Chapter 5
Coral Spawning Behavior and Timing

Michal Sorek and Oren Levy

Abstract One of the most prominent examples of synchronized behavior in corals is spawning, the enormous reproduction event known as the “spawning event,” where the moon choreographs sex among many coral species at the same night, once a year. The timing of annual coral spawning varies geographically around the earth but is consistent and predictable at each location. Several environmental factors such as sea temperature, salinity, tidal periodicity, and daylength have been suggested as inducers for gametogenesis and spawning in reef-building corals, whereas the actual spawning event appears to be triggered by the level of lunar irradiance. The repeated episodes, associated with broadcast spawning year after year, is a classic periodic biological rhythm, which is controled by exogenous *zeitgebers* and by an endogenous biological clock. A key imperative cue is the moon phase and moonlight. Nevertheless, the specific cellular mechanisms mediating this annual synchronization of behavior by reef-building corals has remained elusive, and the fact that cryptochromes may be involved in this process may suggest a role for the circadian clock in this unique phenomenon. Sexual reproduction is one of the most important processes for the persistence of reefs, yet worldwide reef systems are being rapidly degraded and face a multitude of threats, including global climate change and the anthropogenic stressors of artificial light pollution.

Keywords Circadian clock • Circadian masking • Coral reproduction • Cryptochromes • Mass spawning event • Moonlight

5.1 Coral Reefs

Coral reefs are one of the most impressive natural ecosystems in the world and are home to one quarter of the world’s marine biodiversity (Reaka-Kudla et al. 1997). In addition, coral reefs have an extremely important ecological role in the marine

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habitat. They are considered one of the most productive ecosystems on earth. Scleractinians (stony corals) are the major reef-building species and are classified ecologically as hermatypic corals (reef-building corals). These corals are the basis and framework for the entire ecosystem. They are responsible for the calcification process, which contributes calcium carbonate to the reef. Stony corals create homes for a wide variety of organisms and provide other important resources, such as shelter and food, for thousands of species of fish and invertebrates.

5.1.1 Coral Biology

Corals, class Anthozoa within the phylum Cnidaria, exist as solitary polyps or, more commonly, as colonies of many identical individuals. Each polyp consists of the following three basic tissue layers: the epidermis, which is the outer layer; an inner layer of cells lining the gastrovascular cavity, which acts as an internal space for digestion; and the mesoglea layer, which is located between the outer and inner layers (Barnes 1987). Scleractinian corals first appeared during the Triassic period in tropical shallow waters; however, the origin of these coral groups has remained an unsolved mystery of paleontology (Stanley 2003). Corals are known to be predators, and they use their tentacles to trap prey, such as zooplankton and small invertebrates, with stinging cells or nematocysts. However, the majority of their food is supplied by their symbiotic counterparts, endosymbiotic dinoflagellates (Fig. 5.1). The coevolution of corals with endosymbiotic algae, which are also known by the common name zooxanthellae, is responsible for the domination of reefs by corals. This symbiosis is primarily based on metabolic requirements in which the algae provide the corals with photosynthetic products and energy for the rapid calcification of the corals. In return, the algae obtain essential nutrients and shelter provided by the coral hosts. The coral life cycle is simple and includes a long sessile stage in which the coral colony is attached to the substrate and a short planktonic stage consisting of planulae or larvae. After several days, the planula eventually attaches and settles permanently on a hard substratum. It then metamorphoses from the larval form into a juvenile polyp, which produces a skeleton composed of calcium carbonate. Subsequent growth during the juvenile stage leads to the adult form, which can reproduce sexually. This form completes the life cycle (Harrison and Wallace 1990).

5.1.2 Coral Reefs Situation

During the past three decades, coral reefs have been under increasing pressure as a result of dramatic environmental changes (Gardner et al. 2003; Hughes et al. 2003). Acute global climate changes, ocean acidification, temperature increase in the marine environment, disease, and human activities, such as overfishing and coastal development, have destroyed 20 % of the world's 285,000 km^2 of known reefs

