

Broadcast spawning of two species of sea anemone, *Entacmaea quadricolor* and *Heteractis crispa*, that host anemonefish

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Summary

As the sea anemones, *Entacmaea quadricolor* and *Heteractis crispa*, provide essential habitat for obligate symbiotic anemonefish, knowledge of their reproductive biology is crucial to their effective management and conservation. This paper provides the first detailed information on the spawning times, behaviour and mode of gamete release for these host anemone species. Anemones were collected from subtropical reefs in the Solitary Islands Marine Park, eastern Australia, and monitored in outdoor flow-through seawater tanks from 2003 to 2005. Sexually reproductive anemones were either male or female, releasing their gametes into the water column for external fertilisation and development. Spawning of both sexes was predominately synchronous and was restricted to a few nights each year during the austral summer and autumn. Males generally began to release gametes prior to females, suggesting that sperm or some associated product may trigger the females to spawn. Sperm were commonly released in milky white streams or clouds, whereas eggs were released singly or in large masses. Reproductive seasonality and synchrony of gamete release suggests that spawning in both species is coordinated by similar responses of individuals to a range of environmental factors such as seawater temperature, photoperiod and lunar cycles. Incorporating knowledge of the sexual reproductive biology of host sea anemones into management and conservation programs could help ensure the viability of their populations and their resident anemonefish.

Key words: Actiniaria, subtropical reefs, sexual reproduction, spawning, environmental cues

Introduction

Spawning in many anthozoans is the culmination of a long process of gametogenic development, with animals either broadcast spawning their gametes for external fertilisation and development or brooding them to an early developmental stage prior to release (Harrison and Wallace, 1990; Fautin, 1992; Levitan, 1996). Broadcast spawning predominates, with many

hermaphroditic and gonochoric species using this mode of reproduction (Harrison, 1985; Harrison and Jamieson 1999). During spawning, mesogleal and gastrodermal layers rupture, releasing gametes into the gastrovascular cavity before they are passively released, slowly extruded or actively expelled, generally through the polyp mouth (Campbell, 1974; Giese and Kanatani, 1987; Martin and Koss, 2002). Hermaphroditic species

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either release eggs and sperm separately or in tightly-packed spherical egg-sperm bundles (Harrison et al., 1984; Harrison and Jamieson, 1999). In some hermaphroditic actinian species such as *Epiactis japonica*, sperm may be released prior to the discharge of eggs from the same individual (Uchida and Iwata, 1954; Uchida and Yamada, 1968). Gonochoric species release eggs singly or in large masses held together with mucus, whereas sperm are released in large clouds (Gemmill, 1920; Spaulding, 1972; Siebert, 1974).

Most sea anemones studied so far are gonochoric. Spawning of males and females is usually synchronous (e.g. *Anthopleura elegantissima*, see Ford, 1964; Jennison, 1979; Sebens, 1981; *Halcampa duodecimcirrata*, see Nyholm, 1949; *Oulactis mucosa*, see Hunt and Ayre, 1989; Marshall et al., 2004; *Tealia crassicornis*, see Chia and Spaulding, 1972). Synchrony enhances the probability of egg and sperm encounter, maximises outcrossing, increases the probability of fertilisation, and reduces gamete wastage (Campbell, 1974; Harrison and Wallace, 1990; Olive, 1995). It may also increase propagule survival by satiation of active predators and filter feeders (Harrison et al., 1984; Olive, 1995). Many marine invertebrates including sea anemones have limited annual breeding periods. However, the timing and length of the breeding period may differ among species (Campbell, 1974; Giese and Pearse, 1974; Martin and Koss, 2002), years (Giese, 1959; Jennison, 1979), and localities for the same species (Giese and Pearse, 1974). Cues for such periodicity and synchrony vary, and may include a combination of environmental stimuli such as seawater temperature, salinity, tidal regime, lunar phase, photoperiod and food availability (Giese and Kanatani, 1987; Harrison and Wallace, 1990; Fautin, 1992).

