

COMMENT

Spawning synchrony in scleractinian corals: Comment on Mangubhai & Harrison (2008)

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ABSTRACT: Mangubhai & Harrison (2008; Mar Ecol Prog Ser 360:85–96) documented spawning patterns in an equatorial assemblage of *Acropora* spp. in Kenya over a 2 yr period. They concluded that reproductive seasons are more protracted at low latitudes and that ‘mass spawning’ does not occur in equatorial regions, due to a breakdown in spawning synchrony among species. However, this interpretation hinges on the authors’ distinction of ‘mass spawning’ from ‘multi-specific spawning’ for which they provide no ecological rationale. Moreover, they did not cite recent studies that document spawning in synchrony by numerous species in equatorial assemblages. In addition, the authors overlooked work demonstrating that spawning is not as synchronous as typically portrayed on the Great Barrier Reef or in Western Australia. In the context of that literature, reproductive patterns of *Acropora* spp. in Kenya are more similar to sub-tropical reefs in southern Australia rather than to other equatorial reefs. We conclude that the study of reproductive synchrony in corals is being impeded by the lack of a consistent definition that would make it possible to quantify and compare patterns of synchrony at both population and assemblage scales.

KEY WORDS: Coral reefs · Reproduction · Spawning

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INTRODUCTION

Mangubhai & Harrison (2008) used a combination of sequential samples and broad-scale sampling to infer spawning events in 401 colonies in an equatorial assemblage of *Acropora* spp. in Kenya (4°S). They concluded that ‘the overall pattern of coral reproduction in Kenya is one of asynchrony; *Acropora* species release gametes over a 7 mo period’ (p. 85). Based on these findings, and with reference to the literature, they concluded that ‘reproductive seasons may be more protracted towards lower latitudes’ and ‘mass spawning does not occur in equatorial regions’ (p. 91). However, there are 2 problems with these conclusions.

(1) Mangubhai & Harrison (2008) provide no quantitative definition of ‘mass spawning’ without which it is difficult to compare patterns in different regions. Furthermore, their conclusion that mass spawning does

not occur in equatorial assemblages hinges on the distinction they make between ‘mass spawning’ and ‘multispecific spawning’, for which they provide no ecological rationale.

(2) Mangubhai & Harrison (2008) do not cite studies which indicate that spawning is not as synchronous as typically portrayed on the Great Barrier Reef (GBR) and Western Australia (WA), nor recent studies documenting multispecific synchronous spawning in equatorial assemblages.

MULTISPECIFIC SYNCHRONOUS SPAWNING

Mangubhai & Harrison (2008) concluded from their data and reference to Oliver et al. (1988) that mass spawning does not occur in equatorial regions, due to a breakdown in spawning synchrony among species.

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However, Mangubhai & Harrison (2008) accepted that some level of multispecific spawning synchrony occurs in Kenya:

While the exact night of spawning was recorded in 2 *Acropora* species, the narrowing of spawning times to lunar months and lunar quarters, and the overlap between reproducing species during these periods suggests that some degree of multispecific spawning is a characteristic of Kenyan reefs.

(Mangubhai & Harrison 2008, p. 91)

In fact, the spawning period in 12 of 20 *Acropora* species overlapped during February, the peak month of reproductive output. In addition, Mangubhai & Harrison (2008) suggested that species from other genera also breed when the *Acropora* species are breeding. Consequently, their conclusion that mass spawning does not occur in Kenya depends on the authors' distinction of 'mass spawning' from 'multi-specific spawning'. However, no ecological rationale is provided for this distinction, nor is any guide given to how many species, or what proportion of the assemblage constitutes a mass spawning. Mass spawning has previously been defined as 'the synchronous release of gametes by many species of corals, in one evening between dusk and midnight' (Willis et al. 1985, p. 344), and while a more precise definition is clearly required (see below), by this definition mass spawning has been documented in many other equatorial coral assemblages, including the Java Sea (Edinger et al. in Tomascik et al. 1997), Palau (Penland et al. 2004) and Singapore (Guest et al. 2002). Mangubhai & Harrison (2008) also concluded that their data challenge the hypothesis of Guest et al. (2005b) that mass spawning is likely to occur in all speciose coral assemblages. In fact, these data from Kenya support this hypothesis, as do data from other sites throughout the Indo-Pacific (Baird et al. 2001, Carroll et al. 2006, Harrison 2008).

