

Reproductive Synchrony in *Acropora* Assemblages on Reefs of New Caledonia¹

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Abstract: Despite a recent expansion in the geographical focus of studies on coral reproduction, there remain many regions in the Indo-Pacific, such as Melanesia, where research is limited. For example, although New Caledonia in southern Melanesia is home to the world's second largest barrier reef, which has recently been given UNESCO World Heritage listing, almost nothing is known of the reproductive biology of the coral fauna there, in particular the timing of spawning. In this study we sampled *Acropora* assemblages in November 2004 to test for reproductive synchrony at eight sites in New Caledonia separated by up to 200 km. In total, 80% of 1,055 *Acropora* colonies sampled contained mature oocytes, and 34 (92%) of 37 species sampled had at least one mature colony. These data demonstrate that reproduction in *Acropora* is highly synchronous over a large scale in New Caledonia and suggest a multispecies spawning event following the full moon in November coincident with the mass spawning period on the Great Barrier Reef, Australia. The high synchrony of reproductive effort implies that even a brief halt of activities that threaten fertilization and early development of coral propagules, such as discharge of liquid waste from ore processing, could have a major mitigating effect on the potential damage to these globally valued reefs.

CORAL REPRODUCTIVE research in the Indo-Pacific has concentrated on regions close to marine research stations in developed countries, such as the central Great Barrier Reef (Harrison et al. 1984), Guam (Richmond and Hunter 1990), Okinawa (Hayashibara et al. 1993), Hawai'i (Kolinski and Cox 2003), Eilat (Shlesinger et al. 1998), and the

eastern Pacific (Glynn and Ault 2000). Recently, the geographic focus of coral reproductive research has expanded to include more remote and equatorial regions such as Palau (Penland et al. 2004), Singapore (Guest et al. 2005*a*), Indonesia (Baird et al. 2005), Kenya (Mangubhai and Harrison 2008), and the Line Islands (Kenyon 2008). One result of this increase in the geographic focus of research has been a change in our understanding of Indo-Pacific patterns of coral reproductive synchrony (Guest et al. 2005*b*, Baird and Guest 2009) and the processes that regulate the timing of coral reproduction (Mendes and Woodley 2002, van Woesik et al. 2006). For example, it is now clear that highly synchronous spawning both within and among species is not restricted to higher-latitude reefs as earlier hypothesized (Oliver et al. 1988). Multispecies synchronous spawning events (sensu Willis et al. 1985) have now been described from 23 locations globally (Baird and Guest 2009) and appear to be a feature of all speciose coral assemblages (Guest et al. 2005*b*). In addition, coral reproduction in most regions is highly sea-

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sonal, with the vast majority of reproductive activity concentrated within a 2- to 3-month period. This trend holds even in equatorial locations (e.g., Kenya [Mangubhai and Harrison 2008], Singapore [Guest et al. 2005b]) and in regions where breeding periods have previously been described as temporally isolated (e.g., the Red Sea [Hanafy et al. 2010]).

Despite the recent increase in geographic scale of research, coral reproduction remains unexplored in many regions of the globe. For example, there are very few reports from Melanesia, particularly in the primary literature. In Fiji, 22 species of scleractinian corals and three species of soft corals were observed to have spawned between 5 and 7 nights after the full moons in October and November in 1989 (Mildner 1991). In addition, Baird et al. (2001) documented mature oocytes in 28 of 41 *Acropora* species sampled in the Solomon Islands in the week before the full moon on 23 November 1999, and 12 species from four families spawned 3–5 days after the full moon. In New Caledonia Joannot (1990) documented the disappearance of gametes from sequential histological sections between 9 and 11 November 1987, 3–5 nights after the full moon in four taxa: *Acropora millepora*, *A. hyacinthus*, *Favia* sp., and *Porites lutea*. The only in situ reported observation of spawning from New Caledonia is a single faviid colony spawning on 18 November 1989 (M. Adjéroud, pers. comm.).

