

REPLY COMMENT

Extended breeding seasons and asynchronous spawning among equatorial reef corals in Kenya

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ABSTRACT: Patterns of sexual reproduction in scleractinian reef corals have been widely studied, and vary both systematically and biogeographically. Extensive sampling and repeated monitoring of 401 marked colonies of 20 *Acropora* spp. over 2 yr on equatorial lagoon reefs in Kenya (4° S) demonstrated an overall asynchronous spawning pattern extending over a 7 mo period (Mangubhai & Harrison 2008a; Mar Ecol Prog Ser 360:85–96). Spawning occurred during all lunar phases, and during both rising and maximum sea surface temperatures. Although some degree of multispecies spawning occurs on Kenyan reefs, most coral species exhibited relatively asynchronous and extended spawning over 2 to 5 mo with some level of temporal reproductive isolation among species. These data support previous hypotheses of more protracted breeding seasons and a breakdown in spawning synchrony nearer the equator, and contrast markedly with the mass spawning of corals on the Great Barrier Reef and some Western Australian reefs. Baird & Guest (2009, this volume) question this conclusion based on their redefinition of the term 'mass spawning', which they define to encompass lesser multispecies spawning events. They assert that Mangubhai & Harrison (2008a) (1) categorically state that mass spawning does not occur in equatorial regions, and (2) do not cite recent studies that document spawning in synchrony by numerous species in equatorial assemblages; both of these assertions are incorrect. The conclusions in Mangubhai & Harrison (2008a) are valid, and clearly demonstrate an unusually extended and asynchronous spawning pattern among many corals on equatorial reefs in Kenya.

KEY WORDS: Sexual reproduction · Coral spawning · Asynchrony · Mass spawning · Indian Ocean

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INTRODUCTION

A wide range of coral spawning and planulation patterns have been reported from different regions, and the degree and scale of reproductive synchrony varies within and among coral species and assemblages (reviewed in Harrison & Wallace 1990, Richmond & Hunter 1990, Harrison & Booth 2007). Well-documented reproductive patterns range from (1) highly synchronous mass coral spawning events involving coincident spawning by many colonies of many species of reef corals during a relatively small number of nights each year on the Great Barrier Reef (GBR) (Har-

rison et al. 1984, Willis et al. 1985, Babcock et al. 1986) and some reefs in Western Australia (WA) (Simpson 1985, 1991, Babcock et al. 1994), to (2) temporal reproductive isolation in the northern Red Sea (Shlesinger & Loya 1985, Shlesinger et al. 1998). Between these extremes are a variety of complex patterns of spawning and planulation, ranging from (3) coincident multispecific spawning in a few species and (4) temporal isolation of reproduction in other species in the Caribbean and western Atlantic (e.g. Szmant 1986, Gittings et al. 1992, Van Veghel 1993, Hagman et al. 1998, Bastidas et al. 2005), to (5) extensive multispecific spawning and (6) other reproductive patterns in

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some Indo-Pacific tropical and subtropical reef regions, which vary in scale and the extent of breeding seasons (e.g. Hayashibara et al. 1993, Richmond 1997, Baird et al. 2001, Wilson & Harrison 2003, Guest et al. 2005a,b, Penland et al. 2004, Carroll et al. 2006, Harrison 2008, Rosser & Gilmour 2008).

Mangubhai & Harrison (2008a) used extensive sampling and repeated monitoring of 401 marked colonies of 20 *Acropora* spp. over 2 yr on equatorial lagoon patch reefs in Kenya (4° S) to provide detailed information on the timing and levels of spawning synchrony within and among species. The Kenyan data demonstrate an unusually asynchronous spawning pattern within and among *Acropora* spp., with gamete release extending over a 7 mo period from October to April. In contrast to the tightly synchronised mass spawning events that occur following full moon periods on the GBR and in WA and species that split-spawn over successive lunar months or reproduce at other times (Willis et al. 1985), spawning in these equatorial Kenyan corals occurred across all lunar periods (both within and among species), and during both rising and maximum sea surface temperatures over a greatly extended breeding season (Mangubhai & Harrison 2008a). Coincident spawning was observed in 2 *Acropora* species, and some degree of multispecific spawning is likely to be a characteristic of Kenyan reefs. However, most coral species exhibited relatively asynchronous and extended spawning over 2 to 5 mo, with some level of temporal reproductive isolation between species in relation to the lunar phase and month when the main spawning period occurred. Additional data on *Platygyra daedalea*, *Echinopora gemmacea* and *Leptoria phrygia* and pigmented oocytes in 4 other coral species (Mangubhai & Harrison 2006, 2008a,b, Mangubhai 2007) indicate that a variety of other reef corals are also reproductively mature during the East African summer northeast monsoon. Furthermore, some *P. daedalea* colonies exhibited biannual gametogenesis and spawning and also released gametes in August and September (Mangubhai & Harrison 2006, 2008b); hence when all available data on *Acropora* and faviids are combined, spawning occurs over 9 mo from August to April in the Kenyan coral assemblages. Mangubhai & Harrison (2008a) concluded that the Kenyan data support previous hypotheses of more protracted breeding seasons and a breakdown in spawning synchrony in corals near the equator, and contrast markedly with the tightly synchronised mass spawning periods of corals on the GBR and some WA reefs.

