Spawning Season, Lunar-related Spawning and Mating Systems in the Camouflage Grouper Epinephelus polyphekadion at Ishigaki Island, Japan

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Abstract: We examined seasonal changes in the gonadosomatic index of wild fish and detailed the first spawning period of each year of cultured fish over several years to determine the spawning season and lunar-related spawning of camouflage grouper Epinephelus polyphekadion in a subtropical area of southern Japan. Additionally, we observed captive females’ and males’ spawning behavior and elucidated the mating system of this species. The main spawning season of wild fish was April – May of the solar calendar (Gregorian calendar), when gonadosomatic index (GSI) values of females and males peaked. The first spawning periods varied in the solar calendar. However, they were observed from the 19th to 23rd day in the third month of the lunar calendar (lunisolar calendar) during the full moon and the last quarter moon, excluding the years when spawning occurred one month later, because of low water temperatures before the spawning season in those years. This result indicates that camouflage grouper shows lunar-related spawning. The basic mating system of camouflage grouper is pair spawning between the largest dominant male and an ovulated female. However, some non-dominant males undertook sneaker spawning.

Key words: Camouflage grouper; Lunar-related spawning; Mating system; Spawning behavior

Camouflage grouper Epinephelus polyphekadion (Pisces, Perciformes, Serranidae) inhabits shallow waters of coral reefs in subtropical and tropical waters from southern Japan to the Indo-West Pacific region (Heemstra and Randall 1993). This species has been targeted for aquaculture and stock enhancement in Asian and Pacific countries because of its high commercial value. The need exists to develop hatchery technology for mass production of juveniles (Tawada 1989a, b; Debas et al. 1989; Tamaru et al. 1996; James et al. 1997, 1998). However, larval survival rates remain low and mass culture techniques for larval camouflage grouper remain underdeveloped (James et al. 1997).

Wild and captive camouflage grouper reportedly show a lunar-related spawning cycle; they spawn for several days in each successive 2 – 3 month period during the reproductive season (James et al. 1997; Rhodes and Sadovy 2002). Studies of the reproductive biology of camouflage grouper have revealed a wide variation in lunar periodicity and seasonal timing of spawning, i.e. both new-moon and full-moon spawning have been reported and spawning occurs regionally in a specific season in the Indo-Pacific region (Rhodes and Sadovy 2002). In Japan, although Tawada (1989b) first reported...
hormone-induced spawning of captive camouflage grouper, the spawning biology of wild and non-hormone treated camouflage grouper has not been reported.

For several fish species, larger eggs are known to produce larger larvae with a high tolerance for starvation (e.g., Sehgal and Toor 1991; Imai and Tanaka 1998). Kayano et al. (1998) reported that the diameter of eggs from captive red spotted grouper *Epinephelus akaara* that were distributed in temperate waters were larger at low temperatures in the early phase of the spawning season. Larvae that hatched from larger eggs survived longer than those from smaller eggs spawned at higher temperatures later in the spawning season. This phenomenon has also been observed for coral trout *Plectropomus leopardus* distributed in subtropical waters in Japan (Teruya et al. 1992). The diameter of eggs spawned by captive camouflage grouper is reported as $830 \pm 30 \mu m$ (mean $\pm$ SD) at $25 - 30^\circ C$ (Tawada 1989b), $769 - 832 \mu m$ at $27^\circ C$ (Tamaru et al. 1996) and $757 \pm 37 \mu m$ at $29 - 30^\circ C$ (James et al. 1997). Consequently, egg diameters of the camouflage grouper tend to decrease with increasing water temperatures at spawning. Therefore, for subtropical waters, it can be inferred that egg diameters are larger at the lower temperatures that occur early in the spawning season. Prediction of the first spawning period during the spawning season and the use of large eggs obtained during this period would be advantageous for production of camouflage grouper juveniles.