The highly seasonal nature of coral reproduction has important implications for reef ecology and conservation (Guest 2008). Numerous reef organisms, including many fishes, appear to time their reproductive cycles to benefit from this seasonal abundance of nutrients (Pratchett et al. 2001, McCormick 2003). Consequently, knowing when corals spawn can be a good indicator for reproduction in other groups. Also, knowing the timing and synchrony of coral spawning can help explain success or failure in annual coral replenishment due to corresponding climatic conditions during, and soon after, spawning events (Mendes and Woodley 2002). Knowing the time of reproductive events can also allow for more effective management of pulse impacts from

coastal development on coral reef ecosystems (Richmond 1997). For example, human disturbances such as dredging or discharge of liquid waste from heavy industry can be prohibited during spawning events, ensuring that the seasonal production of propagules for reef replenishment is not jeopardized.

New Caledonia lies on the Tropic of Capricorn and hosts one of the three most extensive coral reef systems in the world. Considered as “one of the planet’s best examples of the ecological and biological processes underlying tropical lagoon and coral reef ecosystems,” six clusters of reefs and lagoon were given World Heritage listing by UNESCO in July 2008 (UNESCO 2009). As the world’s third largest producer of nickel (Ni), New Caledonia must be proactive in minimizing the predominant threat of mining and Ni-ore processing to its natural ecosystems (Labrosse et al. 2000). Heavy metals from ore treatment have been shown to produce high levels of Ni (up to 9,000 dissolved ng liter⁻¹) and chromium (Cr) in coastal waters of Noumea (Mignon et al. 2007). A further contentious Ni mining and processing refinery at Prony, on the main island of la Grande Terre (Horowitz 2008), will discharge soluble metals (particularly aluminum [Al], Cr, manganese [Mn], Ni, zinc [Zn]) directly into lagoon waters of the southern UNESCO World Heritage zone, risking impact to the developmental stages of reef biota. Such potential impacts are especially pertinent in areas where corals spawn in summer, a period when they may already be stressed from natural processes such as elevated water temperatures and freshwater runoff from monsoonal rains.

The aims of this study were to document the extent of reproductive activity in *Acropora* assemblages in New Caledonia over a large spatial scale in November 2004. We chose November as the most likely month for *Acropora* to spawn based on observations from other locations in Melanesia as mentioned earlier. We concentrated on the genus *Acropora* because these corals are numerically and ecologically dominant on most reefs throughout the Indo-Pacific. They are also easy to work with, fracturing readily for in situ observations without major damage to

the colony and healing quickly. *Acropora* species are also an excellent proxy of reproductive activity in other broadcast-spawning hermaphroditic scleractinian species in most regions.

MATERIALS AND METHODS

The reproductive condition of *Acropora* colonies was examined at 8 sites at three reefs: two reefs of la Grande Terre, a lagoonal reef around Ilot Konduyo ($21^{\circ} 51' 54.60''$ S, $165^{\circ} 46' 11.79''$ E) and the nearby barrier reef Récif N'Digoro ($21^{\circ} 53' 3.09''$ S, $165^{\circ} 45' 34.20''$ E); and one semisheltered reef of Ile des Pins 200 km farther south ($22^{\circ} 39' 39.89''$ S, $167^{\circ} 26' 12.07''$ E) (Figure 1). All reefs were visited 1–2 weeks before the expected mass-spawning period of corals on the Great Barrier Reef 2–7 days after the full moon on 27 November 2004.

Colonies were sampled haphazardly at each site. Each colony encountered was identified to species and the reproductive condition recorded. Corals of the genus *Acropora* are all broadcast-spawning simultaneous hermaphrodites with one gametogenic cycle per year (Wallace 1999). The reproductive condition of colonies was established by breaking coral branches below expected sterile zones (Wallace 1985) to expose the developing oocytes. Three reproductive conditions were defined based on the color of the oocytes following Baird et al. (2002): mature: oocytes pigmented; immature: oocytes pale (if the oocytes are pale but visible it indicates that they are close to maturity and likely to spawn within 1–3 months); empty: oocytes too small to see or absent (this indicates either that the colony has recently spawned or is unlikely to do so for at least 3 months). The degree of synchrony in the maturation of gametes

