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Varied spawning patterns of reef corals in Nha Trang Bay, Vietnam, western South China Sea

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ABSTRACT

Nha Trang Bay is located in the south-central waters of Vietnam and forms part of the most diverse region within the western South China Sea. Oceanographic studies indicate that this coastal area is not influenced by cold water masses from the north in winter but is subjected to summer upwelling. Coral spawning patterns of four species were monitored by collecting samples of colonies at Hon Mieu Island (12°11'37.31"N and 109°14'1.82"E) and two nearby sites during 2016–2019. Mature eggs were recorded inside polyps *Acropora florida* and *A. robusta* branches sampled prior to and after the full moon of late March to early April in 2018, and March in 2019. Spawning for both species was inferred to have occurred 6–8 nights after full moon in early April 2018, and 2–3 nights after full moon for *A. robusta* in March 2019. Colonies of the tabulate coral *A. hyacinthus* were inferred to have spawned between 6–11 nights after the full moon of March 2019, up to six nights after the spawning of *A. robusta*. In contrast, the spawning time of the massive coral of *Dipsastraea pallida* occurred one month later than that of branching *Acropora* corals, during the period before and after the full moon of late April to early May in 2018, and 4–5 nights after the full moon in April 2019. Monitoring of the ratio of pigmented mature eggs over time and inferred spawning periods of the three *Acropora* species and *D. pallida* indicated that spawning of corals in Nha Trang Bay occurs over an extended spawning period from March to May. Therefore, spawning in these species does not appear to be concentrated during a short mass spawning period over a few nights.

1. Introduction

Nha Trang Bay is positioned in the coastal waters of South Vietnam in the western South China Sea, where the continental shelf is narrow and influenced by two small rivers (Tran et al., 2015). Multi-year data show the average sea temperatures in the bay ranging between 24.0 and 29.5 °C, with two minimums in January and June. The second minimum is due to the influence of upwelling, which occurs annually in the summer in the coastal waters southward of the Nha Trang Bay (Bui, 2011).

The area is renowned as one of the most diverse areas in Vietnam with an array of tropical habitats including coral reefs, soft bottom benthic habitats, seagrass beds, sandy beaches and rocky shores (Vo et al., 2004). Coral reefs are abundant in shallow waters with fringing reefs occurring along the mainland and around all islands. In terms of reef coral diversity, recent studies (Huang et al., 2015; Vo, 2014) indicated that Nha Trang coastal waters make up the most diverse region in the western South China Sea.

Reef-building scleractinian corals exhibit a wide range of sexual reproductive patterns, with the majority of corals (65%) studied to date being broadcast-spawning hermaphrodites (Harrison and Wallace, 1990; Baird et al., 2009; Harrison, 2011). About 20% of corals are gonochoric broadcasters, with the remaining 15% of studied species being brooding corals that develop planula larvae internally within their polyps (Harrison, 2011; Randall et al., 2020). However, some coral species have mixed sexual patterns and modes of development, and some corals can change sex (Harrison, 1985; Loya et al., 2009; Harrison, 2011).

Reef corals also exhibit a wide range of gametogenic cycles and reproductive seasons ranging from single annual cycles to multiple cycles each year, with multiple lunar cycles recorded in some brooding species (Harrison and Wallace, 1990; Randall et al., 2020). Spawning is often synchronized among polyps within each colony and among different colonies of each species, resulting in high concentrations of gametes being released into the sea to enhance fertilization and cross-fertilization (Harrison et al., 1984; Babcock et al., 1986; Levitan et al., 2004).

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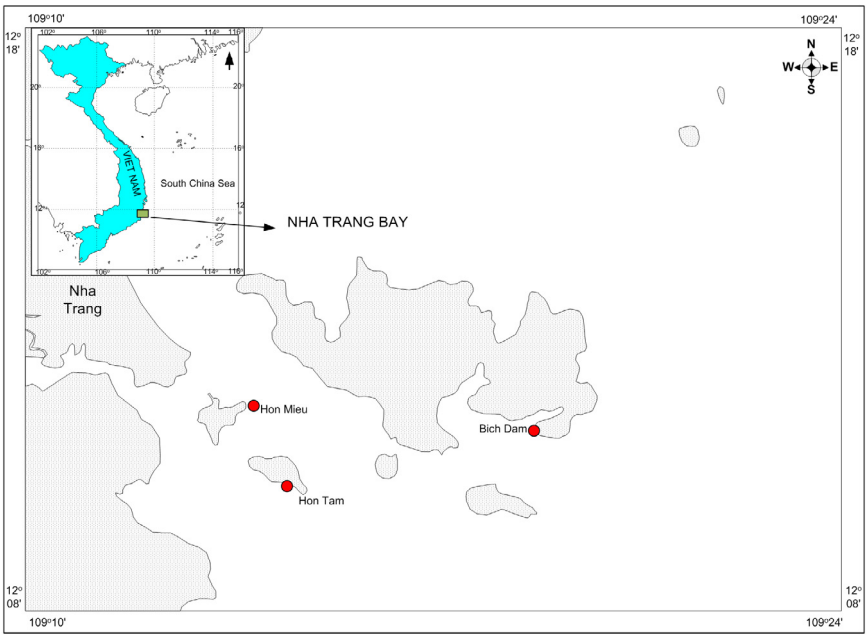

Fig. 1. Map indicating the position of Nha Trang Bay and coral reproduction study sites.