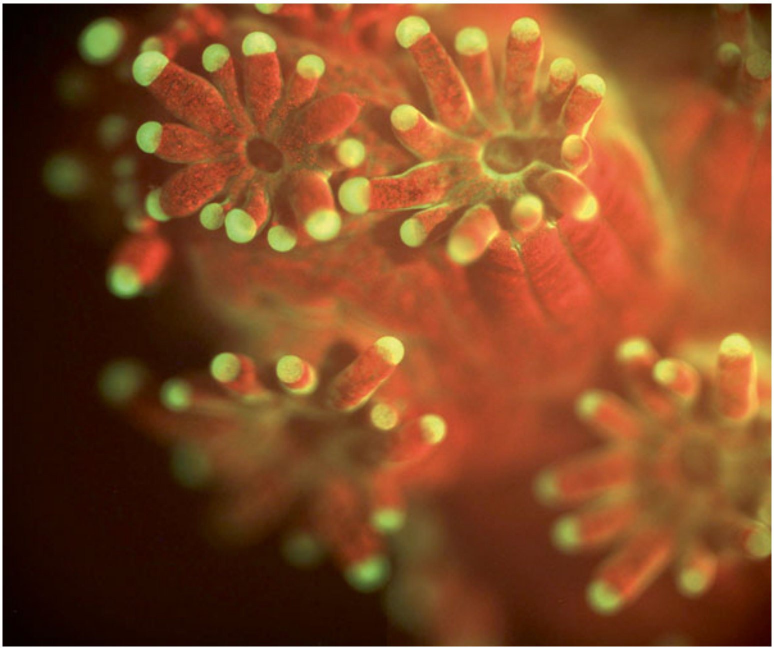

Fig. 5.1 Symbiotic coral *Pocillopora damicornis* polyps, photographed in the laboratory, using a long working distance high-magnification fluorescence imaging setup. (Picture by © Tali Treibitz, Andy Mullen, Jules Jaffe, UC San Diego)

(Pennisi 2007). This worldwide decline in coral reefs has raised major concerns regarding the future of these marine ecosystems and has encouraged additional research to provide a better understanding of coral biology and the conservation of this unique environment. The coral reproductive process holds the key for adjustment to these dramatic global changes, because it appears that coral populations depend almost entirely on the formation of sex cells or gametes along with DNA recombination to form more thermally tolerant genotypes that can adapt to warming ocean waters (van Woesik 2010).

5.2 Coral Reproduction

Coral reproduction has been a major research topic for many years. Much research has attempted to characterize the processes and modes of reproduction for different coral species in a wide variety of geographic locations. Corals are primarily classified based on their sex. They are classified as hermaphroditic, either simultaneous or sequential, with males and females in the same colony, or gonochoric, with all polyps being unisex, either female or male. Hermaphroditism is considered advantageous over gonochorism if the probability of finding members of the opposite sex is low and self-fertilization is possible. Corals are further classified based on two reproductive modes. The first mode is broadcast spawning, in which external fertilization occurs in the water column after the gametes are shed. The second mode is brooding, in which fertilization occurs in the maternal colony (Harrison and Wallace 1990; Richmond and Hunter 1990). The four main patterns of sexuality in corals are hermaphroditic broadcast spawners, hermaphroditic brooders, gonochoristic broadcast spawners, and gonochoristic brooders. Information on sexual reproduction in more than 400 scleractinian species confirms previous data suggesting that hermaphroditic broadcast spawning is the dominant pattern among coral species, whereas there are relatively few hermaphroditic or gonochoric brooding species (Harrison 2011). Characteristics of sexuality are primarily conserved within species, genera, and even families, although exceptions occur for different locations and species. However, not all coral species are readily classified into these four basic patterns because mixed sexual patterns or mixed modes of sexual development have been observed for certain species (Harrison 2011).

Corals can reproduce both asexually and sexually. Asexual reproduction in corals produces genetically identical modules of the original colony and can occur through fragmentation (Highsmith 1982) resulting from storm and wave impacts or other damage to corals; polyp bailout (Sammarco 1982), which occurs when new clonal polyps bud off from the parent polyps after they reach a certain size and expand or begin new colonies (Sumich 1996); or the asexual production of planulae (Stoddart 1983), which may occur during periods when sexual reproduction has ceased (Nakano and Yamazoto 1992; Lam 2000). This process continues throughout the life of the organism (Barnes and Hughes 1999) and primarily occurs when the environment is unable to support sexual reproduction. Another advantage of asexual reproduction is that the increased size of the initial stage reduces the risk of juvenile mortality. Also, this initial stage occupies substantial space on the reefs. In certain cases, this stage may disperse widely and preserve the original genotype.