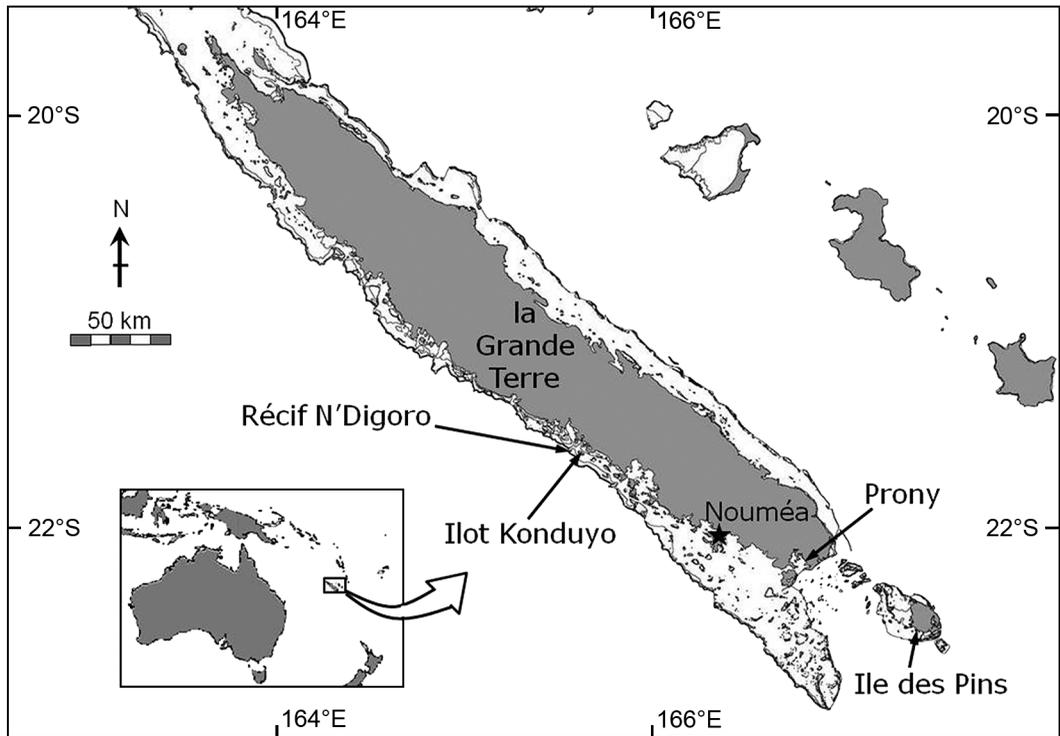


FIGURE 1. Map of New Caledonia showing the lagoonal and barrier reefs around the main island of la Grande Terre and the site of the three study locations.

TABLE 1

Proportion of *Acropora* Colonies in Each of Three Reproductive Conditions in New Caledonia in November 2004

