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Environmental Control of Annual Reproductive Cycle and Spawning Rhythmicity of Spinefoots

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Abstract

Many teleost fishes inhabiting shallow tropical waters exhibit synchronous spawning around species-selective lunar phases during their spawning season. For example, ovaries of the goldlined spinefoot (*Siganus guttatus*) develop during a single period each year from June to July in the Ryukyu Islands, Japan, while those of the goldlined spinefoot in the Karimunjawa Archipelago, Indonesia, develop twice a year from March to May, and then again from September to November. Increases in photoperiod and water temperature are possible cues for the initiation of reproductive activity in the populations around the Ryukyu Islands, while the transition between the rainy and dry season may trigger the initiation of reproductive activity in the Karimunjawa Archipelago populations. Moreover, the goldlined spinefoot releases its gametes around the first quarter moon period of the lunar phase, and since the lunar phase is consistent within the Indo-Pacific Ocean, this species can likely perceive cues from the moon and transcribe them as internal signals. In fact, periodical changes in moonlight intensity are expressed as changes in the plasma levels of melatonin, an endogenous transmitter of environmental light/dark cycles. In addition, the mRNA expression levels of clock genes of neural tissues [*Cryptochrome (Cry3)* and *Period (Per2)*] change according to changes in the lunar cycle. To date, how the lunar cycle may affect endogenous reproductive processes in fish is not fully understood. However, knowledge of lunar spawning periodicity in commercially important species may help in the management of fisheries resources, determining where and when to prohibit fishing (e.g., time and area closures), as well as promoting efficient aquaculture techniques for inducing synchronous spawning.

Introduction

Teleost fish align their reproductive activity to periodical changes in environmental factors. The use of environmental factors for reproductive synchrony is closely related to reproductive strategies of individual fish species, although specific environmental factors used by fish are different among species. For example, the survival rate of newly hatched larvae may be enhanced by ensuring that they hatch during times when food is available, optimizing growth (Bromage et al. 2001). The chance of successful mating increases when the development and release of gametes by

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sexually mature adults occur during the same time period (Robertson 1991). Fish are capable of perceiving changes in environmental factors through their sensory organs, which then translate these cues to stimulate neural and peripheral organs (Takemura et al. 2010; Ikegami et al. 2014). Neurotransmitters and/or hormones synthesized in the brain are likely internal transducers and involved in the regulation of the hypothalamus–pituitary–gonadal (HPG) axis. Consequently, hormones from the HPG axis stimulate gonadal development in accordance with periodical changes in the environment. However questions still remain regarding what kind of internal transducers exist and how they mediate the activating process of the HPG axis.

Regarding annual reproductive cycles, seasonal changes in photoperiod and temperature act as proximal factors in areas of high latitude and play a role in initiating and terminating gonadal development in fish (Pankhurst and Porter 2003) because an amplitude of these factors becomes notable toward the polar zone. In fact, long-day conditions within a suitable range of water temperatures have been demonstrated experimentally to trigger the gonadal development of certain teleost fish (Borg et al. 1986; Bapary et al. 2009). In contrast, less amplitude of photoperiod and temperature may mean that other environmental factors are involved in the initiation and termination of gonadal development in fish adapted to particular latitudinal areas. Johannes (1978) noted the involvement of temperature, plankton productivity, rainfall, and the speed of prevailing currents and winds in seasonal spawning peaks of tropical fish. Reproduction in fish adapted to this global region may be tuned to environmental changes in relation to tropical monsoons.

The spawning cycles of most fish species repeat at regular intervals during a spawning season. For example, the medaka *Oryzias latipes* spawns daily within 1 hour before the onset of light when maintained at 26℃ under long-day conditions (Fukada et al. 1994), suggesting that a diurnal pattern in light plays a role in the continuation of daily spawning. The threespot wrasse *Halichoeres trimaculatus* is also a daily spawner with a preference for high tides (Takemura et al. 2008). In the case of tropical wrasses, the diurnal cycle is likely fundamental for oocyte development, and the tidal cycle is probably superimposed onto this process (Takemura et al. 2008). Semilunar and lunar rhythmicities of spawning patterns have also been demonstrated in certain fish (Takemura et al. 2004b, 2010; Ikegami et al. 2014). These studies showed that cues from the moon's cycle have an impact on spawning rhythmicity, but how these cues regulate the spawning rhythmicity endogenously in fish is not fully understood.