Little is known about the sexual reproductive biology of sea anemones that host anemonefish. This lack of information is due to difficulty in predicting spawning (Giese, 1959) as well as their restricted distribution and the low density of some species (Dunn, 1981). As host sea anemones are ecologically and commercially important, being highly sought after for the marine aquarium trade, their effective management relies on an understanding of the processes that maintain and renew their populations. This paper provides the first comprehensive information on the spawning times, behaviour and mode of gamete release for two species of host anemone, *Entacmaea quadricolor* and *Heteractis crispa*.

Material and Methods

Collection and maintenance of animals

Thirty to forty individuals of both *E. quadricolor* and

H. crispa were collected from subtropical rocky reefs at 9–18 m depth at North Solitary Island, Solitary Islands Marine Park, Australia (29°55'S, 153°23'E). Unlike *H. crispa*, *E. quadricolor* was observed to reproduce asexually by longitudinal fission (A. Scott, pers. obs.), as previously reported (e.g. Godwin and Fautin, 1992). To minimise the collection of *E. quadricolor* clones, various colour morphs of this species were haphazardly selected from at least two metres apart (after Bucklin, 1985; Gomes et al., 2003). *E. quadricolor* and *H. crispa* anemones were carefully removed from the substratum by hand. All individuals of a species were placed into a 3240-L outdoor flow-through seawater tank. Anemones were collected at least one week prior to expected spawnings to enable them to acclimatise to tank conditions. Approximately one-third of all *E. quadricolor* and *H. crispa* individuals were kept throughout the 3-year study period, allowing spawning patterns to be observed over consecutive years. The remaining anemones were returned to the field and replaced at regular intervals, ensuring that the population maintained within the tanks always contained anemones that had recently experienced field conditions.

Tanks were supplied with flow-through seawater at a rate of approximately 20-l min⁻¹, which was sourced from the Solitary Islands Marine Park so that parameters such as temperature, salinity, pH, and nutrient levels were similar to those found at the collection site. Tanks were located outdoors to ensure that the anemones received natural photoperiod and lighting. *E. quadricolor* was provided with rocks, and *H. crispa* with rocks and coarse rubble, mimicking their natural substratum types. Anemones were fed at least every second week on a varied diet of fish, prawns, and scallops. Other potential nutritional sources included dissolved organic material, bacteria and microplankton in the filtered seawater, and the translocation of photosynthetic by-products from mutualistic dinoflagellate zooxanthellae within their tissues.

Monitoring of spawning times and behaviour

Anemones within the tanks were monitored from September 2002 to April 2005. During the first year, observations were made monthly to establish the spawning periods for *E. quadricolor* and *H. crispa*. In subsequent years, intensive monitoring was done one month prior to and during expected spawning periods, and at least one month after spawning was last observed. During these periods, anemones were monitored from the night of the full moon until 12 nights afterwards. Monitoring periods focused on this portion of the lunar cycle based on earlier observations of *E. quadricolor* spawning 8 nights after the full moon at Heron Island

(Scott and Harrison, unpublished data) and the spawning periods of reef corals from the Solitary Islands (Wilson and Harrison, 1997; Wilson and Harrison, 2003).

Using a flashlight covered with a red filter, direct observations were made within the tanks every half hour from dusk until 11 pm each night or until spawning activities had ended. All spawnings were recorded, including the time, date and mode of gamete release, water temperature and prevailing weather conditions. In addition, the outflow of each tank was fitted with an egg catcher comprising of a 200-L plastic tub with 250- μ m mesh panels, immersed in a holding tank. Egg catchers were checked regularly so that if spawning occurred outside of the predicted times, the eggs would be retained and spawning dates could be inferred from the stage of embryo or larval development (Scott and Harrison, 2007).