The egg fertilization rate is an index that is useful to evaluate egg quality in fish broodstock management (e.g., Matsunari et al. 2006). Low fertilization rates of eggs for the red spotted grouper, fluctuating between 10% and 25% for spontaneous spawning, have been a problem in the broodstock management (Okumura 1998). Okumura et al. (2002) investigated the reason for low fertilization rates in spawning tanks of red spotted grouper by observing spawning behavior and found that the low fertilization rate might be caused by limited space, especially insufficient water depth, which might have inhibited normal spawning behavior. Therefore, observation of spawning behavior is important to improve the broodstock management techniques. Nevertheless, camouflage grouper spawning behavior has not been reported. Moreover, observing the spawning behavior would reveal the number of females and males involved in mating, i.e. mating system, which is expected to affect the genetic variability of the offspring strongly given a limited number of effective parents in captivity (Perez-Enriquez et al. 1999; Sekino et al. 2002; Harase and Sekino 2003; Alarcón et al. 2004; Nugroho and Taniguchi 2004). Growing concern surrounds the potential negative effects on wild populations of stock enhancement programs' release of hatchery-produced juveniles with low genetic variation (e.g., Waples 1991; Utter 1998).

To determine the spawning season, lunar-related spawning, timing of the first spawning period during the spawning season, and mating systems of the camouflage grouper in a subtropical area of southern Japan, we: (1) examined the gonadosomatic index of wild fish; (2) determined the first spawning period of cultured fish in a tank; and (3) made preliminary observations of captive females and males' spawning behavior.

**Materials and Methods**

**Gonadosomatic index of wild fish**

Fish were collected by hook-and-line on six occasions during April – October 1986 and on 13 occasions during February – October 1987 off the coast of Ishigaki Island, Okinawa Prefecture, Japan (Fig. 1). Size, sex and gonad weight were determined for 29 fish in 1986 and 40 fish in 1987. Body weight (BW) and total length (TL) of captured individuals were measured respectively to the nearest 10 g and 1 mm. Gonads were removed and weighed to the nearest 0.1 g after paper blotting. Sex was determined by examining a small piece of gonad under a light microscope. To assess the spawning season, the gonadosomatic index (GSI) was calculated for each fish using the formula, $GSI = (gonad weight)/(gonad-free fish weight) \times 100$. 


**Spawning of captive fish**

Broodstock fish were captured by hook-and-line in the coral lagoons of Ishigaki Island in 1985 and 1986. Captured fish were maintained at the Yaeyama Station of the National Center for Stock Enhancement, Fisheries Research Agency (Fig. 1). Spawning investigations were conducted during the first spawning period in April and May of each year during 1989 – 1993. Females and males were seven and four in 1989 and five and five in other years. The mean total length and body weight of the fish in each year are presented in Table 1.

The fish were reared in an outdoor octagonal concrete tank containing 60 kl of seawater (2 m depth) throughout the year. Sand-filtered seawater was supplied to the tank at the rate of 2 – 3 turnovers per day. In 1992 and 1993, fish were stocked in a cubic net cage (5 m wide, 5 m long, 5 m deep) in a coral lagoon and were reared in an octagonal tank during a spawning season. The water temperature and photoperiod were allowed to fluctuate naturally during the rearing period. The seawater salinity was around 35%. Water temperature was measured daily at around 10:00 a.m. The fish were fed to satiation one or two days a week with jack mackerel *Trachurus japonicus* coated with nutrients such as vitamins.

The fish were allowed to spawn naturally. The effluent from the broodstock holding tank was introduced into a rectangular polyester net (0.3 mm mesh) set in an egg collecting tank (0.9 m wide, 2.4 m long, 1.8 m deep) through a 100 mm diameter plastic hose. Whenever spawning occurred, the eggs were collected using a scoop net and transferred into a measuring cylinder with 2 l seawater. The number of eggs was estimated by multiplying the volume of buoyant and sunken eggs in a measuring cylinder by the number of eggs per milliliter of eggs, as counted under a stereoscopic microscope. All buoyant eggs were fertilized, but no fertilized eggs were found among sunken eggs. The fertilization rate of eggs was determined as the percent ratio of the number of buoyant eggs to the total number of buoyant and sunken eggs in each spawning day. The 30 buoyant eggs’ diameters were measured to the nearest micrometer.

