean coast of Panama and these data are revealing a wealth of information about reproductive strategies (Knowlton et al., 1997; Levitan et al., 2004). Several sympatric species spawn on the same night and individuals are remarkably punctual, usually spawning within a few minutes of the time that they spawned in the previous year. Simultaneous spawning of sympatric species can lead to hybridisation among species and it is thought that occasional successful hybridisations have been important in the diversification of reef corals on evolutionary time scales (Willis et al., 2006). However, for three sympatric species (*Montastrea annularis*, *M. faveolata* and *M. franksi*) there are various mechanisms that reduce the chances of hybridisation taking place. For example *M. franksi* spawns some 2 h before the other species, meaning that gametes have drifted away from the reef before the other species spawn, while *M. faveolata* gametes are generally incompatible with gametes from the other species (Levitan et al., 2004). Similar fine scale temporal differences in spawning time and the time taken for egg-sperm bundles to break open may limit opportunities for hybridization in the *Acropora humilis* group on the Great Barrier Reef (Wolstenholme, 2004). Fertilisation success in the *Montastrea* group is highest at the peak time for spawning, suggesting that there are fitness consequences for individuals that spawn earlier or later. Together, the evidence from Panama indicates that synchrony may be driven by strong genetic control of spawning timing coupled with fitness advantages gained through enhanced fertilisation success.

Multi-species Synchronous Coral Spawning

Mass, multi-species spawning of corals is one of nature's most remarkable spectacles and is crucial in the persistence and recovery of coral assemblages (Harrison et al., 1984). Multi-species spawning events have now been documented at a number of reef sites around the world (see review by Guest et al., 2005). However, in a recent overview of coral reproduction, Peter Harrison of Southern Cross University drew a distinction between the mass spawning events that occur on Australia's reefs and multi-specific spawning events that occur elsewhere in the Indo-Pacific and Western Atlantic (Harrison and Booth, 2007). According to Harrison, the Australian coral mass spawn is different from other multi-specific spawning events because of its larger ecological scale; in other words, it is an extreme form of multi-species spawning that involves a large proportion of colonies and species. Harrison also upheld the view that spawning synchrony in broadcast spawning corals tends to breakdown with proximity to the equator (Mangubhai and Harrison, 2008). These views — which developed following the discovery of mass coral spawning on the GBR in the 1980s (Oliver et al., 1988) — are contested by Andrew Baird of James Cook University (Baird and Guest, 2008). Baird argues that the Australian mass coral spawn is not unique and that multi-specific spawning synchrony is probably a feature of most speciose Indo-West Pacific coral assemblages, including those on equatorial reefs (Guest et al., 2005) and those in the Red Sea (Hanafy et al., pers. comm.), which previous work had suggested were characterised by asynchrony among species (Shlesinger and Loya, 1985). To compare patterns of synchrony between sites and among species requires a quantitative definition of synchrony and information on both the proportion of colonies and/or species spawning at the same as well as the length of the spawning season (Baird and Guest, 2008).

Studies of echinoderm reproduction in equatorial Kenya by Nyawira Muthiga of the Wildlife Conservation Society also refute the hypothesis that reproductive synchrony breaks down at the equator. Muthiga and colleagues found that gonad growth was markedly seasonal for the urchin *Echinometra matthaei* and the sea cucumber *Holothuria arenacava* and that the patterns were comparable to other studies at higher latitudes (Muthiga and Kawaka, 2008).

On a similar theme, Baird's data from the GBR reveal that there is some spawning of *Acropora* every month from October to March indicating that the coral spawning season on the GBR is longer than is commonly portrayed (Wolstenholme, 2004). Similarly, Natalie Rosser from RPS Environment in Perth revealed there are two distinct spawning periods in the *Acropora* in Western Australia contrary to previous work, suggesting only an autumn spawn (Rosser and Gilmour, 2008), a pattern that is common throughout the Coral Triangle (Baird et al., 2009).

Effects of Climate Change on Coral Reef Reproduction

Climate change is probably the greatest threat to the future of coral reefs; however, only one study, by Peter Glynn from the University of Miami, has hypothesised about the likely effects of climate change on coral reproduction. Glynn and colleagues have been studying coral reproduction in the Equatorial Eastern Pacific (EEP) for nearly two decades (Glynn et al., 1991). Based on these data (Glynn and Colley, 2008), they propose that broadcasting species in the EEP may fare better then brooding species in the face of global warming because traits they possess increase the probability of survival of sexual recruits and asexual fragments (Glynn and Colley, 2008). Broadcast spawning species outnumber brooding species both in terms of number of species (12 of the 13 studied species) and abundance. They are capable of colonising a diverse range of habitats that experience varying environmental conditions (e.g., upwelling zones and areas with contrasting water clarity and thermal regimes). They also produce large numbers of sexual propagules that have wide dispersal potential and tend to produce greater numbers of asexual fragments compared to brooding species.

Finally, one area that has not been addressed by coral reef ecologists is how changes in environmental cues associated with climate change may affect reproductive timing and fertilisation success in broadcasting species. Plausibly, species that rely on environmental cues to synchronise spawning may become confused with synchrony breaking down resulting in reduced rates of fertilisation, fewer propagules and therefore lower rates of recruitment. This, in turn, may reduce the resilience of coral communities to periodic disturbance, such as mass coral bleaching events. The effect of climate change on reproductive phenology of reef organisms is certainly an area of research requiring urgent attention.

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