Sexual reproduction involves the production of gametes, fertilization, embryo development, and a larval phase that is usually planktonic (Harrison and Wallace 1990). Fertilization may occur either within the maternal polyp (brooding) or externally in the water column after the gametes are shed (broadcast spawning). Sexual reproduction in corals may occur yearly, seasonally, monthly, or not at all. The timing of coral sexual reproduction depends on the species and environmental conditions. Sexual reproduction occurs when female gametes and male gametes combine to create fertilized eggs. Two different methods of sexual reproduction exist in corals. The first method is spawning, in which two parents of different sexes release their gametes into the water and fertilization occurs. The second method is brooding. This method of sexual reproduction is characterized by the presence of embryos and planula larvae within the coelenteron or expanded tentacles of the coral. In this case, the release of the planulae occurs during an advanced stage of larval development. In addition to brooding, corals can also spawn sperm, which fertilizes either the same colony or another colony nearby (Gleason et al. 2001; Okubo et al. 2007; Ayre and Miller 2006). The planulae released from brooding corals into the water column settle within a few hours after release. One important advantage of sexual reproduction in corals is the ability to broadcast gametes, particularly during mass spawning events. This process may promote hybridization among parallel or different pairings. If hybridization is an important feature of coral reproduction, then population-level consequences could rapidly generate new genetic combinations with the potential for increasing the diversity of responses to environmental change. Also, our ideas about the integrity of coral species might be radically altered because experimental laboratory studies of corals have demonstrated that hybrids can be formed (Richmond 1992; Willis et al. 1993, 1997). Sexual reproduction in corals is possibly the most important ecological process for the replenishment of degraded reefs. Sexual reproduction also maintains the coral population and supports evolutionary processes, such as genetic recombination and the production of new coral genotypes, which may enhance fitness.

5.3 The Chronobiology of Coral Spawning and Its Variability in Different Geographic Locations

The phrase "Timing is everything" is often correct and accurate. For coral reproduction, timing can be the key to reproductive success for all reproductive phases. The most tightly synchronized stage of reproduction is the final stage, that of fertilization. If corals use broadcast spawning and release both eggs and sperm into the water column, timing and synchronization are extremely important to ensure successful fertilization. Eggs that are released into the water are available for fertilization for only seconds to minutes before they drift away. For brooding corals, the precise timing of planulae release into the water column may be crucial in that it allows the planulae to find a suitable place to settle. The mechanism by which corals fine tune their spawning and the planulae release times remains unknown. Many environmental factors and stimuli are known to influence the reproductive timing of corals. The key factors are the sea surface temperature, the moon phase, and the daily light cycle. All three factors have been suggested as inducers for gametogenesis and spawning in reef-building corals (Harrison et al. 1984; Babcock et al. 1986, 1994).

These factors are apparently involved in three or more reproduction cycle patterns. The first pattern, the seasonal or annual rhythm, is related to the seasonal variation in sea temperature. Changes in sea temperature are most likely involved in triggering the maturation of eggs and sperm inside the adult (Yonge 1940; Kojis and Quinn 1981; Harrison et al. 1984; Stoddart and Black 1985; Willis et al. 1985; Babcock et al; 1986). The second cycle is the lunar or monthly rhythm, which coordinates the timing of mass spawning. The tidal cycles are important, and it is common for corals to spawn during low-amplitude neap tides (Oliver et al. 1988; Simpson 1991; Babcock 1995; Mendes and Woodley 2002). Spawning during neap tides is an advantageous strategy that reduces gamete dilution because the amount of water movement is low. Related to predicting neap tide, another important cue for corals is the moon phase and moonlight (Jokiel 1985). It is probable that these cues have the largest monthly influence. The third cycle pattern involving the timing of gamete release is the diel light cycle, which is thought to trigger spawning after a precise period of darkness (Harrison and Wallace 1990). An endogenous circadian clock is known to control and entrain several diel phenomena in certain coral species. These phenomena include calcification (Chalker 1977; Chalker and Taylor 1978) and tentacle diel behavior (Sweeney 1976; Sebens and Deriemer 1977; Lasker 1979). However, whether an endogenous circadian clock governs coral reproduction has not yet been clearly demonstrated. The fine tuning that results from the three major cycle patterns is highly important. Although many coral species spawn on the same night, the final spawning time can differ between species. It is possible that these differences in spawning time act as temporal barriers to avoid hybridization between closely related species (Szmant et al. 1997). Corals that occupy different habitats in areas with different climate conditions and latitudes show different life cycles, reproduction modes, and reproductive timing. Currently, it remains impossible to define a universal factor that can provide a good single explanation for the differences in reproductive timing between different geographic localities.