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**Table 1.** Number, body size (mean ± SD), and body weight (mean ± SD) of the captive camouflage groupers

<table>
<thead>
<tr>
<th>Year</th>
<th>Number</th>
<th>Total length (cm)</th>
<th>Body weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>1989</td>
<td>7</td>
<td>4</td>
<td>54.8 ± 3.5</td>
</tr>
<tr>
<td>1990</td>
<td>5</td>
<td>5</td>
<td>52.2 ± 1.5</td>
</tr>
<tr>
<td>1991</td>
<td>5</td>
<td>5</td>
<td>53.3 ± 2.0</td>
</tr>
<tr>
<td>1992</td>
<td>5</td>
<td>5</td>
<td>56.3 ± 2.7</td>
</tr>
<tr>
<td>1993</td>
<td>5</td>
<td>5</td>
<td>56.5 ± 1.1</td>
</tr>
</tbody>
</table>
Spawning behavior of captive fish

Spawning behavior of fish was monitored in detail on May 13, 1993 using an underwater video system inserted into the broodstock holding tank (Eye-ball; Hitachi Zosen Corp., Japan), taking care not to disturb the fish behavior. The spawning behavior was also recorded using a video camera (S-VHS movie camera; Panasonic Inc., Japan) from the water surface. For night recording, two 500 W lights were suspended over the tank. This treatment did not visibly influence the fish spawning behavior.

Statistical analysis

The values of total length of males and females sampled from the wild were compared using Mann-Whitney’s U-test. Significance was inferred for \( P \leq 0.05 \).

Results

Sex and maturity of wild fish

Sex was determined for 41 females and 16 males. Twelve individuals had no visible oocytes or milt; their gender was not determined. The GSI was plotted against the fish TL (Fig. 2). Females and males were, respectively, 35.5 – 60.4 cm and 41.0 – 55.3 cm TL. High GSI values were observed for females and males over the range of body sizes. Females were significantly smaller than males (\( P = 0.0114 \)): they reached maturity at a smaller body size than males.

Changes of GSI of wild fish

The GSI values of females were low (<0.5) in February (Fig. 3), but they then increased rapidly and peaked at 15 – 16 in April and May. Some females showed high GSI values until early July. In September and October, GSI values were less than 0.5. Although the GSI values of males were lower than those of females, the values varied in a cycle similar to that of females. Fish of undetermined gender were observed from late August to February and showed low GSI values of 0.03 – 0.33.

Spawning of captive fish

First spawning of captive fish occurred during different periods in late April and mid-May of the solar calendar (Gregorian calendar). However, it occurred during almost the same period, from the 19th to the 23rd day in the third month of the lunar calendar (lunisolar calendar) during the full moon and the last quarter moon at the age of the moon of ca. 18 – 22, in each year of 1989, 1991, and 1992 (Table 2).
of the pelvic fins of males become black. Five of the dorsal, caudal and anal fins and the tip of the dorsal peduncle patch. In addition, the margins black all over, with marbled patterns, became prominent before the spawning season. During the spawning behavior, sex was not visually determined. 

Spawning behavior of captive fish

Figure 4 shows a schematic diagram of the spawning behavior. Sex was not visually determined before the spawning season. During the spawning season, males turned dark gray to black all over, with marbled patterns, becoming less distinct but displaying a distinct black dorsal peduncle patch. In addition, the margins of the dorsal, caudal and anal fins and the tip of the pelvic fins of males become black. Five

The first spawning period was from the 19th to the 22nd day of the fourth month and from the 20th to the 23rd day of the leap third month of the lunar calendar in 1990 and 1993, respectively. The lunisolar calendar usually has 12 months, but a 13th month is added to the year every two or three years. The leap month takes the same number as the preceding month. In 1993 (leap year), the intercalary month was added after the third month. Hence, the spawning periods in 1990 and 1993 were observed immediately after one month later than other years. Spawning occurred four times; the total number of buoyant eggs spawned in each year was 7 – 53 million with a mean egg diameter of 859 – 923 μm. Fertilization rates of eggs were 28.3 – 94.0%. The water temperature at spawning was 23.0 – 25.9°C.