In many reef regions, some degree of spawning synchrony is also evident between different coral species that spawn together on just a few nights or during specific lunar periods each year (reviewed in Harrison and Wallace, 1990; Richmond and Hunter, 1990; Baird et al., 2009; Harrison, 2011). Global patterns of coral spawning range from highly synchronized mass spawning of many species and families on a few nights each year after full moon periods on the GBR and some Western Australian reefs (Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986, 1994; Gilmour et al., 2016), through to intermediate levels of multi-species spawning synchrony. Multi-species spawning occurs on many reef systems where some populations spawn synchronously but other species spawn over different months or lunar phases (reviewed in Harrison and Wallace, 1990; Richmond and Hunter, 1990; Baird et al., 2009; Harrison, 2011; Baird et al., 2021). In contrast, in some (but not all) equatorial and other reef regions, the available data indicate that spawning may be synchronized within populations of each species, but in some regions spawning is asynchronous between many or most species studied to date, resulting in different species spawning at different lunar cycles or on different months or seasons over more extended spawning seasons (e.g. Shlesinger and Loya, 1985; Szmant, 1986; Oliver et al., 1988; Richmond and Hunter, 1990; Mangubhai and Harrison, 2008; Wijayanti et al., 2019; Gouezo et al., 2020).

Despite increasing numbers of coral reproductive studies in recent decades, very limited data are available for some important reef regions, including Vietnam. For Vietnamese corals, only a paper was newly published on *Acropora* spawning based on observations of gonadogenesis development and variation of egg average sizes (Vo et al., 2022). Therefore, this study aimed to determine seasonal periods when mature gametes were present in some locally abundant reef corals, and the extent of reproductive synchrony among these populations in the Nha Trang Bay area.

2. Materials and methods

Samples of polyps from colonies of four coral species were collected for reproductive studies, mainly at Hon Mieu Island (12°11′37.31″N and 109°14′1.82″E) during 2016–2019 (Fig. 1). Two additional sites for coral collection in 2019 were at Bich Dam and Hon Tam nearby (Fig. 1).

Initially, samples of 3–5 cm long branches were collected from colonies of two *Acropora* coral species twice in January–February 2016, including six specimens per time for *Acropora florida* and nine specimens per time for *Acropora robusta*. To examine the relationship between coral spawning and full moon periods, collection of both species was repeated 10 times in late March 2016 (48 specimens of *A. florida* and 72 specimens of *A. robusta*) and early April 2016 (12 and 18 specimens, respectively), as well as six times during March (31 and 41 specimens) and April (97 and 111 specimens) in 2018. Additional specimens of *A. robusta* were collected seven times in March 2019 to determine the length of the spawning period of this branching coral, with 84 specimens in the total. *Acropora hyacinthus* was selected as a representative tabulate coral to study its reproductive season in 2019. The number of specimens collected included six in January (once), nine in February (once), 108 in March (9 collection periods), and 12 in April 2019 (once). For *Dipsastraea pallida*, small fragments about 3–5 cm wide were chiseled carefully from massive colonies. Due to the increased difficulty and care needed in sampling massive corals, fewer samples of *D. pallida* were collected in 2018, including 11 in March, 29 in April, and 19 in May. An additional sixty samples of *D. pallida* were collected during four sampling periods in April 2019.

Maturing oocytes often become highly pigmented in the weeks before maturation and spawning (Harrison et al., 1984), and changes in oocyte pigmentation were studied by repeatedly sampling branches from some tagged coral colonies. Tagged and repeatedly monitored corals included two colonies of *A. florida* and four colonies for *A. robusta* in 2018, and four colonies of *A. hyacinthus* and four colonies of *A. robusta* in 2019. Observations of pigmented eggs (typically pink color) were done immediately after collection, either on the boat or in a nearby wet lab. All specimens were then preserved in 10% formalin in seawater for egg counting and measurements a week later. Branch samples were then carefully decalcified in dilute acid solutions to remove the calcium carbonate skeletons, embedded in wax, sectioned and stained for histological analysis of egg sizes using standard histological methods.

Measurements of the diameters of eggs were done by measuring the longest and shortest diameters of eggs to provide

Table 1
Numbers of eggs measured for three *Acropora* species and *D. pallida* collected from Nha Trang Bay.

2016	*A. florida*	*A. robusta*	2018	*A. florida*	*A. robusta*	*D. pallida*	2019	*A. robusta*	*A. hyacinthus*	*D. pallida*
18/3	243		1/3	1386	720		22/1		40	
19/3	240	51	6/3	2551	508		18/2		60	
21/3	452	84	26/3	947	1233	102	13/3	80	80	
22/3	455	167	2/4	2371	1346		15/3	80	80	
24/3	114	382	4/4	3290	1474		17/3	80	80	
25/3	382	32	6/4	1913	2179	105	19/3	80	80	
27/3	513	258	9/4	No egg	No egg		21/3	80	80	
28/3	272	170	11/4	No egg	No egg	122	23/3	80	80	
3/4	494		23/4			173	25/3		80	
7/4	2		3/5			187	27/3		80	
			14/5			No egg	29/3		80	
							31/3		80	
							22/4			62
							24/4			91
							26/4			No egg
							28/4			No egg

Table 2
Average diameters of mature pigmented eggs measured from histological samples of three *Acropora* species collected in 2018 and 2019.

Species	Collecting date	Average diameter (μm)	SD	N
A. florida	2, 4, 6 April 2018	429	58	10
A. robusta	2, 4, 6 April 2018	415	66	22
A. hyacinthus	25, 27 March 2019	463	29	80

an average diameter of eggs in images of histological sections of samples using ImageJ software. Average egg diameters were measured for all eggs observed in the branch samples of *A. florida* and *A. robusta* colonies collected in 2016 and 2018 as well as for a number of randomly selected eggs of *A. robusta* and *A. hyacinthus* from the specimens collected in 2019 (Table 1). Measurements of pigmented eggs were done using the same technique for *A. florida* and *A. robusta* branches collected in April 2018, and for *A. hyacinthus* branches collected in March 2019, with a total of 10, 22 and 80 pigmented eggs measured for these species, respectively. Average egg diameters were also measured for all eggs observed in the fragment samples of *D. pallida* colonies collected in 2018 and 2019 (Table 1).