Environmental data

Moon phase and sunset times for the Coffs Harbour region were obtained from XTide Tide Prediction Server (<http://harmonics.unh.edu:8080/>). Mean monthly air temperature range and mean daily rainfall data were provided by the Coffs Harbour Bureau of Meteorology. Photoperiod data on the number of daylight hours between sunrise to sunset were obtained from Geoscience Australia (<http://www.ga.gov.au/geodesy/astro/sunrise.jsp>). Seawater temperature at the collection sites were recorded by half-hourly data logger readings from North Solitary Island, supplied by the Solitary Islands Marine Park Authority.

Results

Spawning behaviour and mode of gamete release

Sexually reproductive *E. quadricolor* and *H. crispa* anemones collected from North Solitary Island were either male or female, broadcast spawning their gametes for external fertilisation and development (Fig. 1). In tanks, male anemones generally began to spawn during the hour prior to the females. Prior to and during spawning, the column of both sexes became fully extended, raising the oral disc above its usual position close to the substratum (Fig. 2a). The oral disc and mouth also became greatly distended, with the mouth usually being elevated in a cone shape above the oral disc (Fig. 1). The spawning posture of the column was clearly visible and prominent in *H. crispa*, whereas it was partly obscured in *E. quadricolor* as the pedal disc was generally attached to the underside of rocks. When expanded, the mesenteries and gonads of *E. quadricolor*

were sometimes visible through the translucent column, allowing the sex of the anemone to be determined prior to spawning, whereas the opaque column of *H. crispa* did not permit this. Whilst spawning, the anemones underwent a series of contractions that were initiated near their base and travelled up towards the oral disc and mouth (Fig. 2b). These contractions forced the sperm or eggs out of the anemone's mouth.

Males emitted sperm vigorously in large repeated bursts, each lasting for up to five minutes in duration. Sperm were released as milky white streams or clouds that dispersed rapidly in the seawater (Fig. 1a, c), or occasionally as highly viscous creamy masses that remained on the oral disc for some time before being dispersed. When spawning was completed, the water within the *E. quadricolor* tank became slightly cloudy with sperm, whereas the seawater was almost opaque and white after *H. crispa* males spawned.

Females of both species released egg masses either held together by mucus or occasionally in small unattached groups (Fig. 1b, d). Egg masses often stayed attached to the anemone for a few minutes before floating towards the surface, breaking up within the water column or once they reached the surface. While most eggs were positively buoyant, some were initially neutrally or even negatively buoyant, but all eggs eventually floated to the surface. Female gametes were occasionally observed inside the tentacle tips of *E. quadricolor* after spawning. However, these constituted a very small proportion of the total number of eggs released.

Several thousand eggs were generally released by each spawning female anemone, although the exact number was not quantified due to rapid dispersion in the large volume of the tank. Numerous gamete releases were observed from each spawning anemone during the night, but not all anemones were seen to release gametes. It was not possible to determine the exact number of individuals that spawned because gamete release could be very rapid, especially in *E. quadricolor*, and the density of gametes released obscured vision in the tanks.

Spawning times and relationship to environmental variables

From 2003 to 2005, spawning of *E. quadricolor* was observed twice a year, 1 to 7 nights after the full moon (NAFM) between February and April (Table 1). Spawning was generally split between two lunar months, with greatest spawning activity occurring from the full moon to the waning gibbous moon. In 2003 and 2004, *H. crispa* spawned three times a year, with spawning being split between two or three lunar months