The majority of the data concerning coral reproduction modes, synchronization, and timing come from the tropical Pacific. The sources of these data include the Great Barrier Reef in Australia and reefs in Western Australia. Data also exist for Guam, Palau, Hawaii, Okinawa, and Panama, as well as the Red Sea and Caribbean. The timing and synchronization of coral reproduction have been most often studied for the Great Barrier Reef. These studies represent an adequate source for understanding the timing of coral reproduction. The major pattern observed in the Great Barrier Reef studies is the remarkable similarity and synchronization of reproductive activity among coral species. The majority (90 %) of species studied broadcast spawn gametes annually during the week following the full moon during the spring (Harrison et al. 1984; Willis et al. 1985). Many individuals of each broadcast spawning species release their gametes during a time window that is approximately 30 min long (Fig. 5.2). On the Great Barrier Reef, spawning synchronization is the most common reproductive mode and occurs for more than 140 species of coral. This type of massive synchronized spawning is familiar from the mass spawning events

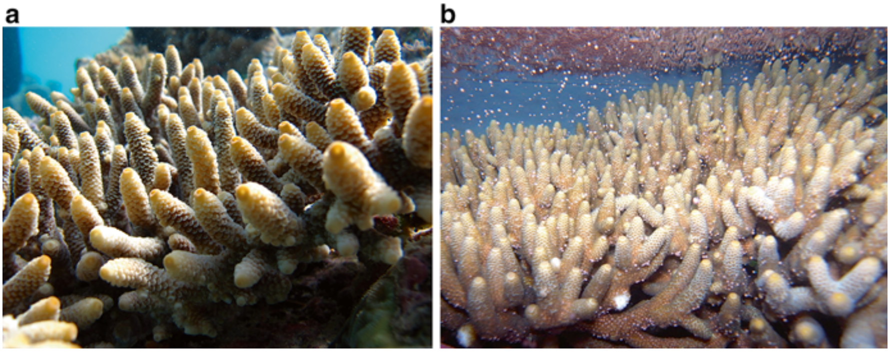

Fig. 5.2 *Acropora millepora* colonies before (**a**) and during (**b**) spawning time at Heron Island, Great Barrier Reef Australia. Spawning was documented around 21:30 during November 2011

that occur for certain reefs on the Great Barrier Reef (Willis et al. 1985; Harrison et al. 1983, 1984; Harrison 1993; Babcock et al. 1986; Wallace et al. 1986; Oliver et al. 1988; Harrison and Wallace 1990) and in western Australia during the austral autumn (Simpson 1985, 1991; Simpson et al. 1993; Babcock et al. 1994; Rosser and Gilmour 2008; Gilmour et al. 2009; Rosser and Baird 2009). These occurrences represent the largest scale synchronous mass spawning events of corals in the world, although the mass spawning that occurs in western Australia is smaller. Other smaller-scale synchronized spawning events involving fewer species or colonies of one or a few coral species have been reported primarily from the Gulf of Mexico and Caribbean region (Gittings et al. 1992; Hagman et al. 1998; Beaver et al. 2004; Bastidas et al. 2005). Several of these events were reported as mass spawning events, but most are considered multispecific spawning events (Harrison and Booth 2007) because they include a much lower number of species. More recently, many reefs in the Indo-Pacific region have been reported to exhibit coral spawning synchronization on a medium scale. These locations include Japan, Taiwan, the Philippines, Singapore, Indonesia, Papua New Guinea, the Solomon Islands, French Polynesia, and the Egyptian Red Sea (reviewed in Harrison 2011).

In contrast to the synchronized spawning events on any scale, the major reproductive activities of the most abundant species in the Red Sea occur during different seasons, different months, or different lunar phases within the same month (Shlesinger and Loya 1985; Rinkevich and Loya 1979). The coral species in the Red Sea exhibit temporal reproductive isolation. Broadcasting species release their gametes during periods of up to six nights, once or twice a year, whereas brooders release their planulae for 3–7 months (Shlesinger and Loya 1985) when the temperature rises or during the summer, when the water temperature is the warmest (Fadlallah 1984). Asynchronous reproduction is also exhibited by most coral species in the Central Pacific, primarily in Okinawa and Hawaii. For the latter corals, the spawning period peaks during the summer months, but spawning continues year round (Kolinski and Cox 2003) for certain brooders. More recently, a reproductive period of 9 months has been reported for a few *Acropora* species in Kenya (Mangubhai and Harrison 2006, 2009; Mangubhai 2009). This lack of synchrony was attributed to a reduction in environmental seasonality and low variability in the ranges of certain environmental parameters (Richmond and Hunter 1990), particularly annual sea surface temperatures and tidal amplitudes (Oliver et al. 1988).