3. Results

Mature eggs of broadcast spawning corals are often highly pigmented, typically with pink or red coloration, but a range of other colors have been reported in some species (Babcock et al., 1986; Harrison and Wallace, 1990). Pink pigmented eggs were observed in *A. florida* and *A. robusta* branch samples collected in Nha Trang Bay during late March to early April (Fig. 2). Mean diameters of pigmented eggs in histological sections from 2018 samples were 429 μm (ranging between 325 and 492 μm) for *A. florida*, 415 μm (ranging between 282 and 522 μm) for *A. robusta*, and 463 μm (ranging between 401 and 549 μm) for *A. hyacinthus* samples from 2019 (Table 2).

Variation in egg diameter and the presence and then absence of large mature eggs in samples from colonies of *A. florida* and *A. robusta* collected in 2016 indicated that spawning occurred between 3rd and 7th April (Fig. 3). The full moon occurred on 23rd March, hence spawning of the sampled colonies likely occurred between 11 to 14 nights After Full Moon (nAFM).

Measurements of egg diameters and the presence of pigmented eggs in samples of *A. florida* and *A. robusta* colony branches collected in March and April 2018 indicated that mature eggs were dominant during the period 26 March to 6 April for both species (Fig. 4). Both tagged colonies of *A. florida* had mature pigmented oocytes on 5th day before the full moon and most branches sampled had mature eggs on 2nd, 4th and 6th after the full moon (Table 3). The four colonies of *A. robusta* repeatedly sampled also had mature eggs during this period, but only 24%–45% of branches sampled had gravid polyps present (Table 3).

Eggs were absent from samples collected on 9 April 2018, indicating that spawning occurred between 6 and 9 April 2018 (Fig. 4). Full moon occurred on 31st March 2018, hence spawning of the sampled colonies is likely to have occurred between 6 to 8 nAFM.

Additional study of *A. robusta* spawning patterns in 2019 indicated that mature eggs were present in sampled colonies from 7 days before until 3 days after full moon, which occurred on 21st March (Fig. 5). Most of the branches sampled from four tagged colonies had gravid polyps with mature eggs present during this period (Table 4). Eggs were absent in samples from 25 March, hence spawning in the sampled colonies is inferred to have occurred between 2 and 3 nAFM in 2019.

Egg maturity and inferred spawning patterns were also studied in *A. hyacinthus* colonies in 2019. The inferred spawning time of this tabulate *Acropora* occurred later than for *A. robusta.* Mature pigmented eggs were recorded in *A. hyacinthus* colonies from March 21 until March 31, corresponding to the period from full moon to 10 days after full moon (Figs. 6, 7). One of the four repeatedly sampled colonies was no longer gravid on 29 March, indicating that this colony had spawned between sampling on 27 March and 29 March, corresponding to 6–7 nAFM (Table 5). Eggs were absent in all samples collected on 2 April 2019 (Fig. 6, Table 5), indicating that spawning in most of the sampled colonies occurred on the 31 March and/or 1st April, corresponding to 10–11 nAFM.

Egg maturity and inferred spawning patterns were initially examined in colonies of the brain coral *D. pallida* in 2018 sampled before and after the full moon on April 30. Changes in the ratios of eggs with larger sizes (Fig. 8) indicated that maturing oocytes were present during the period from 23 April (7th day before full moon) and at least until 3 May (3rd day after the full moon). Eggs were absent in colonies sampled on 14 May hence spawning was inferred to have occurred between 3 and 13 May 2018 corresponding to 3–12 nAFM. More frequent collection of specimens in 2019 (Fig. 9) indicated that the period of egg maturation and spawning in this massive species lasted until April 24 or 25, 4–5 nights after the full moon which occurred on 19 April. These results indicate that mature eggs and spawning of massive *D. pallida* colonies that were sampled in this study occurred one month later than the spawning periods of branching *Acropora* corals.

4. Discussion

The results from this study indicate that the spawning season of the four reef coral species studied in Nha Trang Bay

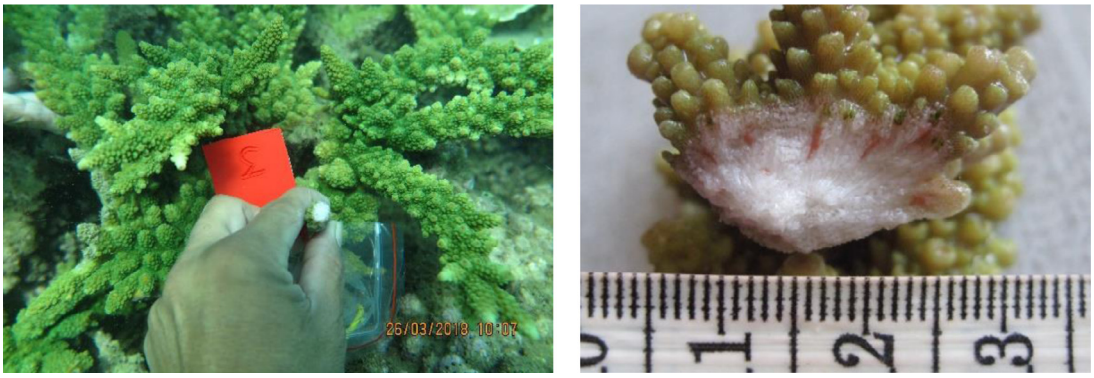

Fig. 2. Tagged colony and pigmented eggs observed in broken branch sections of *A. florida* corals collected in Nha Trang Bay.