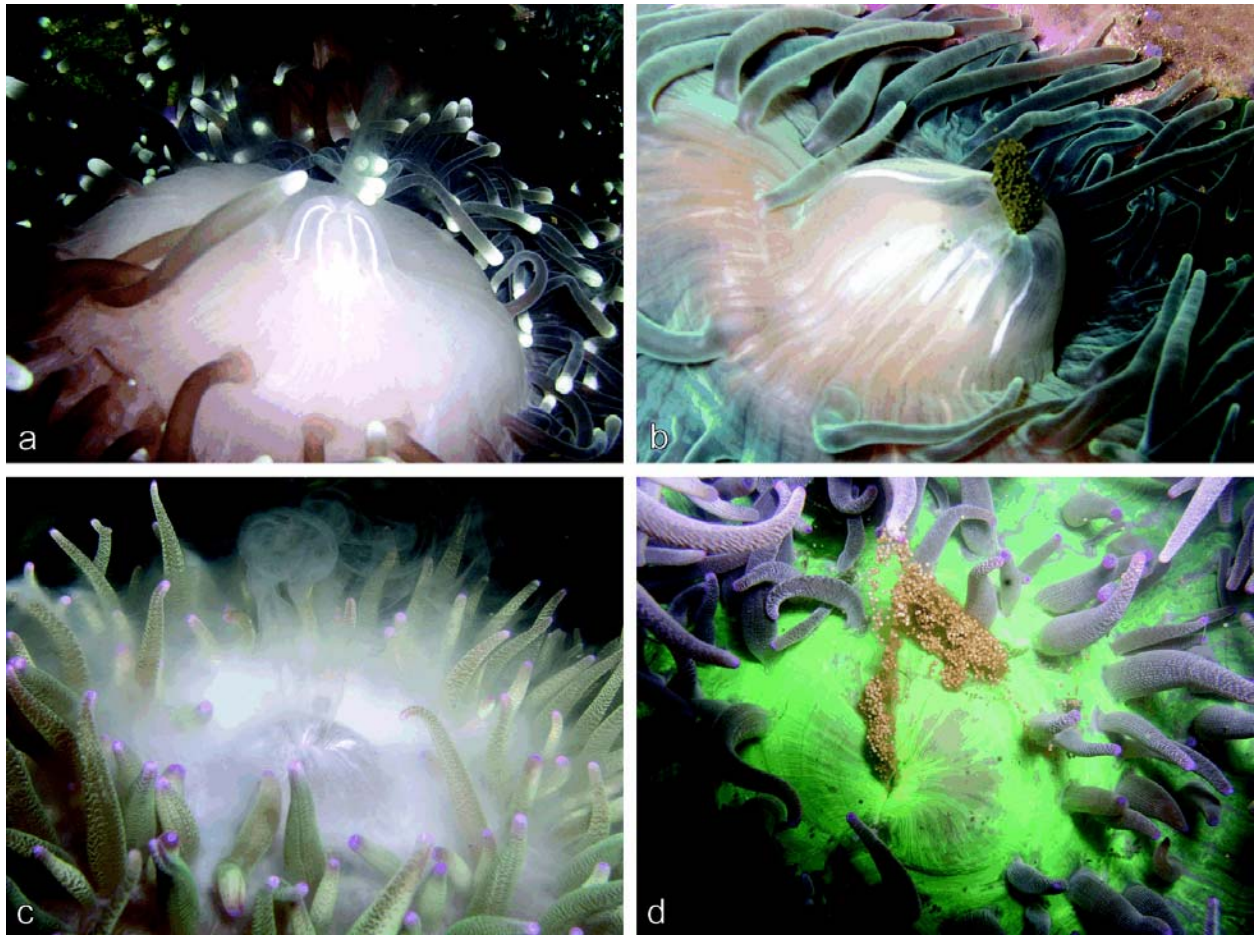


Fig. 1. Broadcast spawning of *E. quadricolor*, a, male, b, female; and of *H. crispa*, c, male, d, female (photograph d, courtesy of C. Damiano).