Several observations show differences in reproductive timing patterns within the same species in different locations. For example, *Stylophora pistillata*, the most dominant stony coral on the reefs of the Red Sea, was found not to be controlled by the lunar periodicity in this area (Rinkevich and Loya 1979), although later research (Zakai et al. 2006) indicated a degree of lunar cycle influence on planulae release. This same species was controlled by the lunar periodicity of planulation in Palau (Atoda 1947). Another example of different timing of planulae release in *S. pistillata* within the Great Barrier Reef was found on Heron and Lizard Islands. This species releases planulae during the summer, the timing of which does not follow the lunar cycle for planulation (Tanner 1996; Loya 1983). Recent reports from the Egyptian Red Sea have described the highly synchronous maturation of gametes among many

Acropora species (Hanafy et al. 2010) with multispecific spawning on a medium scale, whereas *Acropora* in the northern part of the Red Sea, for example, in Eilat, does not show a similar pattern (Shlesinger and Loya 1985; Shlesinger et al. 1998). These two examples of *S. pistillata* coral and the *Acropora* corals demonstrate variations in reproductive timing modes at different locations. Differences in timing among allopatric populations of a species may represent adaptations to both local environmental factors and specific cues (Richmond and Hunter 1990). Differences between the synchronized and unsynchronized timing of spawning among corals at the equator compared to high and low latitudes may be caused by a lower variability in temperature close to the equator. Analyzing the existing data regarding latitudinal trends may explain the differences in timing behavior among the same species in different locations for some but not all reefs.

During recent years, global changes have affected coral reef conditions dramatically. The decline in the condition of the environment has produced accelerated research into coral reproductive behavior and timing. The current information on this subject is based on more than 400 corals from many different locations and includes new sites and research topics.

5.4 Environmental Factors Affecting Synchronized Coral Reproduction

We have shown that an important feature of coral reproduction is synchronization. Many proximate factors have been hypothesized to influence spawning and planulae release at different levels and times, including the aforementioned key factors of sea temperature (Glynn et al. 1991; Hayashibara et al. 1993), tidal regime (Wyers et al. 1991) and lunar phase (Guest et al 2002), and onset of darkness (Harriott 1983; Babcock et al. 1986; Hunter 1989). Additionally suggested factors include a near-zero solar insolation derivative (van Woesik et al. 2006), the duration of regional calm periods of wind that may enhance fertilization and synchronization (van Woesik 2010), food availability (Fadlallah 1981), the amount of rainfall combined with temperature (Mendes and Woodley 2002), twilight chromaticity (Sweeney et al. 2011), and salinity (Jokiel 1985). It is not yet clear whether and how all these factors work with each other or with internal components of the endogenous clock in corals, serving as input signals from external stimuli during synchronization.

The most common hypothesis (Glynn et al. 1991; Babcock et al. 1986) points to water temperature as the most influential factor, with rising temperatures stimulating the production and maturation of gametes in many invertebrates. The second cue is the full moon, with the process of spawning occurring primarily a few days after the full moon at a precise time after sunset, which is considered the third cue. However, the principal difficulty with this hypothesis is that it cannot provide a good explanation for any reef in any region. For years, attention was centered on reefs in the mid-latitudes, where changes in temperature are significant and can provide a good explanation for the determination of the timing of spawning. In the tropics, however, the temperature varies very little and cannot be considered a major cue for coral spawning. On certain reefs, coral spawning does not occur when the water is the warmest. For example, the corals on the west coast of Australia reproduce during the late summer and autumn (Simpson 1985, 1991; Simpson et al. 1993; Babcock et al. 1994), whereas reproduction of the corals on the east coast occurs during the spring. However, the water temperature begins to increase in both regions during the summer. Richmond and Hunter (1990) have demonstrated a correlation between the percentage of synchronized coral species and the annual variation in the seawater temperature, although there are exceptions. The attempt to find the ultimate cue for synchronization has revealed many differences between corals at high and low latitudes, with corals in the lower latitudes showing spawning synchrony that appears to be weaker compared to corals at high latitudes (Richmond and Hunter 1990).