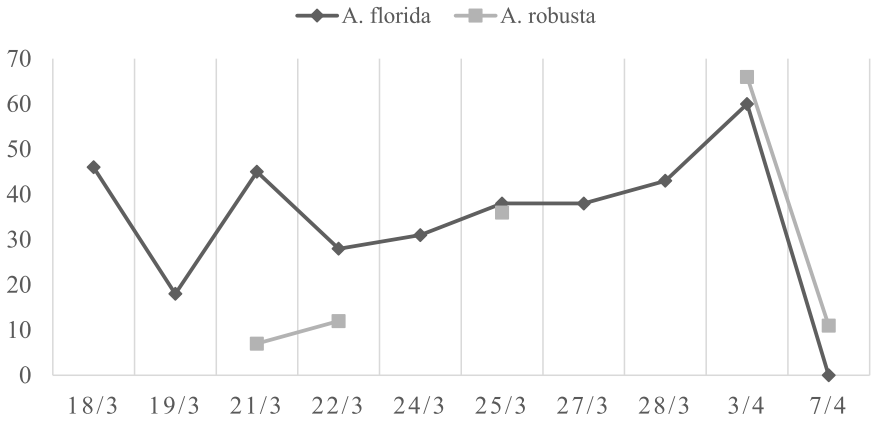

Fig. 3. Variation in the ratio (%) of egg diameter > 400 μm in branch samples of *A. florida* and *A. robusta* in 2016.

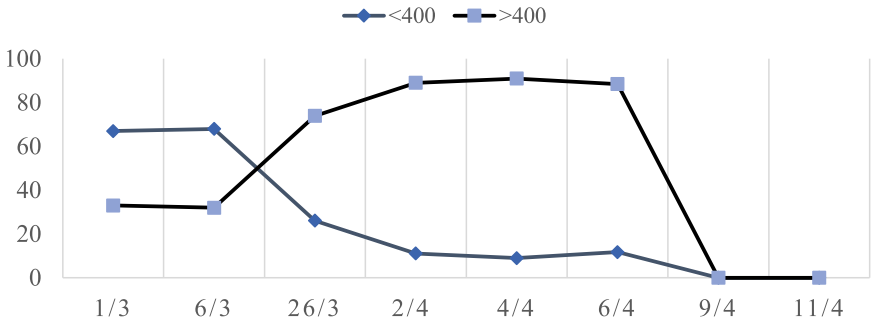

Fig. 4. Variation in the ratios (%) of mature egg diameters > 400 μm in branch samples of *A. florida* and *A. robusta* in 2018.

Table 3
Proportion of branches sampled from colonies of two *Acropora* species with mature (pigmented) eggs in 2018.

Collecting date	*A. florida*		*A. robusta*	
	Eggs present in branch sampled	Per colony	Eggs present in branch sampled	Per colony
26 March	4/11	2/2	8/21	3/4
2 April	10/17	2/2	5/18	4/4
4 April	23/26	2/2	7/29	3/4
6 April	14/16	2/2	12/26	4/4

occurred between March and May each year. Similar spawning periods have been reported in some other studies of reef coral reproduction in the Southeast Asia region. Up to 18 species of *Acropora* have been recorded spawning between 8–13 nAFM in synchronous multispecies spawning events on reef areas in the northern Philippines in March resulting in surface aggregations of coral spawn slicks (Jamodiong et al., 2018; Harrison et al., 2021), with additional *Acropora* species recorded spawning in April and June (dela Cruz and Harrison, 2017, 2020). Spawning has been reported in March to April for Merulinidae in the Western Gulf of Thailand (Kongjandtre et al., 2009), during April for *Acropora* spp. in Kuantan, Malaysia (Hanapiah et al., 2020), and during March and April for multiple species of *Acropora*, Merulinidae and some other species in Singapore (Guest et al., 2005). Multispecies coral

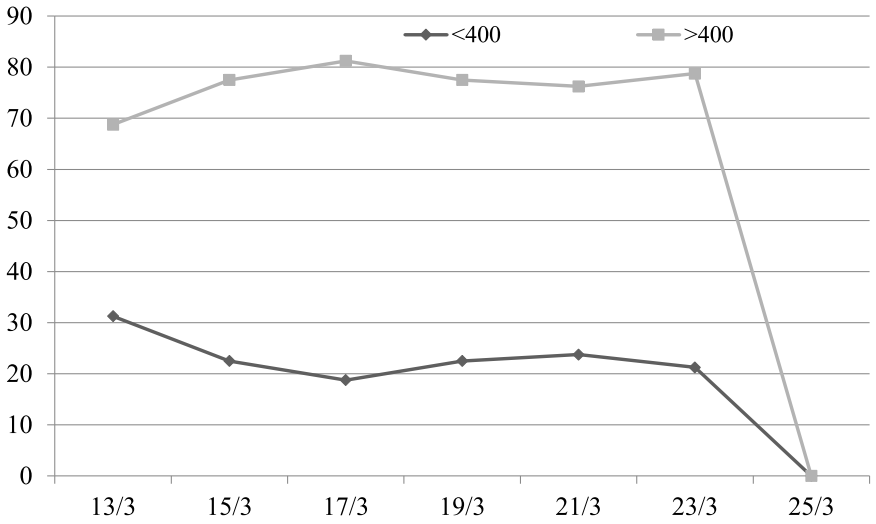

Fig. 5. Variation in the ratios (%) of egg diameters < 400 μm and > 400 μm in branch samples of *A. robusta* in 2019.