Spinefoots (rabbitfishes) belong to the perciform group in the family Siganidae and are native to shallow waters, mainly in the Indo-Pacific region. Since spinefoots have a high fisheries value in this region, appropriate management of their resources would be beneficial for their sustainable use. This study aimed to provide an overview of the annual reproductive cycle and spawning rhythmicity of certain spinefoots inhabiting the tropical and subtropical waters of the Indo-Pacific region. In addition, this study sought to understand how certain spinefoots entrain their reproductive activity to rhythmic changes in low-latitude aquatic environments. Physiological mechanisms for the possible perception and transduction of environmental factors by low-latitude spinefoot species are also discussed.

Annual reproductive cycle

The gonadosomatic index (GSI) is a conventional indicator of gonadal development, and monthly changes in this index were investigated to clarify the annual reproductive cycle of four spinefoot species inhabiting the waters of the Ryukyu Islands, Okinawa, Japan (subtropical area; Fig. 1). As a result, a rise in GSI was observed once a year for 3 months from May to July for the streamlined spinefoot (forktail rabbitfish; *Siganus argenteus*) (Rahman et al. 2000a), for 3

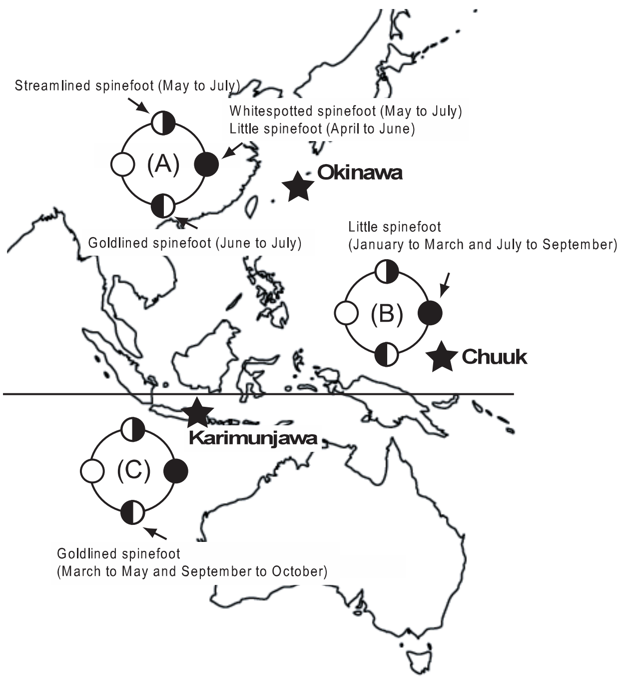

Fig.1. Geographical comparisons of annual reproductive cycle and spawning rhythmicity in spinefoot species in Indo-Pacific region. Stars indicate sampling sites; (A) Okinawa (Japan), (B) Chuuk (Micronesia), (C) Karimunjawa, Indonesia). Circles show lunar phase. ○; full moon, ◑; last quarter moon, ●; new moon, and ◐; first quarter moon. Spawning lunar phase in each place is indicated by arrows.

months from April to June for the white-spotted spinefoot (seagrass rabbitfish; *Siganus canaliculatus*; Hoque et al. 1999), for 3 months from May to July for the little spinefoot (spiny rabbitfish; *Siganus spinus*; Harahap et al. 2001), and for 2 months from June to July for the goldlined spinefoot (golden rabbitfish; *Siganus guttatus*; Rahman et al. 2000a, b). Yolk-laden oocytes were observed in the ovaries of females with a high GSI during these months. Concomitant with the development of oocytes at vitellogenic stages, increases in the plasma levels of vitellogenin (Vtg), a precursor form of yolk proteins, as well as estradiol-17 β (E2) were recorded (Rahman et al. 2000a, b). The findings clearly suggested that vitellogenesis is actively occurring during months with a high GSI (Rahman et al. 2000b; Hoque et al. 1999). During months when vitellogenic processes were steadily in progress, the photoperiod and water temperature around the Ryukyu Islands peaked in June and July, respectively. Spinefoot species adapted to these subtropical conditions clearly utilize increases in these environmental factors for gametogenesis.