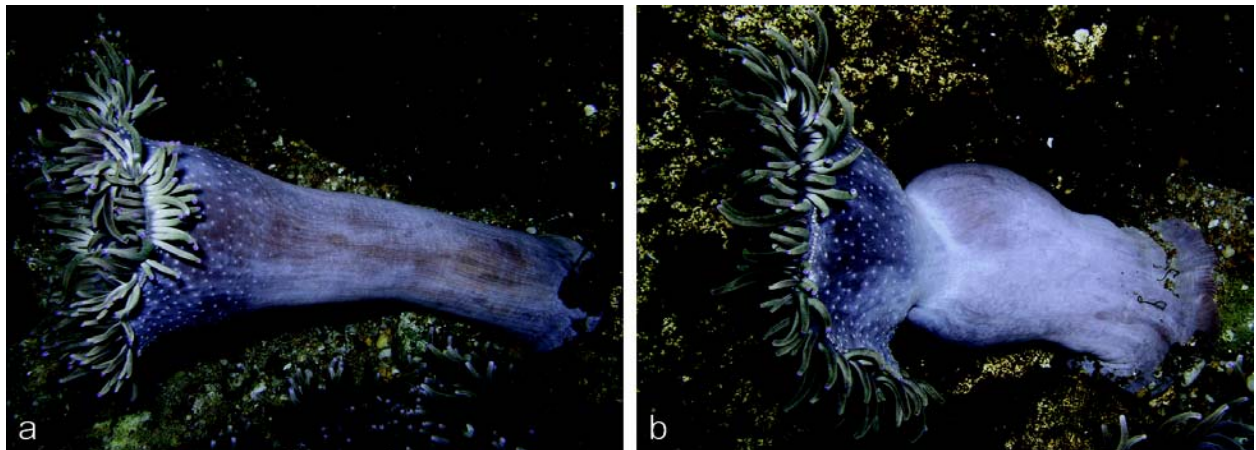


Fig. 2. *H. crispa* spawning posture: a, column greatly extended and oral disc raised above the substratum; b, contraction moving up the column prior to gamete release.

(Table 1). In 2005, spawning was observed four times over four lunar months. One spawning occurred in the first and third lunar months during this period, and two spawnings occurred in the fourth lunar month.

Spawning of *H. crispa* was observed 0 to 9 NAFM (i.e. full moon to last quarter), between January and May (Table 1).

Table 1. Spawning times of *E. quadricolor* and *H. crispera* from 2003 to 2005. Anemones collected from North Solitary Island, Solitary Islands Marine Park and observed in outdoor flow-through seawater tanks.

Species	Month	Nights after the full moon		
		2003	2004	2005
<i>E. quadricolor</i>	February			7, 1
	March	2, 3	1	
	April		3 ^a	
<i>H. crispera</i>	January			6
	February		6 ^b	
	March ^c	7	1, 2	7, 0 ^b , 4
	April	9		
	May	6		

^aInferred spawning, timing based on larval development.

^bOnly males observed to spawn.

^cTwo full moons occurred during March 2005.