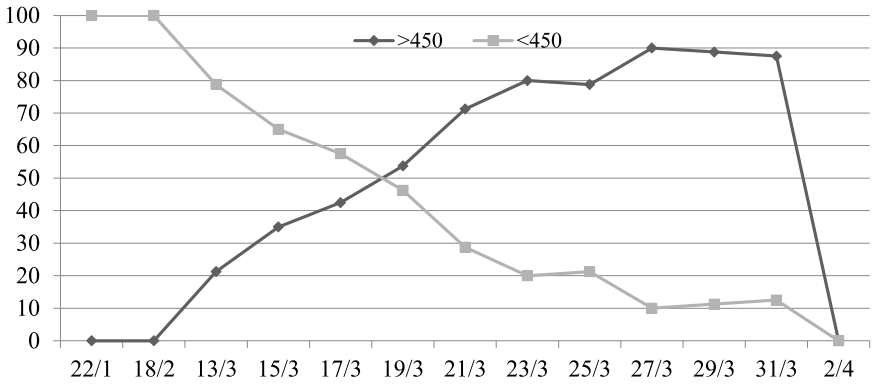

Fig. 6. Variation in the ratios (%) of egg diameters < 450 μm and > 450 μm in branch samples of *A. hyacinthus* in 2019.

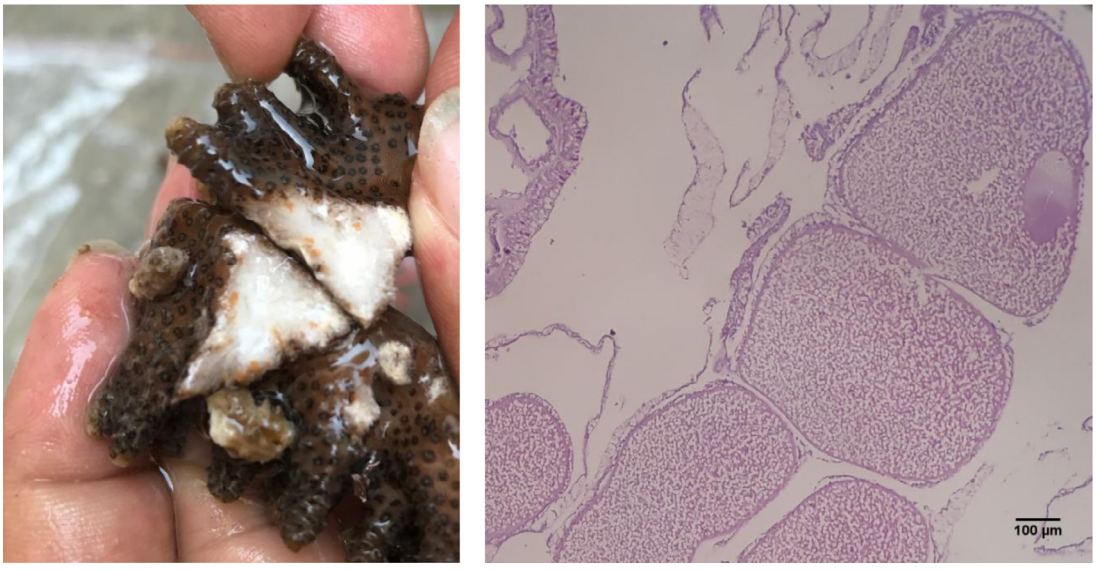

Fig. 7. A sample of *A. hyacinthus* collected on March 25, 2019 showing pigmented mature eggs in the polyps (left image) and photomicrograph of a histological section of eggs (right image) from this sample (scale bar = 100 μm).

spawning events and some coral spawn slicks were recorded on Indonesian reefs during March and April, and in September and October, coinciding with two seasonal periods of warming sea temperatures (Wijayanti et al., 2019).

The coral pawning periods inferred in the present study from March to May occurred within the transition period from the Northeast to the Southwest monsoon in South Vietnam, which is characterized by increased seawater temperature. Oceanographic

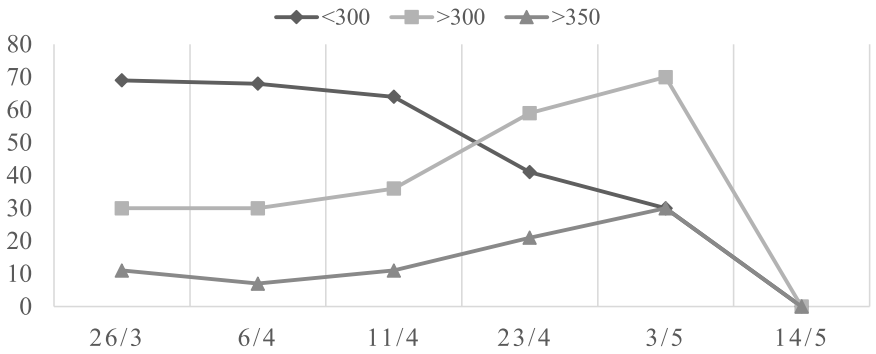

Fig. 8. Variation in the ratios (%) of egg diameters < 300 μm, > 300 and > 350 μm in samples of *D. pallida* in 2018.