<i>Acropora</i> species	Mature	Immature	Empty	Gravid	<i>n</i>
<i>digitifera</i>	79	0	21	79	230
<i>muricata</i>	84	5	10	90	154
<i>nasuta</i>	97	0	3	97	104
<i>valida</i>	59	3	38	62	97
<i>hyacinthus</i>	90	0	10	90	70
<i>pukbra</i>	66	2	33	67	58
<i>intermedia</i>	83	0	17	83	47
<i>millepora</i>	100	0	0	100	31
<i>lutkeni</i>	76	3	21	79	29
<i>nana</i>	85	0	15	85	26
<i>gemmifera</i>	96	4	0	100	23
<i>aspera</i>	50	5	45	55	22
<i>listeri</i>	86	0	14	86	21
<i>humilis</i>	75	0	25	75	16
<i>robusta</i>	81	0	19	81	16
<i>monticulosa</i>	92	0	8	92	12
<i>anthocercis</i>	100	0	0	100	10
<i>secale</i>	90	0	10	90	10
<i>latistella</i>	22	0	78	22	9
<i>austera</i>	88	0	13	88	8
<i>yongei</i>	63	0	38	63	8
<i>florida</i>	0	0	100	0	7
<i>microphthalma</i>	29	0	71	29	7
<i>tenuis</i>	86	0	14	86	7
<i>microclados</i>	100	0	0	100	5
<i>nas/cer</i>	80	0	20	80	5
<i>abrotanoides</i>	100	0	0	100	3
<i>acuminata</i>	0	0	100	0	3
<i>cytherea</i>	33	0	67	33	3
<i>cerealis</i>	50	0	50	50	2
<i>divaricata</i>	0	0	100	0	2
<i>samoensis</i>	100	0	0	100	2
<i>spicifera</i>	0	0	100	0	2
<i>verweyi</i>	0	100	0	100	2
<i>polystoma</i>	100	0	0	100	1
<i>selago</i>	100	0	0	100	1
<i>spatulata</i>	100	0	0	100	1
<i>valenciennesi</i>	100	0	0	100	1
Total					1,055

among polyps within a colony is generally very high (Wallace 1985). However, not every fracture of the branch will penetrate a polyp. Consequently, up to three branches were broken per colony, and colonies were only scored as empty if all three branches were empty. All the available evidence indicates that the vast majority of colonies will release gametes after the full moon subsequent to their maturation (Willis et al. 1985, Babcock et al. 1986, Oliver et al. 1988), which is indicated by pigmentation in the oocytes and

is readily recognizable underwater (Harrison et al. 1984).

RESULTS AND DISCUSSION

Eighty percent of 1,055 *Acropora* colonies sampled contained mature oocytes, and a further 2% had immature oocytes (Table 1). Thirty-three of 38 species checked (87%) had at least one colony with mature oocytes (Table 1). We predict that spawning times of these *Acropora* species are likely to be sim-

TABLE 2

Spatial Variation in Reproductive Condition of Colonies and Species in *Acropora* Assemblages in New Caledonia

Region	Reef	Site	Proportion of Colonies					<i>n</i>	Species		Total
			Mature	Immature	Empty	Gravid	No. Mature		Proportion Mature		
Grand Terre	Ilot Konduyo	1	70	0	30	70	132	16	76	21	
		2	62	0	38	62	154	14	70	20	
	Ilot Konduyo Total		66	0	34	66	286		73	26	
		N'Digoro	1	92	1	7	93	91	19	95	20
	2		91	3	7	93	106	18	86	22	
	3		92	2	6	94	142	16	89	19	
N'Digoro Total		91	2	6	94	339		93	27		
	Grand Terre total		80	1	19	81	625		81	37	
Ile des Pins		1	73	4	23	77	142	8	80	10	
		2	74	2	24	76	144	12	86	14	
		3	85	1	14	86	144	16	73	22	
Ile des Pins total			78	2	20	80	430		86	22	
Grand total			79	2	20	80	1055	33	92	37	

ilar to those on the Great Barrier Reef (i.e., somewhere between 3 and 5 days after the full moon in November. Of the remaining five species, all colonies of *A. florida*, *A. acuminata*, *A. divaricata*, and *A. spicifera* were empty, and *A. verweyi* had only immature oocytes.

The proportion of mature colonies varied little among sites within reefs (Table 2). At Ilot Konduyo the proportion ranged from 62% to 70%; at Récif N'Digoro from 91% to 92%; at Ile des Pins from 73% to 85%. However, the differences among reefs were substantial, ranging from 66% at Ilot Konduyo to 91% at Récif N'Digoro, indicating that spawning synchrony was lower at Ilot Konduyo when compared with the other reefs. It is interesting that the differences in proportion of mature colonies among sites correspond to their relative exposure to oceanic hydrology (i.e., oceanic exposure at Ilot Konduyo < Ile des Pins < Récif N'Digoro) (Figure 1). The high proportion of colonies without visible oocytes at Ilot Konduyo suggests that some colonies there may have spawned a month earlier, in October, than those on the Récif N'Digoro. This pattern is similar to that observed on the Great Barrier

Reef, where in some years the peak spawning on inner-shelf reefs precedes that on midshore and offshore reefs by a month, a pattern linked to sea-surface temperatures, which begin to rise a month earlier in the shallower inshore waters (Willis et al. 1985). Alternatively, these colonies could be sterile, or have bred at other times of the year.