Spawning behavior of captive fish

Figure 4 shows a schematic diagram of the spawning behavior. Sex was not visually determined before the spawning season. During the spawning season, males turned dark gray to black all over, with marbled patterns, becoming less distinct but displaying a distinct black dorsal peduncle patch. In addition, the margins of the dorsal, caudal and anal fins and the tip of the pelvic fins of males become black. Five 

Table 2. Spawning data for captive camouflage groupers

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of spawning times</th>
<th>Date of spawning</th>
<th>Water temperature at spawning (°C)</th>
<th>Number of eggs spawned (×10⁴)</th>
<th>Fertilization rate (%)</th>
<th>Mean egg diameter ± SD (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Solar calendar</td>
<td>Lunar calendar</td>
<td>Lunar phase</td>
<td>Buoyant eggs</td>
<td>Sunken eggs</td>
<td></td>
</tr>
<tr>
<td>1989</td>
<td>1</td>
<td>25-Apr</td>
<td>20th third month</td>
<td>19.0</td>
<td>24.0</td>
<td>20875</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>26-Apr</td>
<td>21st third month</td>
<td>20.0</td>
<td>24.1</td>
<td>22600</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>27-Apr</td>
<td>22nd third month</td>
<td>21.0</td>
<td>24.2</td>
<td>2340</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>28-Apr</td>
<td>23rd third month</td>
<td>22.0</td>
<td>24.5</td>
<td>6740</td>
</tr>
<tr>
<td>1990</td>
<td>1</td>
<td>13-May</td>
<td>19th fourth month</td>
<td>17.9</td>
<td>24.5</td>
<td>1150</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>14-May</td>
<td>20th fourth month</td>
<td>18.9</td>
<td>24.2</td>
<td>5070</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>15-May</td>
<td>21st fourth month</td>
<td>19.9</td>
<td>25.3</td>
<td>1500</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>16-May</td>
<td>22nd fourth month</td>
<td>20.9</td>
<td>24.8</td>
<td>375</td>
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<tr>
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<td>1</td>
<td>3-May</td>
<td>20th third month</td>
<td>18.3</td>
<td>23.0</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>4-May</td>
<td>20th third month</td>
<td>19.3</td>
<td>23.2</td>
<td>5920</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>5-May</td>
<td>21st third month</td>
<td>20.3</td>
<td>23.4</td>
<td>1360</td>
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<td>6-May</td>
<td>22nd third month</td>
<td>21.3</td>
<td>23.6</td>
<td>50</td>
</tr>
<tr>
<td>1992</td>
<td>1</td>
<td>21-Apr</td>
<td>19th third month</td>
<td>17.9</td>
<td>24.2</td>
<td>836</td>
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<tr>
<td></td>
<td>2</td>
<td>22-Apr</td>
<td>20th third month</td>
<td>18.9</td>
<td>24.3</td>
<td>12900</td>
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<td></td>
<td>3</td>
<td>23-Apr</td>
<td>21st third month</td>
<td>19.9</td>
<td>24.3</td>
<td>6050</td>
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<td></td>
<td>4</td>
<td>24-Apr</td>
<td>22nd third month</td>
<td>20.9</td>
<td>24.4</td>
<td>1430</td>
</tr>
<tr>
<td>1993</td>
<td>1</td>
<td>11-May</td>
<td>20th leap third month</td>
<td>19.1</td>
<td>25.9</td>
<td>180</td>
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<tr>
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<td>22nd leap third month</td>
<td>21.1</td>
<td>25.8</td>
<td>7540</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>14-May</td>
<td>23rd leap third month</td>
<td>22.1</td>
<td>25.8</td>
<td>132</td>
</tr>
</tbody>
</table>
**Discussion**

**Maturity, spawning season and lunar-related spawning**

All camouflage groupers captured in this study were sexually mature. High GSI values were observed respectively for females and males over a range of body sizes: 35.5 – 60.4 cm and 41.0 – 55.3 cm TL (Fig. 2). Females also reached maturity at a smaller body size than males; this phenomenon is closely related to the camouflage grouper being a protogynous hermaphrodite (Debas et al. 1989).