Surveys on the reproductive season of these spinefoot species have been also carried out in tropical regions of the Indo-Pacific Ocean (Fig. 1). The reproductive season of the streamlined spinefoot lasts from February to September in the Philippines (Luchavez and Carumbana 1982) and from May to June in Micronesia (Park et al. 2006a). The major reproductive season of the white-spotted spinefoot occurs from January to April in Singapore (Soh and Lam 1973), from April to August in Palau (Bryan et al. 1975), from March to May in the Arabian Gulf (Al-Ghais 1993; El-Sayed and Bary 1994), and from March to June in Hong Kong (Tseng and Chan 1982). A second, or minor, reproductive season was identified for some spinefoot species in the tropical regions. For example, monthly collection of the barred spinefoot (pencil-streaked rabbitfish; *Siganus doliatus*) around the Chuuk Lagoon, Micronesia, showed increases in GSI from March to May and in August (Park et al. 2006a). The GSI of the goldlined spinefoot collected around coral reefs off the Karimunjawa Archipelago, Indonesia, increased twice from March to May (a minor peak) and from September to November (a major peak) (Sri Susilo et al. 2009). Regarding the natural conditions of the latter study area, the photoperiod and water temperature changed with a range of 0.37 h and 2.5℃, respectively. Profiles of the photoperiod and water temperature did not correlate with changes in the GSI for goldlined spinefoots. However, when the annual change in the GSI of this species was compared with the annual change in rainfall, minor and major increases in GSI were observed around the terminal phase and initial phase, respectively, of the rainy season (Sri Susilo et al. 2009), which suggests that changes in aquatic environments in relation to the tropical monsoon may cue the reproduction of this spinefoot species. In this regard, freshwater input in relation to rainfall reportedly becomes a nutrient source for stimulating local pulses of primary production in nearshore tropical marine environments (Taylor and Stanton 1995). Food abundance in aquatic environments is closely linked to a subsequent improvement in nutritional status, and consequently, results in valuable gamete production by adults (Lambert et al. 2000), as well as in the survival and growth of offspring. The importance of food availability in gamete production was experimentally demonstrated by Bapary et al. (2012), who found that restricted feeding and subsequent refeeding resulted in the suppression and rescue, respectively, of ovarian development in the sapphire devil *Chrysiptera cyanea* during the reproductive season. Therefore, food availability may act as a driver of reproductive activity if other environmental factors are within an appropriate range for gonadal development. Pankhurst and Porter (2003) defined food availability (nutrition) as a “permissive” factor whose effects are exercised against the driving effects of “proximate” cues such as the photoperiod.

Spawning rhythmicity

During the spawning season, fish spawn repeatedly at regular intervals, and spinefoot species exhibit lunar-related spawning rhythmicity. Collecting fish on a weekly basis according to the lunar cycle assists in determining which lunar phase is used for synchronous spawning. For populations of streamlined spinefoot in waters surrounding the Ryukyu Islands, the GSI increased toward, peaked around, and dropped after the last quarter moon period, indicating that spawning occurred during this particular moon period (Rahman et al. 2003a, b). Based on observations from a weekly profile of the GSI, a peak of spawning of the white-spotted spinefoot and the little spinefoot was observed around the new moon period (Hoque et al. 1999; Harahap et al. 2001). Spawning of the goldlined spinefoot occurred around the first quarter moon period (Rahman et al. 2000b; Fig. 1), and differences in the spawning lunar phase among these spinefoot species may indicate the evolutionary acquisition of chronologically based reproductive isolation (Takemura et al. 2010).