5.5 Experiments Under Controlled Laboratory Conditions

Over the years, many researchers have classified and characterized areas of coral reefs for timing and synchronization of reproduction characteristics. To understand the mechanism of reproductive timing, corals were subsequently studied under controlled laboratory conditions. Under laboratory conditions, it is possible to isolate specific factors and to determine the influence of each factor on reproductive timing in corals. It is also possible to determine the influence of these factors on different cycle periods. Several researchers have attempted to determine whether spawning and planulae release in corals is a circadian behavior or is controlled directly by light. Manipulation of daylight and moonlight in the coral *Pocillopora damicornis* was conducted by Jokiel (1985) to investigate the influence of light on the timing of coral spawning. Corals were kept under natural light during the day. By night, one part of the experiment corresponded to artificial full moon light and another to new moon light (darkness). Corals in both treatments showed a loss of synchrony in monthly larval production. These results showed that spawning is synchronized by night irradiance cues that are essential for synchronization. Published evidence (Babcock 1984, 1988; Hunter 1989) indicates that coral spawning timing can be shifted by an early artificial sunset a few days before spawning occurs. This finding demonstrates two important principles. The first is that the light–dark (LD) cycle is responsible for the fine tuning of spawning at the level of hours and minutes, and the second is that light (not particular endogenous components that measure time) regulates the timing of spawning. Brady et al. (2009) demonstrated earlier spawning in *Montastraea franksi* under an earlier artificial sunset on the day of spawning. These results indicate that in this case either that the timing of spawning is directly controlled by the local solar light cycle, at least for the precise tuning of the hours of spawning, or that light masks an endogenous circadian rhythm. In support of the idea of weak circadian clocks, Levy et al. (2007) showed that the expression of two circadian clock genes (*cry1* and *cry2*) did not show sustained circadian rhythms under continuous darkness (Fig. 5.3) (see following).

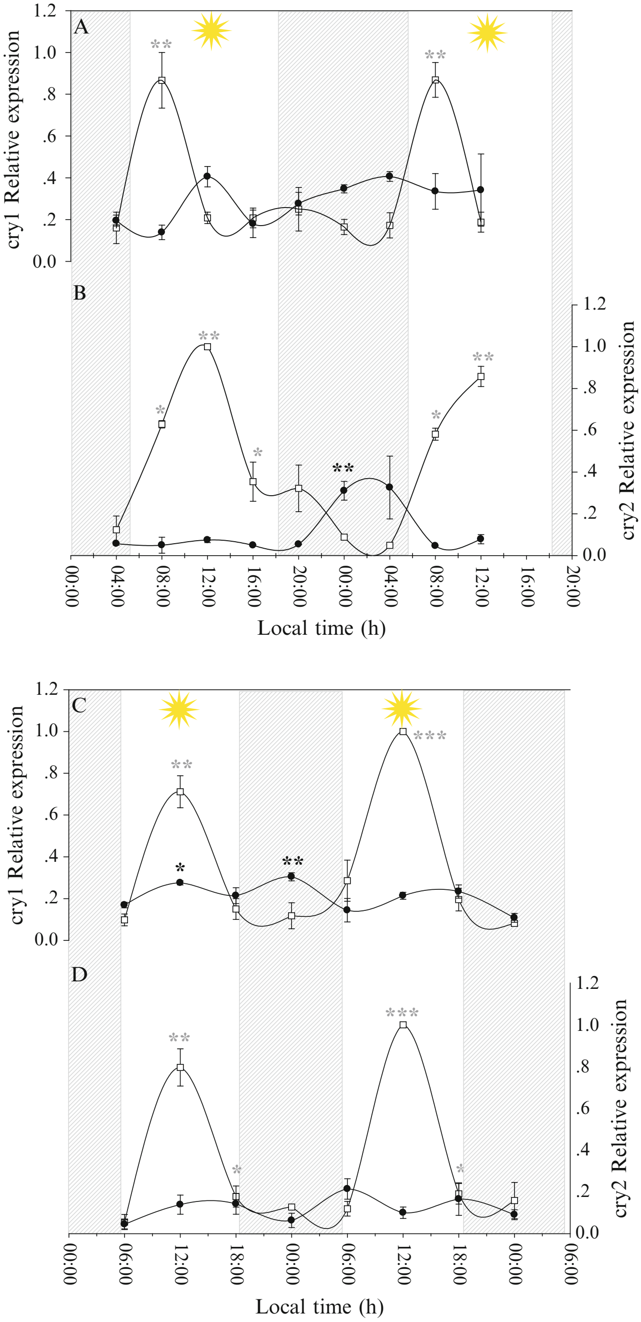

Fig. 5.3 Temporal expression patterns of *cry1* and *cry2* in *A. millepora* under light–dark (LD) (*open squares*) and DD (*filled circles*) cycles using quantitative polymerase chain reaction (PCR). (**a**, **b**) A 32-h cycle with sampling intervals of 4 h. (**a**) Quantitative analysis of *cry1* revealed a