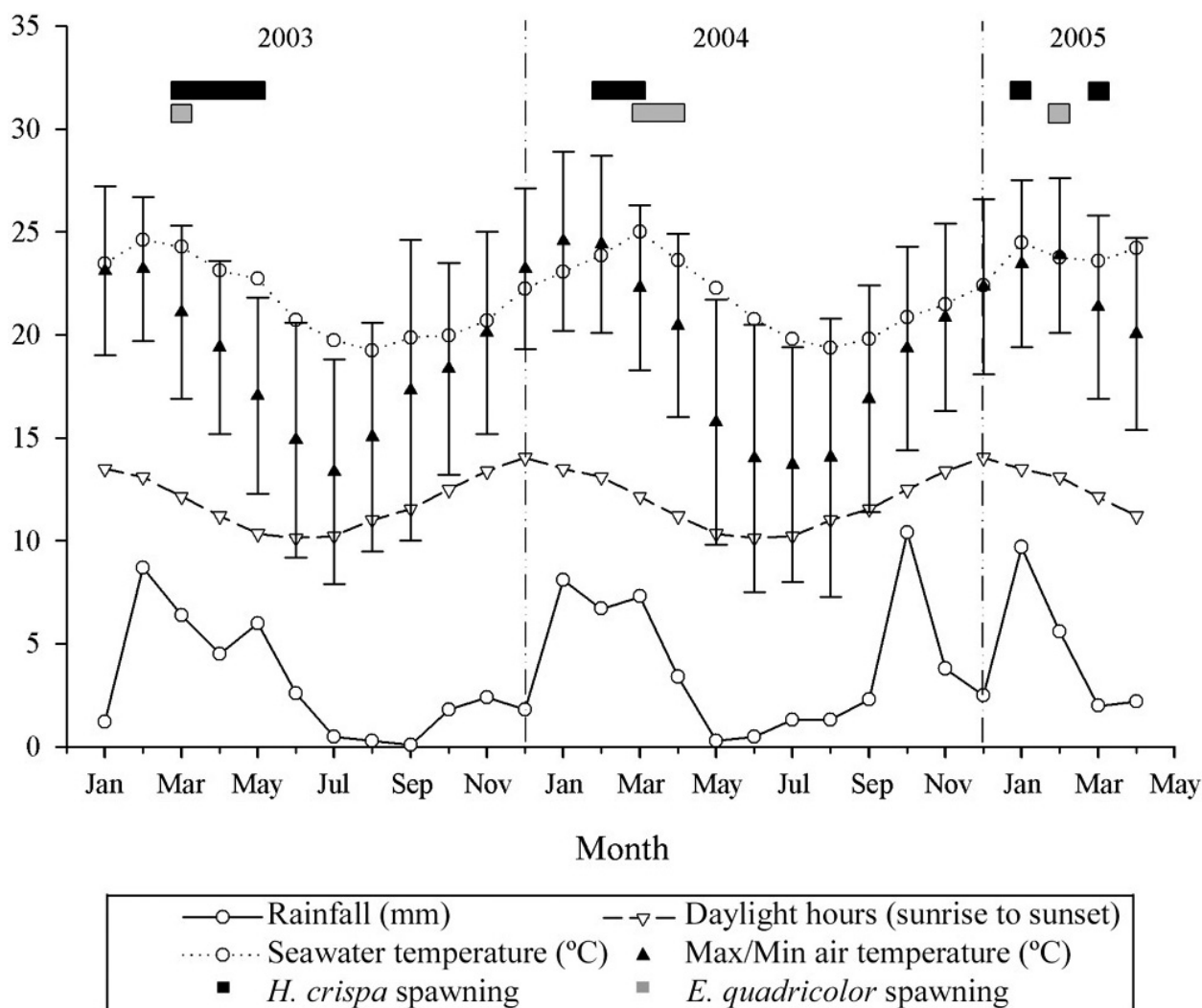


Fig. 3. Environmental parameters (mean rainfall, temperature, and photoperiod) and the spawning periods of *E. quadricolor* and *H. crispera* at the Solitary Islands.

Spawning occurred in the evening, starting between dusk and 3 or 6 h after sunset for *E. quadricolor* and *H. crispa*, respectively, and lasted for 1.5 to 3 h. Male and female anemones spawned on the same nights, except on two occasions when only *H. crispa* males spawned (Table 1). Spawning of females was never observed without males spawning. Recently-collected anemones and those kept for over one year were observed to spawn at the same time. One male *H. crispa* spawned in consecutive years, and another was observed to spawn during two consecutive spawning nights within the same lunar month. The exact numbers of anemones that spawned during consecutive years, months or spawning nights could not be determined due to the mobility of the anemones, the short duration of gamete release and restricted visibility from the high volume of gametes within the tanks.

Distinct annual patterns of rainfall, photoperiod, seawater and air temperatures occurred within the Solitary Islands study region (Fig. 3). Average monthly seawater temperatures ranged from 19.2°C to 25.0°C at North Solitary Island from January 2003 to April 2005. The minimum and maximum seawater temperatures recorded during this time were 17.9°C and 26.9°C, respectively. Spawning of *E. quadricolor* and *H. crispa* occurred when average monthly seawater temperatures were equal to or above 23.6°C and 22.7°C, respectively, which was at or near their annual maximum. Mean monthly air temperature was generally decreasing during spawning periods. Throughout the study, spawning periods of both species occurred during relatively high rainfall and decreasing photoperiod. Spawning of *H. crispa* on 30 March 2005 (4 NAFM) coincided with heavy rain, resulting in mortality of some of the positively buoyant gametes due to low salinity of the surface water. Photoperiod was near its annual minimum by the end of the spawning period for *H. crispa* in 2003.