The effect of the moon phase on reproduction can also be observed histologically. Ovaries from the above-mentioned spinefoot species were observed with vitellogenic oocytes that synchronously developed toward, and ovulated eggs were released around, the species-selective spawning moon phase (Hoque et al. 1999; Rahman et al. 2000b; Harahap et al. 2001). Concomitant with the synchronous development of vitellogenic oocytes in an ovary, plasma levels of E2 and Vtg increased toward the species-selective spawning moon phase (Rahman et al. 2000b). Similarly, 17 α 20 β -dihydroxy-4-

pregnen-3-one (DHP), a maturation-inducing hormone in teleost fish (Nagahama et al. 1994), peaked around the species-selective spawning moon phase (Rahman et al. 2000b). *In vitro* culture of ovarian tissue of the goldlined spinefoot revealed that human chorionic gonadotropin (hCG) stimulated the synthesis of E2 around the new moon period. Alternatively, the synthesis of DHP occurred around the first quarter moon period (Rahman et al. 2002, 2003a). These reports indicated that the spinefoot species is a lunar-synchronous spawner and that the HPG axis is activated according to the lunar cycle (Takemura et al. 2010; Ikegami et al. 2014).

A weekly collection of spinefoot species was also conducted in the Indo-Pacific region. The little spinefoot and the barred spinefoot in Micronesia spawned around the new moon period and the first quarter moon period, respectively (Park et al. 2006a,b). In contrast, the synchronous spawnings of the goldlined spinefoot in Indonesia (Sri Susilo et al. 2009) and the Philippines (Harvey et al. 1985; Hara et al. 1986) were observed around the first quarter moon period. Populations of this species likely utilize the same lunar phase for repetitive synchronous spawning, even if the habitats are geographically far from each other (Fig. 1). Therefore, similar cues from the moon may be perceived by the sensory organs of spinefoots overall and utilized for synchrony of reproduction.

Note that juveniles of the little spinefoot and the white-spotted spinefoot migrate to coastal regions around the new moon period (Soliman and Yamaoka 2010), suggesting that immature fish can also use the same moon phase for migration. Cues from the moon may be perceived and transduced in the brain located at the upstream region of the HPG axis. As an example of the application of this information for fishery management, the age at settlement of the little spinefoot estimated from juveniles at about 20 days (Soliman et al. 2010) can be used to determine the date of spawning, thereby determining when a closed season can be legislated. Adding 1-2 days for duration of egg development to the age at settlement, the date of spawning of the fish was calculated to be 21-22 days from settlement. With settlement occurring around a new moon, the spawning falls around the period of the first quarter moon. Since the white-spotted spinefoot, little spinefoot, and streamlined spinefoot co-occur at the settlement in Lagonoy Gulf in the Philippines (Soliman and Yamaoka 2010), a local government bordering the gulf declared a closed season prohibiting the catching of spinefoots during the first quarter moon in March to May based on this information (e.g., see Soliman 2013).

Perception and utilization of cues from the moon

What kinds of cues from the moon are perceived by lunar-synchronized spawners? Several cycles occur in relation to the moon, which are roughly categorized into three cycles: the lunar cycle, semilunar cycle, and tidal cycle (Takemura et al. 2010). The lunar cycle involves a periodical change repeated at 1-month intervals, and the biological activities of organisms peak around the species-selective lunar phase (this cycle is observed in spinefoots and groupers). The semilunar cycle is a periodical activity that seems to appear at a 14.7-day interval (this cycle is observed in California grunions and mummichogs). In many cases of this cycle, peaks of biological activity occur twice within a month. The tidal cycle at a 12.4-h interval also involves moon-related activity (this cycle is observed in wrasses and European flounders), which is well correlated with a daily tidal cycle and caused by the combined effects of gravitational forces exerted by the moon and the sun, along with the rotation of the Earth (Leatherland et al. 1992). Since the spawning of spinefoots at a 1-month interval is cycled with a peak around the species-selective moon phase during the spawning season, they are capable of perceiving and utilizing periodical changes in cues from the moon. Cues from the moon may be periodical changes in moonlight illumination (Horning and Trillmich 1999) and geomagnetic fields (Stolov 1965; Bell and Defouw 1966) because they cycle at an interval of 1 month and peak around the full moon and the last quarter moon, respectively.