Boch et al. (2011) analyzed the contributions of separate components of light dynamics because the effects of twilight and lunar light on coral spawning synchrony have previously been conflated. The alternative hypothesis, so far untested, was that twilight and lunar light have differential contributions as proximate cues. Boch et al. (2011) showed that under controlled conditions lunar photoperiod cues are most likely the major driver of spawning synchrony on a given night of the lunar cycle and at a specific time of night. The differences in spectral dynamics have secondary effects on spawning. Petersen et al. (2007) identified specific differences between broadcast and brooding corals. Twenty-four coral species from nine families under artificial conditions in an aquarium system were observed to show reproductive behavior. Broadcast spawners reproduced primarily in open systems under natural light conditions, whereas brooders showed less sensitivity toward certain environmental factors that are known to trigger reproduction in field populations, such as moonlight and temperature fluctuations. It has been suggested that spectral light composition affects the timing of gamete release, particularly during twilight. Under laboratory conditions, when the daylength was artificially extended by 6 h for two coral species, *Acropora millepora* and *Acropora aspera*, from the Great Barrier Reef, the corals demonstrated a phase shift in their spawning time. Coral colonies that were illuminated by red light did not show any delay in the spawning time compared to the same species under natural conditions in situ. In contrast, colonies irradiated by blue, green, and white (PAR) light spectra had a phase shift in their spawning time relative to the spawning time of the control colonies and corals of the same species found on the reef. These findings suggest that artificial light contamination in the blue and green spectral regions can mismatch and delay spawning, whereas red light has no effect on spawning behavior (Levy et al., unpublished data). These results suggest the presence of blue-light photoreceptors known as cryptochromes that could mediate this spawning behavior (Levy et al. 2007).

These findings could improve the understanding of the threats to coral reefs. Sexual reproduction is one of the most important processes for the persistence of reefs; yet worldwide coral reef systems are being rapidly degraded and face a multitude of threats. The interplay between an endogenous clock and external light cues for the timing of reproduction may be compromised in the era of industrialization and global change, where the moon is not the only source of light at night. Buildings, street lamps, lighthouses, cars, boats, and oil platforms provide obvious evident examples of artificial sources of light at night that can eventually affect reproductive timing and fertilization success in broadcasting species.

Fig. 5.3 (continued) significant effect of light (*L*) and dark (*D*) (L/D, $P=0.035$), as well as a significant effect of 'sampling time' (time, $P<0.001$). (**b**) Expression of *cry2* (L/D, $P=0.026$, time $P<0.001$). Each value was normalized to **β**-actin and converted to percentage of maximal level for each gene. Values (mean ± SE) were tested by ANOVA with linear contrast method within groups to distinguish between the LD/DD rhythm amplitude of *cry1* and *cry2*. *cry1* DD ($P>0.01$), *cry1* LD ($P<0.01$). *cry2* DD ($P>0.05$), LD ($P<0.01$). Time points with asterisks are significantly different (*grey asterisks* LD, *black asterisks* DD; * $P<0.05$, ** $P<0.01$, *** $P<0.001$). Sample size = 3. (From Levy et al. 2007)

5.6 What Do We Know About Molecular Aspects of Reproductive Timing?

The phenomenon of synchronized spawning of corals in different locations, species, and scales, particularly in the context of unique large-scale mass spawning events, remains an issue with many unanswered questions. It is not yet known whether and how corals sense the environment and how internal components of the endogenous clock assist the timing and synchronization of external stimuli. Continuous progress in molecular methods for studying corals is very important for understanding the timing of coral reproduction. Understanding the molecular mechanism will contribute to our knowledge of reproductive chronobiology and will provide a general mechanism for many reefs throughout the world. Gorbunov and Falkowski (2002) have suggested that detection of the blue region of moonlight by corals may cue the specific night of spawning because several species of corals are extremely sensitive to the blue region of the light spectrum. Molecular research based on the coral *A. millepora* has identified the central gene components of corals that are part of the central clock loops. The major photoreceptor genes known as cryptochromes (*cry*) have also been identified and are hypothesized to mediate the moonlight signal in the environment for reception by the central clock (Levy et al. 2007). As shown above Fig. 5.3, *cry1* and *cry2* genes were found to be rhythmic under light–dark conditions but not under constant darkness. *cry2* may entrain the intrinsic clock on a monthly basis because its expression increases massively on full moon nights compared to new moon nights (Levy et al. 2007; Fig 5.4). However, the expression of this gene has not yet been determined during mass spawning events.