Discussion

Male and female *E. quadricolor* and *H. crispa* anemones broadcast spawn their gametes for external fertilisation and development. Spawning of both sexes was predominately synchronous, occurring in the austral summer and autumn. Scleractinian corals also spawn during this time in the Solitary Islands (Wilson and Harrison, 1997, 2003). Spawning always occurred after sunset, between full and waxing crescent moon. Like some other marine invertebrates (Babcock et al., 1992), not all individual anemones were observed to spawn simultaneously. During a spawning event, some individuals did not spawn and in many cases the spawning animals constituted the minority of individuals present.

Spawning behaviour and cues

E. quadricolor and *H. crispa* become very inflated prior to and during spawning, a behaviour commonly noted in other broadcast spawning anemones including the host sea anemones, *Heteractis magnifica* and *Stichodactyla gigantea* (Babcock et al., 1992). As spawning requires the forceful emission of gametes (Giese and Pearse, 1974), it is likely that inflation provides hydrostatic pressure that facilitates gamete release, which is aided by rhythmical contractions of the columnar muscles in the species studied.

Spawning of *E. quadricolor* and *H. crispa* occurred spontaneously in outdoor flow-through seawater tanks. Males generally began to release their gametes prior to the females. Similar findings have been reported in other species of anemone (Uchida and Yamada, 1968; Clark and Dewel, 1974; Spaulding, 1974; Marshall et al., 2004), suggesting that sperm or some associated product may trigger the females to spawn. Chemical exudates from either sex of the same species synchronise spawning in some other cnidarians (Giese and Pearse, 1974). Knowledge of possible chemical cues used by *E. quadricolor* and *H. crispa* could help elucidate methods to stimulate spawning. Such insights could allow experimental induction of spawning, facilitating easier access to gametes for experimentation or possible aquarium culture.

Spawning times and relationship to environmental variables

E. quadricolor and *H. crispa* had annual spawning seasons. The onset and termination of the spawning season varied among years and between species. *E. quadricolor* spawned over a more restricted period, usually during a single month at the beginning of the year, whereas the spawning period of *H. crispa* lasted for up to three months. Although spawning seasons occurred over a period of months, the actual spawnings were restricted to only a few nights per year. Partitioning of spawning may increase larval survival and settlement as long as enough individuals spawn together to ensure fertilisation (Shlesinger and Loya, 1985). Spawning over an extended period of time may be beneficial at the Solitary Islands as the highly variable water currents may result in gamete wastage due to transportation of larvae to unfavourable settlement sites (Wilson, 1998). Furthermore, partitioning of spawning may be advantageous if adverse environmental conditions are encountered on a particular spawning night. For example, low salinity of the surface water after rain killed buoyant anemone gametes in this study. Heavy rain has also been observed to destroy coral gametes, negating the annual reproductive effort during a mass

reef coral spawning event at Magnetic Island on the Great Barrier Reef (Harrison et al., 1984).

Many species have been reported to spawn in synchrony with lunar phases, with annually reproducing broadcast spawning species tending to spawn on the same lunar phase each year at the same locality (Giese and Pearse, 1974; Harrison and Wallace, 1990). *E. quadricolor* and *H. crispa* spawned between 1 and 7 NAFM and 0 and 9 NAFM, respectively. This is similar to most reef coral species that spawn during the full or last-quarter moon phases (Harrison and Wallace, 1990).