When the goldlined spinefoot were reared for 2 months under illumination conditions of natural, artificial full moon, and artificial new moon nights, fish under natural conditions were confirmed to spawn around the predicted spawning dates (around the first quarter moon period). In contrast, the synchronous spawnings of fish under artificial full and new moon conditions were suppressed or disrupted (Takemura et al. 2004a), indicating that fish can utilize periodical changes in “brightness at night” for synchrony of reproductive activity, although the importance of the geomagnetic field in synchronous spawning cycle was not evaluated. Utilization of “brightness at night” during the full moon period has been reported in the spawning behavior of certain cichlids inhabiting Lake Tanganyika (Rossiter 1991; Watanabe 2000a, b). In this case, “brightness at night” was explained to facilitate parental care of the young against predators (Rossiter 1991).

Melatonin is an indoleamine hormone synthesized mainly in the pineal organ and retina through an action of arylalkylamine *N*-acetyltransferase (aaNAT), which is the rate-limiting enzyme of melatonin synthesis (Falcón et al. 2010). Melatonin from the pineal organ is believed to be secreted to the blood circulation and is due to a physiological function in neural and peripheral organs because the plasma levels of melatonin increase during nighttime and decrease during the day (Bromage et al. 2001). When plasma concentrations of melatonin were measured from the goldlined spinefoot and the white-spotted spinefoot, definitive daily fluctuations were observed with an increase during nighttime and a decrease during the day (Rahman et al. 2004; Takemura et al. 2004a), which has also been reported for many teleost fish (Bromage et al. 2001). Notably, the plasma levels of melatonin at midnight during the new moon period were higher than those during the full moon period (Rahman et al. 2004; Takemura et al. 2004a; Fig. 2A). An *in vitro* culture study revealed that exposing the isolated pineal organs to illuminance during the full moon period resulted in the suppression of melatonin synthesis (Takemura et al. 2006). Concomitant with melatonin fluctuation, mRNA expression of aaNAT in the retina of the goldlined spinefoot was higher at night during the new moon period than during the full moon period (Kashiwagi et al. 2013). These findings clearly suggest that plasma levels of melatonin change in accordance with periodical changes in “brightness at night” and that little difference exists in the amplitude of melatonin levels between the full moon period and the new moon period. Therefore, melatonin likely acts as a neuroendocrine transducer of moonlight cues.

The actions of melatonin in the cells of neural and peripheral organs are mediated via melatonin receptors belonging to the G protein-coupled receptor superfamily (Iigo et al. 1994; Reppert et al. 1996). Melatonin receptor subtypes have been cloned and characterized in the goldlined spinefoot to assess whether they are involved in lunar-synchronized spawning activities (Park et al. 2006c, 2007a, b, 2014). Park et al. (2014) reported that among three subtypes of melatonin receptors known in vertebrates (MT1, MT2, and Mel1c), MT1 and Mel1c mRNA abundances in the pineal organ of the goldlined spinefoot were higher during the new moon period than the full moon period (Fig. 2B, C). In addition, exposing fish to intense moonlight during the full moon period lowered Mel1c mRNA abundance in the pineal organ within 1 hour (Park et al. 2014). These results suggest that the mRNA abundance of melatonin receptors fluctuate in accordance with periodical changes in the “brightness at night.” Since a profile of melatonin synthesis correlated well with that of Mel_{1c} mRNA abundance in the cultured pineal organ, melatonin may partially mediate the mRNA expression of its receptors (Park et al. 2007b).

In this review, we have mainly discussed a possible involvement of “brightness at night” and its transducing system through melatonin. However, other cues may come from the moon to exert lunar-related rhythmicity. In this regard, note the lunar rhythmicity in smolts of the chinook salmon *Oncorhynchus tshawytscha*, in which the timing of salt water entry from a river was closely related to the date of lunar apogee (the farthest distance from the earth to the moon), followed by the date of quarter moons (DeVries et al. 2004). Salmonid fish can likely perceive changes in lunar gravitation for the start of migration.