Baird & Guest (2009, this volume) do not question the validity of our (Mangubhai & Harrison 2008a) extensive data, but instead question our conclusions that the Kenyan data support previously published hypotheses of more protracted reproductive seasons at lower lati-

tudes and a breakdown in spawning synchrony near the equator. Baird & Guest's (2009) conclusions are complicated by their redefinition of the term 'mass coral spawning' to include a wide range of lesser multispecific spawning events involving few species and colonies, and their use of this new definition to conclude that mass coral spawning 'is probably a feature of all speciose coral assemblages' (Guest et al. 2005b, p. 215), despite substantial and increasing evidence to the contrary. Baird & Guest (2009) selectively quote from statements made in Mangubhai & Harrison (2008a) to infer that we categorically state that mass spawning does not occur in equatorial regions, which was not our conclusion. Baird & Guest (2009) also state that we did not cite recent studies that document synchronous spawning by numerous species in other equatorial assemblages, and overlooked studies inferring that spawning is not as synchronous as typically portrayed on the GBR and in WA; these assertions are also incorrect. Accordingly, we systematically highlight and discuss the statements by Baird & Guest (2009), to clarify these issues.

MASS CORAL SPAWNING VERSUS MULTISPECIFIC SPAWNING PATTERNS

Baird & Guest (2009 p. 301) questioned our definition of 'mass coral spawning': 'Mangubhai & Harrison (2008) [2008a herein] provide no quantitative definition of 'mass spawning' without which it is difficult to compare patterns in different regions.' We used the term 'mass spawning' in the sense of its original published, very widely cited and accepted definition (*sensu* Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, Oliver et al. 1988, Harrison & Wallace 1990). The term 'mass spawning' was partly 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), to emphasise the large numbers of species involved in these mass spawning events on peak spawning nights. However, as evidenced by the extensive published data (*op. cit.*), and noted by Rosser & Gilmour (2008, p. 345), 'implicit in this definition of mass spawning is the involvement of both many species and a high proportion of colonies within species, in contrast to instances of multispecific spawning that involve some species and a lower proportion of colonies'. Thus, 'mass spawning' is distinguished from other lesser multispecific spawning patterns by its much larger ecological scale (Harrison & Booth 2007), and represents an extreme form of multispecific synchronous spawning involving a large proportion of colonies of many species (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). Together, these 3 papers

describing the extensive data on mass coral spawning on the GBR have been very widely cited (>650 citations since 1993 recorded by ISI Web of Science), and therefore this definition is both widely understood and accepted by most researchers.

Mass coral spawning on the GBR typically occurs in the week following full moon periods in the austral late spring or summer (Harrison et al. 1984), and can involve synchronous nocturnal spawning by more than 20 to 30 species during peak nights, including all or most colonies of some extensively sampled populations (Willis et al. 1985, Babcock et al. 1986). Although many or most colonies within the sampled populations tend to spawn during a single night, some colonies and species spawn over a few nights, and some populations tend to 'split-spawn' during a few nights over 2 consecutive lunar cycles (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). Subsequent research showed that mass spawning events of similar magnitude involving up to 24 species occur on some WA reefs (Simpson 1985, 1991, Babcock et al. 1994), but these occur in the austral autumn in contrast to the mass spawning periods on the GBR. Perhaps due to the extraordinarily large scale of the mass spawning events, data on species that have other reproductive patterns are sometimes overlooked. For example, some other species spawn within a few nights before or after these mass spawning events, and therefore participate in single species or multispecific spawning events that are of much smaller scale compared with mass spawning episodes (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, 1994). Further, some colonies and species that spawn during mass spawning events on the GBR also spawn at other times, and some species do not participate in mass spawning after full moon periods, but spawn or planulate at other lunar phases or during other seasons (see data in Kojis & Quinn 1981, Harrison et al. 1984, Wallace 1985, Willis et al. 1985, Babcock et al. 1986, Willis 1987, Oliver et al. 1988, Stobart et al. 1992, Wolstenholme 2004, among others).