Seasonal variation in sea temperature has been widely accepted as one of the most important environmental factors controlling reproduction in marine invertebrates (Orton, 1920; Giese and Pearse, 1974; Harrison and Wallace, 1990). Spawning of several species of anemone has been linked with seawater temperature (Jennison, 1978, 1979; Shaw, 1989; Fukui, 1991). *E. quadricolor* and *H. crispa* spawned during the warmer months of the year when sea and air temperatures were near their annual peaks. Spawning during times of higher temperatures may increase the rate of embryo and larval development (Dahan and Benayahu, 1998; Bassim et al., 2002) and enhance settlement rates (Martin and Archer, 1986; Wilson and Harrison, 1998; Nozawa and Harrison, 2005).

E. quadricolor and *H. crispa* spawned during months of high rainfall in summer and autumn, which are correlated with decreasing day length. Giese and Pearse (1974) suggested that photoperiod could serve as an ideal synchroniser for spawning as it shows so little variation for a particular date from year to year at the same latitude. Spawning always occurred after sunset, suggesting that *E. quadricolor* and *H. crispa* respond to variation in light intensity, and that the onset of darkness acts as the final cue for gamete release. Spawning in many scleractinian reef corals is also triggered by darkness (Harrison and Wallace, 1990). Spawning after sunset may reduce gamete predation by visual predators (Babcock et al., 1986) and avoid potential UV damage during early development (Epel et al., 1999; Wellington and Fitt, 2003).

Reproductive seasonality and synchrony of gamete release suggest that spawning of *E. quadricolor* and *H. crispa* is probably coordinated by similar responses of individuals to environmental factors. As numerous environmental factors are generally involved in the synchronisation and coordination of spawning by marine invertebrates, it is probable that several factors work simultaneously or in succession (Giese, 1959; Harrison and Wallace, 1990; Olive, 1995; Martin and Koss, 2002).

Comparison of tank-based observations and inferred field spawnings

The timing of observed tank-based spawnings for *E. quadricolor* corresponds well with field spawning periods inferred from gametogenic samples taken at North Solitary Island (Scott, unpublished data). Spawning synchrony between the laboratory and the field has also been found for many coral species (Harrison et al., 1984; Babcock et al., 1986; Carroll et al., 2006). In 2003 and 2004, all observed spawning dates for *E. quadricolor* corresponded with inferred field spawning periods. Of the two spawnings observed in 2005, one fell within and the other fell approximately two weeks after the spawning period that was inferred to have occurred in the field. In contrast, spawning was not observed during the first inferred field spawnings of 2003 and 2004. Similarity between tank and inferred field spawning periods of *E. quadricolor* reinforces the hypothesis of an annual spawning period, regulated by environmental variables, over a few months at the beginning of the year at the Solitary Islands.

Management implications

Information on the reproductive biology of host sea anemones is central to understanding the processes that maintain and renew populations of these ecologically and commercially important species. As the reproductive characteristics of an organism are strongly correlated with their distribution, persistence, and ecological requirements, such knowledge is needed to guide management and conservation programs (Whitehead et al., 1986; Wabnitz et al., 2003; Gutierrez-Rodriguez and Lasker, 2004). Ensuring the stability of host sea anemone populations is important not only for the anemones, but also for their obligate symbionts, as the viability of anemonefish populations depends in part on host dynamics (Porat and Chadwick-Furman, 2004; Shuman et al., 2005).

For aquarium harvesting rates to be sustainable, they must not exceed the ability of the anemones to repopulate impacted regions (Shuman et al., 2005). This study has shown that *E. quadricolor* and *H. crispa* have limited annual breeding seasons and successful recruitment of these species is thought to be rare (Fautin and Allen, 1992). High demand and lucrative economic returns generated from collecting these species, combined with poor survival rates in captivity, further increase their susceptibility to over-exploitation (Wabnitz et al., 2003). Fertilisation success of broadcast spawning species, such as *E. quadricolor* and *H. crispa*, is influenced by the factors that affect the chances of egg sperm encounter (Levitan, 1995; Coma and Lasker,

1997). If the density of these species is reduced too much, individuals may become reproductively isolated from one another, effectively reducing the likelihood of sexual reproductive success and further exacerbating the problems caused by collecting pressures.

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