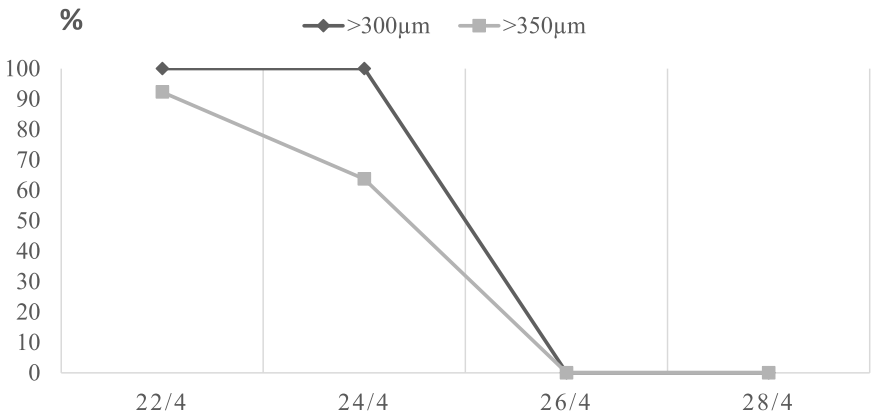

Fig. 9. Variation in the ratios (%) of egg diameters > 300 and > 350 μm in samples of *D. pallida* in 2019.

Table 4
Proportion of branches sampled from four colonies of *Acropora robusta* with mature (pigmented) eggs in 2019.

Collecting date	Eggs present in branch sampled	Per colony
13 March	9/12	4/4
15 March	9/12	4/4
17 March	12/12	4/4
19 March	12/12	4/4
21 March	9/12	3/4
23 March	6/12	2/4
25 March	0/12	0/4

Table 5
Proportion of branches sampled from four colonies of *Acropora hyacinthus* with mature (pigmented) eggs in 2019.

Collecting date	Eggs present in branch sampled	Per colonies
25 March	12/12	4/4
27 March	12/12	4/4
29 March	10/12	3/4
2 April	0/12	0/4

research (Bui, 2011), has recorded average sea temperatures in the Nha Trang Bay to range between 24.0 and 29.5 °C, with two minimum periods in January and June, and two maximum temperature periods in May and September (Fig. 10). Reproductive cycles of many coral species are thought to be influenced by seasonal changes in sea temperatures, with gamete maturation and spawning periods coinciding with warming sea temperatures (Willis et al., 1985; Babcock et al., 1986; Harrison and Wallace, 1990; Randall et al., 2020). The study by Dai et al. (1992) indicated that reef corals in the South of Taiwan (21°N) where the reef environment is characterized by warmer waters and lower ranges in sea temperature, released their gametes one to two months earlier compared with corals from cooler reefs in the North of Taiwan (25°N).

Some other environmental factors are also thought to influence coral reproductive cycles, including seasonal changes in solar insolation (Penland et al., 2004), and day length which entrains a molecular clock to produce an endogenous rhythm in some corals (Hoadley et al., 2016). The inferred spawning periods of the corals studied in Nha Trang Bay between March and May coincided with the months of increased photoperiod and the highest radiation (Fig. 11). Recent studies have suggested that a combination of environmental factors including rising sea temperature and increased photoperiod and radiation may act as proximate cues to synchronize spawning in reef corals (Randall et al., 2020). Therefore, further research is needed to determine whether some reef corals from Vietnam spawn in response to the second period of warming sea temperatures after upwelling but decreasing photoperiod and radiation during September and October each year.

The present study of coral reproduction in Nha Trang Bay highlighted the complexity in the relationship between coral spawning and lunar cycles among the four species studied. Many corals have been recorded to spawn in the week after full moon periods (Harrison and Wallace, 1990; Richmond and Hunter, 1990; Baird et al., 2021), and moonlight can be detected through photoreceptors in coral tissues that may entrain lunar cycles of spawning (Levy et al., 2007; Hoadley et al., 2016). Spawning of *A. robusta* colonies was inferred to have occurred between 2–3 nAFM in March 2019, but inferred spawning of *A. hyacinthus* colonies occurred later in the same lunar cycle (10–11 nAFM). An intermediate lunar period of spawning between 6–8 nAFM was inferred for *A. florida* and *A. robusta* colonies in 2018, and it is possible that some colonies of both species spawned synchronously. Colonies of the brain coral *D. pallida* corals were inferred to spawn 4–5

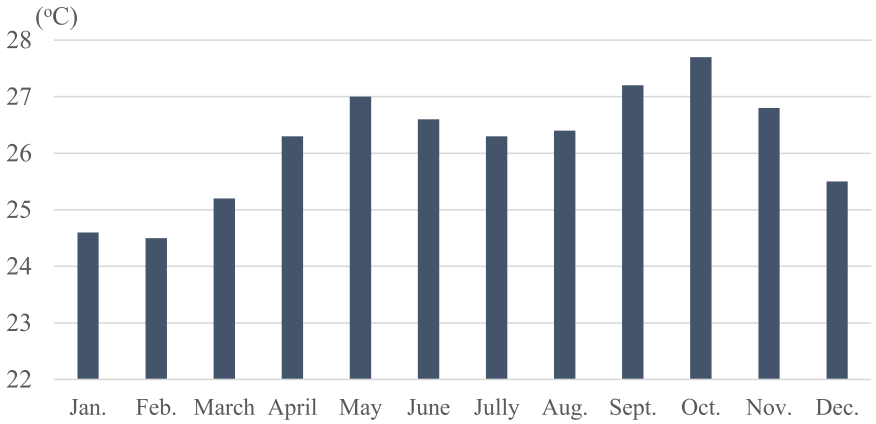

Fig. 10. Variation in average sea surface temperature in Nha Trang Bay (based on data from HyCOM-NOOA 1992–2017).