LENGTH OF THE REPRODUCTIVE SEASON

The patterns of reproduction in Kenya were contrasted with the patterns on the GBR and in WA, where mass spawning events were said to be 'unusual in relation to their magnitude and geographic scale' (Mangubhai & Harrison 2008, p. 85). However, spawning in *Acropora* assemblages is not as synchronous as typically portrayed for the GBR and WA (Harrison & Wallace 1990). On the GBR, a number of *Acropora* species spawn outside of the mass spawning period as defined by Willis et al. (1985). For example, in a 2 yr study of 9 *Acropora* spp. on Big Broadhurst Reef in the central GBR, *A. granulosa* spawned in March, 4 mo after the mass spawning period, and some colonies of *A. sarmen-tosa* were mature in February, August and November (Wallace 1985). Furthermore, in a 3 yr study of spawn-

ing times in 12 morphospecies of the *Acropora humilis* group, a second substantial spawning event occurred 3 mo after the November mass spawning period, with 11 of the 12 taxa participating in both events (Wolstenholme 2004). Colonies of *A. samoensis* spawned in December, January and February; the majority of colonies of *A. digitifera* spawned in February, and mature colonies of *A. gemmifera* were present over a 4 mo period (Wolstenholme 2004). High synchrony within populations over a broad spatial scale is the exception on the GBR, rather than the rule. In 3 regions spanning the length of the GBR, most *Acropora* populations sampled in the week before the mass spawning period had a proportion of colonies in each of 3 reproductive conditions (mature, immature and empty), indicating that spawning in these populations extended over at least 2 mo (Baird et al. 2002). Similarly, the proportion of mature colonies of 3 species of *Acropora* varied dramatically among 6 regions on the GBR and among years, indicating major regional and annual differences in within-population reproductive synchrony (Hughes et al. 2000). Non-*Acropora* species known to broadcast spawn outside the accepted mass spawning period on the GBR include: 3 species of *Montipora*, some colonies of which spawn in both October and March in the central GBR (Stobart et al. 1993); *Porites cylindrica* and *P. lutea*, which spawn in January in the Capricorn Bunker Group on the southern GBR (Kojis & Quinn 1982); and *Turbinaria mesenterina*, some colonies of which release gametes over a 4 mo period starting in February in the central GBR (Willis 1987). In addition, the first study to claim broad synchrony in spawning among coral assemblages on the GBR actually indicates that spawning was split between November and December on at least 5 of the 12 reefs evaluated, and the number of empty colonies on many reefs suggests that these colonies were breeding at other times of the year (Oliver et al. 1988; their Table 1, p. 805). Similarly, on the west coast of Australia at least 11 species of *Acropora* spawn in spring (Rosser & Gilmour 2008), i.e. 6 mo after the accepted mass spawning period (Simpson 1985).

How unusual is a 7 mo reproductive season in the Kenyan *Acropora* assemblage? Only 2 GBR studies have sampled *Acropora* assemblages throughout an entire season: on Lizard Island the spawning season lasted at least 5 mo from October to February (Wolstenholme 2004), and on Little Broadhurst Reef spawning was inferred in at least 4 mo between August and March (Wallace 1985). In light of these 2 studies, the length of the reproductive season in *Acropora* spp. in Kenya is not so extraordinary. Indeed, describing the reproductive season in Kenya as 7 mo long does not capture the fact that peak reproductive output is concentrated in a much shorter period; 80% of *Acropora*

reproductive output occurred between January and March, with 5% or fewer colonies spawning in October, November, December or April (Mangubhai & Harrison 2008). The most unusual aspect of the spawning patterns in Kenya is the proportion of species spawning over an extended period: 8 of the 20 species spawn over 3 mo or more, including species such as *A. nasuta*, *A. tenuis* and *A. valida*, which typically have high within-population synchrony in other regions (Babcock et al. 1986, Hayashibara et al. 1993). In this respect, spawning patterns in Kenya are more similar to those at sub-tropical sites in southern Australia (Solitary Islands, 30°S; Wilson & Harrison 2003), than other equatorial reefs such as Singapore (Guest et al. 2005a). In the Solitary Islands, 9 of the 14 species of *Acropora* inferred to spawn between December and April released gametes during 3 to 5 mo (Wilson & Harrison 2003).

A QUANTITATIVE APPROACH TO COMPARING SPAWNING SYNCHRONY AMONG REGIONS

Reproductive synchrony can occur at several levels, e.g. individual (intra-colony synchrony), species (population synchrony) and coral assemblage (multispecific synchronous spawning or mass spawning). Synchrony may be defined according to the question of interest. For example, if the potential for hybridization among species is the focus, then synchrony must be defined on a time frame that allows cross fertilisation (Levitan et al. 2004, Wolstenholme 2004), and any spawning of more than 1 closely related species is a mass spawning in this context. If we are interested in proximate cues that co-ordinate the day of the month on which a coral species spawns, then a definition of synchrony on the scale of days will suffice. If we are interested in proximate cues for the seasonality of spawning, the month of spawning will suffice.

A quantitative approach is essential for comparing synchrony between sites and among species. For studying seasonality, an index should be devised that incorporates the proportion of the population that spawns in any one month and the number of months of the year in which spawning occurs; averaging the values for all species sampled would provide an index of the seasonality of spawning in the assemblage. Mangubhai & Harrison (2008) provide important new information on the patterns of coral spawning in equatorial Kenya, but these patterns do not demonstrate that spawning synchrony breaks down near the equator. Testing of this hypothesis requires more than 1 equatorial site and an equivalent examination of replicate assemblages at higher latitudes. Furthermore, a quantitative definition of synchrony is a prerequisite for

testing such a hypothesis. We conclude that progress towards understanding the proximate and ultimate cues that synchronise coral spawning requires more rigour in defining spawning synchrony.

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