The fact that some corals or species reproduce outside of mass spawning periods is not new, nor unexpected, and the original papers describing mass coral spawning did not claim that all species on the GBR or WA reefs participated in mass spawning events (nor did Mangubhai & Harrison 2008a). Recent research indicating that some additional species spawn or planulate outside mass spawning periods does not support Baird & Guest's (2009, p. 302) conclusion that spawning is now demonstrated to be less synchronous on the GBR or WA than previously indicated, as the data on mass spawning have not been invalidated by recent studies. Rather, subsequent research has confirmed that highly synchronous mass coral spawning events are a feature of many reefs in the GBR and along WA, and have increased the numbers of species recorded

spawning during mass spawning events (reviewed in Harrison & Wallace 1990, Harrison & Booth 2007), while some other studies have confirmed that some populations split-spawn or that a much smaller number of colonies or species reproduce at other times (e.g. Stobart et al. 1992, Hughes et al. 2000, Baird et al. 2002, Wolstenholme 2004, Rosser & Gilmour 2008). Therefore, although Baird & Guest (2009) highlight some exceptions to the mass-spawning paradigm, these exceptions were mostly already known, or simply add more recent information on a few other species.

In total, more than 140 scleractinian species from 11 scleractinian families have been recorded to participate in mass spawning events or spawn during mass spawning periods occurring in the week following full moons (Willis et al. 1985, Babcock et al. 1986). Mass spawning has been observed on many reefs in the GBR region, with synchronous coral spawnings recorded over a 9° range of latitude on reefs up to 1200 km apart (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, Oliver et al. 1988). Therefore, it is the scale of synchronous spawning during one or a few nights by a very large proportion of colonies of many species that separates 'mass spawning' from other lesser multispecific spawning events, or larger multispecific spawning events that extend over many months (reviewed in Harrison & Wallace 1990, Harrison & Booth 2007). This is why the term 'mass spawning' has been, and should continue to be, restricted to describing these extreme synchronous multispecific spawning events, rather than including all multispecific spawning (cf. Guest et al. 2005b, Baird & Guest 2009).

Furthermore, it is not the use or definition of the term 'mass spawning' that is restricting meaningful comparison of spawning patterns in different regions. Rather, it is the fact that there have been insufficient rigorous long-term studies that provide detailed quantitative data based on repeated monitoring of identified colonies plus extensive observations of coral spawning to clearly establish spawning periods and the degree of synchrony within and among populations of many scleractinian species (see, e.g. Harrison et al. 1984, Willis et al. 1985, Shlesinger & Loya 1985, Babcock et al. 1986, Oliver et al. 1988, Simpson 1991, Hayashibara et al. 1993, Babcock et al. 1994, Wilson & Harrison 2003, Shlesinger et al. 1998, Penland et al. 2004, Mangubhai & Harrison 2006, 2008a), which is inhibiting comparisons of reproductive patterns among reef coral assemblages in different Indo-Pacific reef regions.

EQUATORIAL SPAWNING PATTERNS

Baird & Guest (2009, p. 301) also state: 'Furthermore, their [Mangubhai & Harrison 2008a] 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.' We did not categorically state that 'mass spawning does not occur in equatorial assemblages'. The full statements from Mangubhai & Harrison (2008a, p. 91) are: 'However, the suggestion that mass spawning is a characteristic of equatorial reefs (Guest et al. 2005b) is not supported by the coral reproductive data from this study or from Oliver et al. (1988)', and 'Furthermore, the findings of this study support the hypotheses that reproductive seasons may be more protracted towards lower latitudes (Orton 1920, Pearse 1974) and that mass spawning does not occur in equatorial regions due to a breakdown in spawning synchrony (Oliver et al. 1988)'. There is an important but subtle distinction between what we stated and the partially quoted text highlighted by Baird & Guest (2009). We did not conclude that mass spawning does not occur on equatorial reefs, but note that the available published data are insufficient to unambiguously prove that mass spawning, at a scale similar to mass spawning events on the GBR and in some WA reefs, occurs on equatorial reefs. However, this does not preclude the possibility that mass spawning events could occur on some equatorial reefs, and further detailed research in equatorial regions where large multispecific spawning events have been reported (e.g. Baird et al. 2001, Guest et al. 2005a,b, Penland et al. 2004), may prove that mass spawning does occur in some equatorial regions.