It can be concluded that at Ishigaki Island, the main spawning season of the wild camouflage grouper is April – May, when GSI values of females and males peak (Fig. 3). Some fish showed higher GSI values until early July. Therefore, the spawning season seems to continue for 3 – 4 months in the field. The spawning season of serranids differs depending on the geographical area and species (e.g., James et al. 1997; Lee et al. 2002; Rhodes and Sadovy 2002). Rhodes and Sadovy (2002) summarized that the spawning season of camouflage groupers at several sites from the northern to southern hemispheres typically occurs over a 2 – 3 month period with great seasonal variation. The spawning period of wild camouflage grouper at Ishigaki Island approximates that of other sites; the main spawning season at Ishigaki Island resembles those at Kuwait and Saudi Arabia (Rhodes and Sadovy 2002).

Camouflage grouper males and females aggregate in large numbers to spawn at specific times and locations each year in Pohnpei, Micronesia (Rhodes and Sadovy 2002). They use lunar periodicity to adjust the specific times of spawning, i.e., to complete the synchronous spawning at specific locations, as inferred for other grouper species (Toledo et al. 1993; Lee et al. 2002). Lunar-related spawning cycles have been reported for camouflage grouper at several sites, with a wide variation in lunar periodicity, i.e., both new-moon and full-moon spawning depending on the site (Rhodes and Sadovy 2002). In this study, the first spawning period of cultured camouflage grouper was observed from the 19th to the 23rd day in the third or fourth month of the lunar calendar during the full moon and the last quarter moon in each year during 1989 – 1993 (Table 2). Spawning after the full moon is inferred for wild camouflage grouper in Pohnpei and New Caledonia (Rhodes and Sadovy 2002).

**Prediction of the first spawning period**

In 1990 and 1993, spawning occurred just one month later than during other years (Table 2). Water temperature is well known as an important environmental factor affecting the gonad maturation and spawning of fish (Scott 1979; Migaud et al. 2002; Clark et al. 2005). Figure 5 shows changes in water temperature in a broodstock holding tank in each year during 1989 – 1993. Temperature changes showed a similar trend during the five years and fluctuated between ca. 19 and 22°C from mid-January to late February and then rapidly decreased from 22 – 23°C to ≤ 20°C from late February to early March. The cumulative temperature was calculated from the day the temperature decreased to ≤ 20°C in these periods for each year (Fig. 5). In
each year, first spawning occurred during the full moon to the last quarter moon after the cumulative temperature exceeded ca. 1000–1100 °. Delayed spawning in 1990 and 1993 is attributable to the low water temperatures before the spawning season (Fig. 5). Consequently, in Ishigaki Island, we can predict that the first spawning of captive camouflage grouper occurs around the 19th day of the lunar calendar during the full moon to the last quarter moon after the cumulative temperature, as calculated based on the minimum temperature during late February and early March of the solar calendar, exceeds ca. 1000–1100 °.

**Spawning behavior and mating systems**

This study first documented the spawning behavior of camouflage grouper in captivity (Fig. 4). In the spawning season, the whole body of males turned dark gray to black with marbled patterns. The largest male, the most dominant and aggressive of the males, guarded a territory on the tank floor and formed a pair with an ovulated female. Body color changes were observed for wild camouflage groupers at spawning aggregation sites in Pohnpei (Rhodes and Sadovy 2002). Reportedly, the male frequently changes color in what appears to be territory-defining behavior.

Spawning behavior of captive camouflage groupers resembled that of other grouper species such as chocolate hind *Cephalopholis boenack* (Donaldson 1989), pigmy grouper *C. spiloparaea* (Donaldson 1995), coral trout (Teruya et al. 1992), and red spotted grouper (Okumura et al. 2002). According to Okumura et al. (2002), red spotted grouper dashed vertically in a pair from the bottom to the water surface and released gametes at the surface in a tank. The pair sometimes jumped from the surface and swam horizontally on the water surface before or after spawning. That behavior suggests that the low fertilization rate (19%) of eggs from captive red spotted grouper might be the result of this jumping behavior from water surface during spawning in the limited space of a tank with insufficient water depth. In this study, jumping behavior during spawning was

![Fig. 5. Changes in daily water temperature (wavy lines) and cumulative temperature (straight lines) in the camouflage grouper culture tank during January and May of the solar calendar in each year during 1989–1991. Symbols show the lunar phase: ●, new moon; ○, full moon. Horizontal broken arrows indicate days the temperature decreased to ≤20°C during late February and early March; the cumulative temperature was calculated from this day. Vertical bars indicate the period when the cumulative temperature exceeded 1000–1100 °. Vertical arrows indicate the cumulative temperature when the first spawning period begins.](image-url)
not observed for the camouflage grouper (Fig. 4). The variation of fertilization rates between 28.3% and 94.0% among camouflage groupers in this study (Table 2) might be attributable to the quality of gametes, which depends on other factors such as the nutritional value of food for the broodstock.