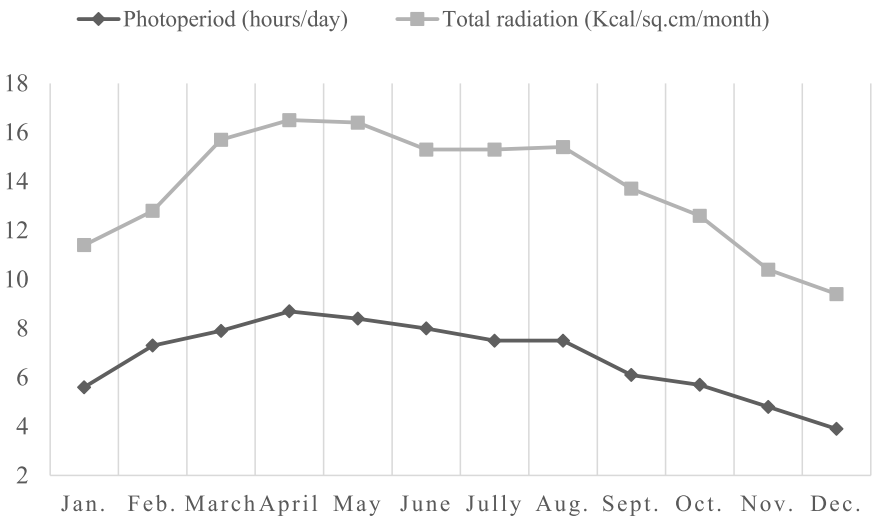

Fig. 11. Variation in average photoperiod and total radiation monthly in the Nha Trang area (data from DOST-KhanhHoa, 2020).

nAFM in late April 2019, one lunar cycle later than the *Acropora* species spawning period in 2019. Inter-annual variation in the lunar nights of spawning has been reported among *Acropora* species in other regions, and seems to be more prevalent among these branching corals than for some groups of massive corals which are more consistent in their lunar periodicity of spawning (Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986; Hayashibara et al., 1993).

5. Conclusion

This study provided the first internationally published data on coral spawning in Vietnamese waters, indicating egg maturity and inferred spawning patterns of three *Acropora* species and the brain coral *D. pallida*. Analysis of the inferred spawning periods of these species indicated that spawning of corals in Nha Trang Bay occurs at different lunar periods over an extended spawning period from March to May. Therefore, their spawning does not appear to be concentrated during a short mass spawning period over a few nights, as occurs in some reef regions in the Indo–Pacific. Further research is required to determine the extent of spawning synchrony within populations of these species and between different coral species and families within the coral assemblages in Nha Trang Bay and elsewhere in Vietnamese reefs.

CRediT authorship contribution statement

Si Tuan Vo: Conceptualization, Methodology, Investigation, Data analysis, Writing – original draft. **Son Lam Ho:** Methodology, Data analysis, Reviewing. **Kim Hoang Phan:** Investigation, Field observation, Data analysis and curation. **Van Than Doan:** Investigation, Lab observation, Data analysis and curation. **Tran Tu Tram Đang:** Egg measurement, Data analysis and curation. **Van Long Nguyen:** Reviewing. **Peter Lynton Harrison:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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References

Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.K., Wallace, C.C., Willis, B.L., 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90, 379–394.

Babcock, R.C., Wills, B.L., Simpson, C.J., 1994. Mass spawning of corals on high latitude coral reef. Coral Reefs 13, 161–169.

Baird, A.H., Guest, J.R., Edwards, A.J., et al., 2021. An Indo-Pacific coral spawning database. Sci. Data 8 (35).

Baird, A.H., Guest, J.R., Willis, B.L., 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu. Rev. Ecol. Evol. Syst. 40, 551–571.

Bui, H.L., 2011. HandBook for South Central Waters of Vietnam. Publishing House of Natural Science and Technology, Ha Noi, p. 208 (in Vietnamese).

dela Cruz, D.W., Harrison, P.L., 2017. Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. Sci. Rep. 7, 13985. http://dx.doi.org/10.1038/s41598-017-14546-y.

dela Cruz, D., Harrison, P.L., 2020. Enhancing coral recruitment through assisted mass settlement of cultured coral larvae. PLoS One 0242847.

Dai, C.F, Soong, K., Fan, T.Y., 1992. Sexual reproduction of corals in northern and Southern Taiwan. Guam, In: Proceedings of the 7th International Coral Reef Symposium, vol. 1, pp. 448–455.

DOST-KhanhHoa, 2020. Characteristics on Climate and Hydrology of Khanh Hoa Province. Published by Department of Information and Communication, Khanh Hoa Province, p. 259 (in Vietnamese).

Gilmour, J.P., Underwood, J.N., Howells, E.J., Gates, E., Heyward, A.J., 2016. Biannual spawning and temporal reproductive isolation in *Acropora* corals. PLoS One 11, e0150916.

Gouezo, M., Doropoulos, C., Fabricius, K., Olsudong, D., Nestor, V., Kurihara, H., Golbuu, Y., Harrison, P.L., 2020. Multispecific coral spawning events and extended breeding periods on an equatorial reef. Coral Reefs 39, 1107–1123.

Guest, J.R., Chou, L.M., Baird, A.H., Goh, B.P.L., 2005. Seasonal reproduction in equatorial reef corals. Invertebr. Repr. Dev. 48, 207–218.

Hanapiah, Muhammad Faiz Mohd, Saad, Shahbudin, Ahmad, Zuhairi, 2020. Dispersal pattern of coral larvae in Kuantan Coastal waters, Malaysia. Sci. Herit. J. 4 (1), 13–18.

Harrison, P.L., 1985. Sexual characteristics of scleractinian corals: Systematic and evolutionary implications. In: Proceedings of the 5th International Coral Reef Congress, Tahiti, vol. 4, pp. 337–342.

Harrison, P.L., 2011. Sexual reproduction of scleractinian corals. In: Dubinsky, Z., Stambler, N. (Eds.), Coral Reefs: An Ecosystem in Transition Part 3. Springer Publishers, pp. 59–85.

Harrison, P.L., Babcock, R.C., Bull, G.D., Oliver, J.K., Wallace, C.C., Willis, B.L., 1984. Mass spawning in tropical reef corals. Science 223, 1186–1189.