Kenyan spawning patterns are fundamentally different to those on the GBR and many other regions where spawning is highly synchronous within populations of each species, regardless of the degree of overlap in spawning times among species (reviewed in Harrison & Wallace 1990, Harrison & Booth 2007). The Kenyan data clearly show that populations of *Acropora* spp. spawned relatively asynchronously, with different colonies spawning during different lunar phases and over more than 1 lunar phase, and spawning in 8 species occurring over an extended period of 3 mo or more, which Baird & Guest (2009) acknowledge as unusual. A similar pattern of mostly asynchronous and extended spawning over multiple lunar cycles has recently been observed among many *Acropora* spp., faviids and other coral taxa on equatorial reefs in the Maldives (Harrison & Hakeem 2007). Furthermore, the Kenyan data showed that different coral species displayed some degree of temporal reproductive isolation with respect to the main month and lunar period of spawning; a pattern noted in the northern Red Sea, but where spawning is more synchronous within populations (Shlesinger & Loya 1985, Shlesinger et al. 1998). Thus, the asynchronous spawning patterns extending

over 9 mo exhibited by Kenyan corals studied to date (Mangubhai & Harrison 2006, 2008a,b, Mangubhai 2007), contrast strongly with the tightly synchronised mass spawning patterns of many colonies of many species studied on the GBR and some WA reefs, and provide additional strong ecological rationale for separating 'multispecific spawning' from 'mass spawning' patterns.

FUTURE STUDIES OF CORAL REPRODUCTION

An important limitation of the recent studies highlighted by Baird & Guest (2009) to support their claim that spawning is not as synchronous on the GBR and WA as previously indicated, is that those studies used a rapid assessment technique in the field, where egg maturity is determined visually by the presence or absence of pigmentation in large oocytes on randomly selected coral fragments or branches (e.g. Baird et al. 2002, Wolstenholme 2004, Guest et al. 2005a), which does not accurately quantify the degree of synchrony or asynchrony found within coral assemblages. When field assessment of oocyte colour was first developed to aid assessment of coral reproductive maturity, oocyte colour was used in conjunction with repeated sampling of tagged coral colonies and direct observations of colonies at night, plus microscopic assessment of sperm maturity to determine spawning periods (Harrison et al. 1984).

Using field observations of broken sections of randomly sampled colonies, white eggs have been classified as immature, and colonies that appear non-reproductive are assumed to have recently spawned or are unlikely to spawn for at least 3 mo (Baird et al. 2002). However, this method makes a number of assumptions that do not always hold true: (1) colonies that are empty have recently spawned, or spawn at different times of the year, and (2) only coloured eggs are mature. The absence of oocytes and spermaries in broken sections of coral colonies may indicate that the colony has already spawned, or that it is non-reproductive, or may have been stressed during the gametogenic cycle and, therefore, could have resorbed most or all of its gametes (reviewed in Harrison & Wallace 1990). Pale and smaller oocytes can be difficult to see in some broken coral sections, which may introduce error into these rapid field assessments. Furthermore, our study in Kenya showed that mature white or pale oocytes were recorded in 14% of mature gravid colonies and in 63% of the species studied (Mangubhai & Harrison 2008a). Therefore, significant errors can occur when relying on such techniques as rapid assessments of coloured eggs as a means of inferring spawning periods.

More importantly, random samples of corals do not clearly identify when corals spawn, and random observations of colonies spawning do not prove whether or not the whole colony only spawns at the same time, or whether it spawns on subsequent nights or split spawns over 2 lunar cycles. These issues limit the interpretation of findings relating to the degree of synchrony or asynchrony of spawning between geographic locations based on rapid assessments of coral reproductive maturity only using oocyte colouration, and the degree to which mass spawning occurs on different reefs (cf. Baird et al. 2002, Guest et al. 2005a). The repeated sampling and monitoring of tagged or mapped colonies (see methods in Mangubhai & Harrison 2008a) provides the best option for minimising the probability of mature eggs being misdiagnosed as immature oocytes in future studies, and provides a more accurate picture of spawning patterns within and among colonies, populations and species.

In conclusion, improved understanding of the proximate cues and ultimate causes resulting in different patterns of spawning synchrony within and among scleractinian coral colonies, populations and assemblages is important. However, rather than focussing on semantic debates about redefining 'mass spawning' (Baird & Guest 2009), improved scientific understanding of coral reproduction patterns in different reef regions requires rigorous long-term quantitative studies using repeated sampling and monitoring of the reproductive condition of marked or mapped corals and detailed observations of coral spawning, to determine the scale and extent of spawning seasons and synchrony within and among populations of species. This is particularly important in equatorial reefs where there is increasing evidence of asynchronous and extended spawning periods both within and among scleractinian coral colonies, populations and species in some equatorial reef regions (Oliver et al. 1988, Mangubhai & Harrison 2006, 2008a,b, Harrison & Hakeem 2007).

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