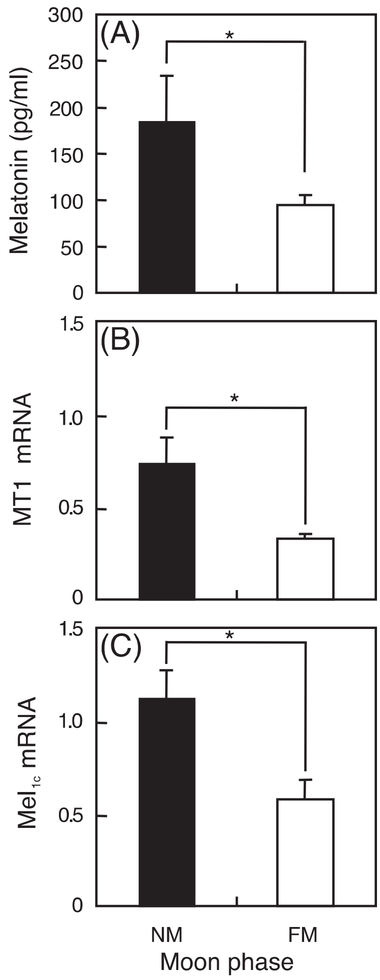

Fig. 2. Comparisons of melatonin concentration in the plasma (A), melatonin receptor, (MT1) gene expression in the pineal organ (B), and melatonin receptor (Mel_{1c}) gene expression in the pineal organ (C) of the goldlined spinefoot between the new moon (NM) and full moon (FM). The plasma sample and the pineal organ were taken from fish at midnight during the new moon (■) and full moon (□). Melatonin levels in the plasma were measured by time-resolved immunofluoroassay. Expressions of MT1 and Mel_{1c} mRNA in the pineal gland were determined by quantitative real-time PCR and normalized by the amount of *β-actin* mRNA. Values are means ± SEM. Asterisk indicates a significant difference ($p < 0.05$) between the new moon and full moon. Modified from Ikegami et al. (2014).

Closing remarks

Recently, a study reported a relationship between the lunar cycle and clock genes in the reef-built coral *Acropora millepora* (Levy et al. 2007) and the goldlined spinefoot (Sugama et al. 2008; Fukushiro et al. 2011; Toda et al. 2014). In the case of *A. millepora,* which spawns around the full moon period, the mRNA abundance of light-responsible genes (*Cryptochrome, Cry1* and *Cry2*) fluctuated with an increase during daytime under a light/dark cycle. The mRNA abundance of *Cry2* was higher around full moon nights than around the new moon period (Levy et al. 2007). In contrast, in the gold-lined spinefoot, the light-responsive gene *Period (Per2)* mRNA abundance in the pineal organ was higher at the culmination of the full moon period than during the new moon period (Sugama et al. 2008). Moreover, the mRNA abundance of *Cry1* and *Cry3* in the brain (mesencephalon and diencephalon) fluctuated weekly with a peak around the first quarter moon (Fukushiro et al. 2011), which is a spawning lunar phase of the gold-lined spinefoot. More recently, not only *Cry3* but also *Per4* mRNA levels in the diencephalon showed lunar phase-dependent variation without depending on light conditions at night (Toda et al. 2014). The presence of an endogenous lunar clock may be not eliminated if lunar synchronized spawning is repeated during the reproductive season. Further studies are needed to more fully elucidate the physiological mechanism of the lunar system in fish.

Using the spinefoot species as experimental models, this review focused on the annual reproductive cycle and its environmental regulation, as well as the spawning rhythmicity in relation to the lunar cycle and the possible roles of moonlight as an external cue and melatonin as an internal cue. Since many fish in tropical and subtropical waters (i.e., low-latitude regions) exhibit a clear lunar cycle during the restricted spawning season (Takemura et al. 2010), this review provides useful information on the duration and time of reproductive activity in commercially important species in these regions. Therefore, we hope that this review will assist in the appropriate management of fisheries resources for sustainable development in Kuroshio.

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