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Author(s)	Takahashi, Tetsumi
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1 **Different degrees of lunar synchronization of ovary development between two**  
2 **morphs of a Tanganyikan cichlid fish**

3

4 **Tetsumi Takahashi**

5 Graduate School of Science, Kyoto University, Kitashirakawa-Oiwake, Sakyo, Kyoto

6 606-8502, Japan

7 E-mail: [tetsumi@terra.zool.kyoto-u.ac.jp](mailto:tetsumi@terra.zool.kyoto-u.ac.jp)

8

9 *Key words:* Cichlidae; gonado-somatic index; lunar cyclic spawning; spawning nest;  
10 predator avoidance strategy

11

12 Two gray-scale figures, no tables, no appendix.

13

14 This paper has not been submitted elsewhere in identical or similar form, nor will it be  
15 during the first three months after its submission to *Hydrobiologia*.

16 **Abstract** The degree of lunar synchronization of spawning is thought to be related to  
17 a strategy that decreases predation on the brood in Tanganyikan substrate-brooding  
18 cichlids. Here, I examined the periodic change of ovary development in two morphs of  
19 *Telmatochromis temporalis*: the normal morph uses burrows under stones as spawning  
20 nests, whereas the dwarf morph uses holes within empty snail shells. The normal morph  
21 showed a significant lunar synchronization of ovary development, but the dwarf morph  
22 did not. In the normal morph, spawning prior to the full moon probably decreases the  
23 incidence of approaching brood predators and increases the guarding efficiency of  
24 parents. In the dwarf morph, however, lunar cyclic spawning may be dispensable,  
25 because the spawning nests within shells are probably highly effective for predator  
26 avoidance. These two morphs are closely related, and then will be a good model to  
27 clarify the widely observed phenomenon of lunar cyclic spawning.

28 **Introduction**

29

30 Although biological rhythmicity that is synchronized with lunar or semi-lunar cycles is  
31 a widespread phenomenon in marine organisms (Leatherland et al., 1992; Hernández-  
32 León, 2008), it is rare among organisms inhabiting freshwater bodies, where tidal  
33 fluctuation is limited or absent. However, lunar cyclic spawning has been reported in  
34 nine substrate-brooding species of cichlid fish belonging to the tribe Lamprologini in  
35 Lake Tanganyika, Africa (Nakai et al., 1990; Rossiter, 1991). In these species, a pair of  
36 parents or a female guards the eggs and yolk-sac larvae, which cannot easily escape  
37 from predators by themselves. The spawning cycles of these species are thought to  
38 improve the survival of the vulnerable brood (eggs and yolk-sac larvae) or dispersing  
39 young (Nakai et al., 1990; Rossiter, 1991). Three possible explanations have been  
40 proposed: 1) spawning prior to the full moon reduces the predation on the vulnerable  
41 brood by nocturnal predators (bagrid catfish) that are not active during the full moon  
42 (Rossiter, 1991), 2) spawning prior to the full moon enhances the effectiveness of  
43 nocturnal parental guarding of the vulnerable brood under the maximum lunar  
44 illumination during the full moon (Nakai et al., 1990; Rossiter, 1991), and 3) dispersal  
45 of young during the fourth quarter of the lunar cycle and the new moon improves the  
46 survival of young dispersing under the cover of darkness (Nakai et al., 1990). If any of  
47 these explanations is true, the degree of lunar synchronization of spawning will vary  
48 according to the strategies for decreasing predation on the vulnerable brood and/or  
49 dispersing young. Comparison between more closely related populations is better to test  
50 this hypothesis because it will minimize the effect of phylogeny.

51 The algae-feeding Tanganyikan cichlid, *Telmatochromis temporalis* Boulenger,

52 is an iteroparous substrate brooder. Like other substrate-brooding species that are  
53 known to exhibit lunar synchronized spawning, this fish also belongs to the tribe  
54 Lamprologini (Takahashi, 2003). *T. temporalis* is dimorphic for body size. The two  
55 morphs dwell in different habitats, lay eggs and guard the brood in different types of  
56 nest, and hide in different types of shelter, respectively (Takahashi, 2004; Takahashi et  
57 al., 2009). The normal morph possesses a moderate-sized body for a Tanganyikan rock-  
58 dwelling cichlid [88 mm in standard length at maximum size ( $SL_{max}$ ) in males, 62 mm  
59  $SL_{max}$  in females] and is one of the most common fish on rocky shorelines. This morph  
60 uses burrows under stones as spawning nests and shelters (Mboko & Kohda, 1999;  
61 Katoh et al., 2005). The dwarf morph is about half of the normal morph in body size (45  
62 mm  $SL_{max}$  in males, 29 mm  $SL_{max}$  in females) and invariably inhabits shell beds, in  
63 which the lake bottom is covered by a high density of empty snail shells of the  
64 gastropod *Neothauma tanganyicense* Smith (Takahashi et al., 2009: fig. 1d). This morph  
65 uses the empty shells as spawning nests and shelters. A population genetic study showed  
66 that the normal and dwarf morphs from Wonzye (08°43'31" S; 31°07'55" E; near  
67 Mpulungu, Zambia, at the southern end of the lake) were closely related but isolated  
68 from each other, although their geographical distributions partly overlap (Takahashi et  
69 al., 2009).