Sweeney et al. (2011) have also determined that shifts in twilight color and intensity during nighttime and between nights immediately before and after the full moon, as well as an increase in the blue-light spectrum underwater during twilight after the night of the full moon, correlated significantly with observations of spawning in corals. In contrast, molecular studies of the coral *Favia fragum* regarding the *cry1*, *cry2*, *clock*, and *cycle* genes showed a diel oscillation for *cry1* and *cry2* but did not identify any relationship between the elevated expression of one of the *cry* genes and a monthly cycle specifically connected to the day of spawning (Hoadley et al. 2011). This finding suggests that the *cry* genes are not involved in the entrainment of reproductive cycles to lunar light cycles in *F. fragum*. Because of the ongoing debate and the deficiency of solid data related to the role of circadian clock in cueing broadcast spawning synchronization, as an alternative option "masking" should also be investigated. The term "masking" (Aschoff and Vongoetz 1989) describes an immediate effect of a stimulus that overrides the expression of an animal's endogenous clock. Under natural conditions, masking has the adaptive value of confining animals to their appropriate temporal niche and may complement the circadian clock in fine-tuning activity patterns in response to environmental stimuli (Redlin 2001). Thus, masking might be an important mechanism in the response of species to moonlight. The possible detection of a masking response under field conditions will provide evolutionary insights into its true adaptive value, which may or may not occur in coral reef spawning events. To define endogenous rhythms, the rhythm

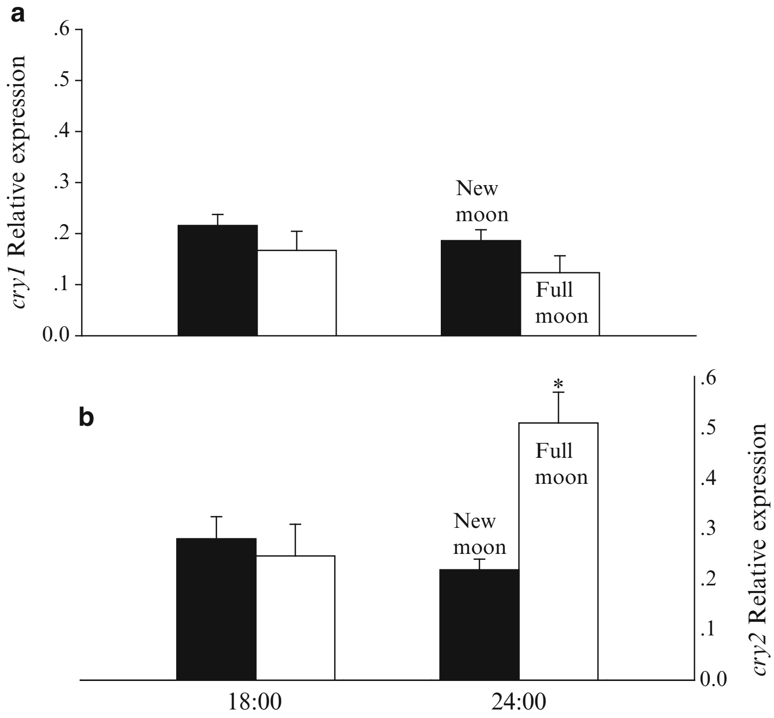

Fig. 5.4 (**a**, **b**) Quantitative analysis of *cry1* and *cry2* of two consecutive months, August and September 2005, comparing new moon nights (5 August and 4 September) to full moon nights (20 August and 18 September) at time points of 18:00 and 00:00. Each value is the average time point of the two respective sampling events (mean ± SE). ANOVA RM, $P > 0.05$ *cry1*, $^*P < 0.05$ *cry2*; sample size = 4. (From Levy et al. 2007)

itself must continue under constant conditions in the absence of stimuli. The published molecular studies regarding lunar rhythms, so far, cannot necessarily be attributed to an endogenous biological clock. Whether the phenomenon of synchronized spawning is environmentally triggered or controlled by endogenous mechanisms remains an unanswered question. Understanding how corals perceive and integrate information regarding environmental cues to regulate their reproductive cycles may solve one of earth's biggest mysteries and help maintain the coral reef environment in marine ecosystems.

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