Harrison, P.L., dela Cruz, D.W., Cameron, K.A., Cabaitan, P.C., 2021. Increased coral larval supply enhances recruitment for coral and fish habitat restoration. Front. Mar. Sci. 8, 750210.

Harrison, P.L., Wallace, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp. 133–207.

Hayashibara, T., Shimoike, K., Kimura, T., Hosaka, S., Heyward, A., Harrison, P., Kudo, K., Omori, M., 1993. Patterns of coral spawning at Akajima Island, Okinawa Japan. Mar. Ecol. Prog. Ser. 101, 253–262.

Hoadley, K.D., Vize, P.D., Pyott, S.J., 2016. Current understanding of the circadian clock within Cnidaria. In: The Cnidaria, Past, Present and Future. pp. 511–520.

Huang, D., Licuanan, W.Y., Hoeksema, B.W., Chen, C.A., Ang, P.O., Huang, H., Lane, D.J.W., Vo, S.T., Waheed, Z., Affendi, Y.A., Yeemin, T., Chou, L.M., 2015. Extraordinary diversity of reef corals in the South China Sea. Mar. Biodivers. 45 (2), 157–168.

Jamodiong, E.A., Maboloc, E.A., Villanuaeva, R.D., Cabaitan, P.C., 2018. Gametogenesis and inter-annual variability in the spawning pattern of *Acropora hyacinthus* in Northwestern Philippines. Zool. Stud. 57 (46), http://dx.doi.org/10.6620/zs.2018.57-46.

Kongjandtre, N., Ridgway, T., Ward, S., Hoegh-Guldberg, O., 2009. Broadcast spawning patterns of *favia* species on the inshore reefs of Thailand. Coral Reefs http://dx.doi.org/10.1007/s00338-009-0551-3.

Levitan, D.R., Fukami, H., Jara, J., Kline, D., McGovern, T.M., McGhee, K.E., Swanson, C.A., Knowlton, N., 2004. Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. Evolution 58, 308–323.

Levy, O., Appelbaum, L., Leggat, W., Gothlif, Y., Hayward, D.C., Miller, D.J., Hoegh-Guldberg, O., 2007. Light-responsive cryptochromes from a simple multicellular animal, the coral *Acropora millepora*. Science 318, 467–470.

Loya, Y., Sakai, K., Heyward, A., 2009. Reproductive patterns of fungiid corals in Okinawa, Japan. Galaxea 11, 119–129.

Mangubhai, S., Harrison, P.L., 2008. Asynchronous coral spawning patterns on equatorial reefs in Kenya. Mar. Ecol. Prog. Ser. 360, 85–96.

Oliver, J.K., Babcock, R.C., Harrison, P.L., Willis, B.L., 1988. Geographic extent of mass coral spawning: Clues to ultimate causal factors. In: Proceedings of the 6th International Coral Reef Symposium, Townsville, vol. 2, pp. 803–810.

Penland, L., Kloulechad, J., Idip, D., van Woesik, R., 2004. Coral spawning in the western Pacific Ocean is related to solar insolation: Evidence of multiple spawning events in Palau. Coral Reefs 23, 133–140.

Randall, C.J., Negri, A.P., Quigley, K.M., Foster, T., Ricardo, G.F., Webster, N.S., Bay, L.K., Harrison, P.L., Babcock, R.C., Heyward, A.J., 2020. Sexual production of corals for reef restoration in the Anthropocene. Mar. Ecol. Prog. Ser. 635, 203–232.

Richmond, R.H., Hunter, C.L., 1990. Reproduction and recruitment of corals: Comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. Mar. Ecol. Prog. Ser. 60, 185–203.

Shlesinger, Y., Loya, Y., 1985. Coral community reproductive patterns: Red sea versus the great barrier reef. Science 228, 1333–1335.

Szmant, A.M., 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5, 43–54.

Tran, V.B., Nguyen, D.D., Pham, B.T., Tran, M.C., 2015. Geomorphological characteristics of Nha Trang bay and adjacent area. Coll. Mar. Res. Works 21 (2), 42–54 (in Vietnamese).

Vo, S.T., 2014. Fauna of reef corals in the Vietnam marine areas. In: Proceeding of the Second National Conference on Marine Biology and Sustainable Development. Publishing House of Natural Science and Technology, Ha Noi, pp. 315–322 (in Vietnamese).

Vo, S.T., DeVantier, L.M., Nguyen, V.L., Hua, T.T., Nguyen, X.H., 2004. Coral reefs of the Hon Mun Marine Protected Area. Nha Trang Bay, Vietnam: Species composition, community structure, status and management recommendation. In: Proceedings of the Scientific Conference Bien Dong-2002, Nha Trang - Vietnam. pp. 649-690.

Vo, S.T., Lam, H.S., Dang, T.T.T., Phan, K.H., Doan, V.T, Mai, X.D., 2022. A study on the spawning season of 3 *Acropora* species in Nha Trang bay, Southern waters of Vietnam. Vietnam J. Mar. Sci. Tech. 22 (1), 21–28.

Wijayanti, D.P., Indrayanti, E., Wirasatriya, A., Haryanto, A., Haryanti, D., Sembiring, A., Fajrianzah, T.A., Bhagooli, R., 2019. Reproductive seasonality of coral assemblages in the Karimunjawa Archipelago, Indonesia. Front. Mar. Sci. 6, 195.

Willis, B.L., Babcock, R.C., Harrison, P.L., Oliver, J.K., Wallace, C.C., 1985. Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. Tahiti, In: Proceedings of the 5th International Coral Reef Congress, vol. 4, pp. 343–348.