The proportion of species with at least one mature colony was also consistently high, ranging from 70% to 95% and varied little among sites within reefs (Table 2). If these *Acropora* species behave like they do elsewhere in the Indo-Pacific it is highly probable that there will be multispecies spawning events some time after the full moon in November at all these sites. These data indicate highly synchronous coral reproduction, even greater than typically recorded on reefs on the Great Barrier Reef (e.g., Baird et al. 2002) and certainly greater than in the Solomon Islands (Baird et al. 2001). To some extent these data support the prediction that synchrony is higher at higher latitudes, although comparisons with sites farther south, such as Lord Howe Island (Harrison 2008), are difficult due to differences in the ways these data are presented.

Within-species synchrony in oocyte maturation was generally high (Table 1). However, of the 18 species where at least 10 colonies were sampled, six (33%) lacked visible oocytes in more than 20% of colonies: *A. humilis*, *A. digitifera*, *A. valida*, *A. lutkeni*, *A. aspera*, and *A. pulchra* (Table 1). Empty colonies may have bred a month earlier or be sterile as was suggested for colonies at Ilot Konduyo. Alternatively, either these colonies are not breeding during this annual gametogenic cycle, or they are breeding at other times of the year. A high proportion of colonies spawning outside the main reproductive season could be evidence of cryptic species, with colonies of the cryptic species spawning at different times of the year. For example, in Japan, colonies of one of two morphological groups of *A. digitifera* spawn a month later than colonies of a second morphological group that is now recognized as a separate species (Hayashibara and Shimoike 2002). Similarly, *A. digitifera* has two distinct spawning peaks 3 months apart, in November and February, at Lizard Island on the Great Barrier Reef (Wolstenholme 2004). Alternatively, a low proportion of the population breeding each year could be evidence of a different life history strategy (i.e., investing more heavily in growth and asexual reproduction rather than sexual reproduction). For example, *A. valida* often reproduces asexually via fragmentation, as evidenced by its occasional high local abundance and highly clonal population structure (Ayre and Hughes 2000). Similarly, *A. aspera* and *A. pulchra* are arborescent species that potentially direct energy toward linear growth of branches to promote asexual reproduction via fragmentation at the expense of reproduction (Smith and Hughes 1999, Okubo et al. 2007). Species within the *A. humilis* group, including *A. digitifera* and *A. humilis*, often have a highly encrusting morphology, particularly in high-energy areas like those at most of our sites. Species with this morphology possibly direct energy to lateral growth in preference to sexual reproduction to improve the strength of attachment (Jackson and Hughes 1985), and this may explain the high number of individuals without visible oocytes.

The highly seasonal nature of coral spawning around the globe (Guest et al. 2005b) affords environmental managers the opportunity to place temporal restrictions on human impacts that undermine the fertilization and early development of coral larvae. For example, the nickel refinery at Prony, located between our study sites (Figure 1), will expose reefs within New Caledonia's lagoon to soluble metals in effluent discharge (Horowitz 2008). The development of coral eggs and larvae is particularly sensitive to metal pollutants (Heyward 1988, Negri and Heyward 2001, Reichelt-Brushett and Harrison 2005). Although many aspects of coastal development and heavy industry often have continuous (or press) effects on marine systems, short-term recurrent (or pulse) threats, such as dredging, can be timed to minimize environmental damage. Our findings of synchronous reproduction in New Caledonia could, therefore, provide a basis for resource managers to dictate short periods for curtailing effluent discharge from ore treatment and other human-induced pulse impacts on fertilization and early development of coral larvae to help safeguard the resilience and persistence of these World Heritage-listed coral reefs.

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