The basic mating system for the camouflage grouper was pair spawning, which resembles that of several grouper species (Donaldson 1989, 1995; Teruya et al. 1992; Zabala et al. 1997; Okumura et al. 2002). However, in this study, we observed sneaker males (Gross 1996), which released their own gametes while a spawning pair was releasing theirs (Fig. 4). This behavior has not been reported for other serranids. Consequently, sperm competition, the competition between the ejaculates of different males for the fertilization of an ovum (Parker 1970), is expected to occur among camouflage grouper males. A positive relation between the intensity of sperm competition (= type of mating system) and relative sperm production has been found in fish (Stockley et al. 1997; Balshine et al. 2001). Marino et al. (2001) explained this relationship for serranids using examples of two grouper species. The mating system of wild dusky grouper *E. marginatus* is pair spawning in single-male/multi-female social units during the reproductive season (Zabala et al. 1997); the males have extremely small ripe testes, attaining only 0.6% of their body weight (Marino et al. 2001). The wild Nassau grouper *E. striatus* is a group spawner (Whaylen et al. 2004). Consequently, males have large ripe testes, attaining 10% of body weight (Sadovy and Colín 1995). The testes and male camouflage grouper account for 0.5 - 5.5% of body weight (mean value, 2.2%; calculated as testis weight/ body weight × 100 using data of Fig. 3) during the high reproductive season in late May. Therefore, the mating system and relative testes weight of camouflage grouper were moderate between dusky grouper and Nassau grouper. This finding supports the relation between the intensity of sperm competition (= type of mating system) and relative sperm production in serranids, as described by Marino et al. (2001).

Under extreme polygyny, in which very few males accomplish almost all matings, high variance in male reproductive success results in a low effective population size (Fessehaye et al. 2006). The effective population size is always much smaller than in comparable monogamous populations when marked inequalities in the reproductive success occur (Nunney 1993). Consequently, genetic variation of the offspring would be reduced in the mating system of camouflage grouper under culture conditions with a limited number of broodstock. However, the presence of sneaker males might contribute to increased genetic variability of the offspring in camouflage grouper reared in tanks. In future studies, the paternity of fertilized eggs and/or hatched larvae must be confirmed using genetic markers.

**Acknowledgments**

We would like to thank all the staff of the Yaeyama Station, National Center for Stock enhancement for their advice and encouragement. Cordial thanks are extended to S. Shimoji (Uminchu Saburo) for collecting the fish samples.

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石垣島におけるマダラハタの産卵期,
月齢に同調した産卵および配偶システム

照屋和久・升間主計・本藤 靖・浜崎活幸

石垣島におけるマダラハタの産卵期および産卵開始時期を明らかにする目的で, 天然魚の生殖腺指数を調査するとともに, 天然魚を数年間飼育した親魚の水槽内における産卵開始時期を5年間にわたり調査した。さらに, 親魚の産卵行動を観察し, 本種の配偶システムを明らかにすることを試みた。天然魚の主要な産卵期は, 雌雄とも生殖腺指数がピークに達する4月〜5月（太陽暦）であると推察された。産卵期初めの親魚の産卵が, 満月から下弦の月にかけての3月19日〜23日（太陽暦）に集中した。ただし, 産卵期前の水温が低い年の産卵は, 1カ月後の満月から下弦の月の期間にシフトした。このように, マダラハタの産卵は月齢に同調していた。水槽内では最大の雌1個体がわばりを形成し, その個体と成熟雄によるペア産卵が行われたが, 小型雄によるスニーキングも観察された。