70 In the present study, I observed the periodic changes of ovary development in  
71 the normal and dwarf morphs from Wonzye, and examined whether the ovary  
72 development was synchronized with the lunar cycle. Based on my findings, I discuss the  
73 relationship between the degree of lunar synchronization of ovary development and  
74 predator avoidance strategies.

75

76

77 **Materials and Methods**

78

79 Sampling of fish

80

81 Using SCUBA diving, 6 to 11 females of the normal morph were collected every 3 to 5  
82 days between 27 September and 2 December of 2005 on rocky shorelines at 1.0 to 4.9  
83 m depth ( $N = 173$ ), and 5 to 12 females of the dwarf morph were collected every 3 or 4  
84 days between 29 September and 1 December of 2005 on shell beds at 9.5 to 10.3 m  
85 depth ( $N = 174$ ). Fish were transported to the laboratory at Mpulungu and killed in a  
86 solution of anesthesia FA 100 (Takeda Pharmaceutical Co. Ltd.) within 6 hours after  
87 collection. The ovaries were extracted from all females. The bodies and ovaries were  
88 dabbed on tissue paper to remove excess moisture before weighing, and were weighed  
89 to the nearest 1 mg. When the ovary was lighter than the minimum readable weight of  
90 the electronic balance (1 mg), the weight was taken to be 0 mg. However, zero values  
91 cannot be subjected to log-transformation. To avoid this problem, I added 1 mg to all  
92 ovary weights. The gonado-somatic index was calculated as  $I_G = 100 W_O W_B^{-1}$  (%),  
93 where  $W_B$  is body weight (mg), and  $W_O$  is ovary weight + 1 (mg). Note that  $I_G$  is not a  
94 useful descriptor of gonad investment in some organisms (Tomkins and Simmons,  
95 2002). However, this index was used in the present study, because the normal and dwarf  
96 morphs showed isometric relationships between  $W_B$  and  $W_O$  (see below in Results).

97

98 Test of lunar synchronization

99

100  $I_G$  was approximated to a cosine curve:

101

$$102 \quad f(T_i) = a \cos[2\pi (T_i - x) / l] + y$$

$$103 \quad [f(T_i) \geq 0, 0 \leq x < l],$$

104

105 where  $T_i$  is the number of days from 27 September (the first day of sampling) to the day  
106 that individual  $i$  was collected,  $a$ ,  $x$  and  $l$  are amplitude, phase and length of the cosine  
107 curve, respectively, and  $y$  is a corrected average of  $I_G$ . Appropriate values for parameters  
108 were searched by the method of least squares in three models: full model (four  
109 parameters:  $a$ ,  $x$ ,  $l$  and  $y$ ), lunar-cyclic model with  $l = 29.5$  (three parameters:  $a$ ,  $x$  and  $y$ )  
110 and non-cyclic model with  $a = 0$  (one parameter:  $y$ ). The  $F$ -test was used to compare  
111 these three models for each morph.

112

113

## 114 **Results**

115

116 Body weight and ovary weight

117

118 The relationship between  $W_B$  and  $W_O$  is shown in Fig. 1. In the normal morph, all small  
119 females lighter than 1000 mg possessed light ovaries. These small females were  
120 considered to be immature and were excluded from the following analyses. Some large  
121 females heavier than 1000 mg also had light ovaries. However, these females were  
122 considered to be mature females having undeveloped ovaries, for example, females just  
123 after spawning, and were not excluded from the following analyses. In the dwarf morph,

124 all females were likely mature, although their  $W_B$  was much lighter than that of the  
125 mature females of the normal morph. The average  $W_B$  of the mature females was 2050  
126 mg ( $N = 160$ ) in the normal morph and 259 mg ( $N = 174$ ) in the dwarf morph.

127 Tomkins and Simons (2002) pointed out that  $I_G$  was not a useful descriptor of  
128 gonad investment in organisms that showed an allometric relationship between the  
129 gonad and somatic weights. In the present study, however, the isometric function  
130 provided a significantly better fit than the allometric function for explaining the  
131 relationship between  $W_B$  and  $W_O$  in each morph (Fig. 1) (test of difference between  
132 allometric and isometric functions:  $F = 0.483$ ,  $df = 1$  and  $158$ ,  $P = 0.488$  in the normal  
133 morph;  $F = 0.034$ ,  $df = 1$  and  $172$ ,  $P = 0.854$  in the dwarf morph). This result means that  
134  $I_G$  is not significantly affected by  $W_B$  after maturity; therefore,  $I_G$  was used as the  
135 descriptor of gonad investment in the present study. In the normal morph, the variance  
136 of  $\log(W_O)$  seemed to increase with  $\log(W_B)$  (Fig. 1), but this tendency was not  
137 significant [the correlation coefficient between  $\log(W_B)$  and squared deviates was  $r =$   
138  $0.071$ ,  $P = 0.370$ ].

139

140 Lunar synchronization of ovary development

141

142 In mature females of the normal morph,  $I_G$  showed a marginally significant difference  
143 among sampling days (Kruskal-Wallis:  $\chi^2 = 33.3$ ,  $df = 19$ ,  $P = 0.022$ ) and a significant  
144 fit to the lunar-cyclic model (Fig. 2A) [full model versus lunar-cyclic model:  $F = 0.819$ ,  
145  $df = 1$  and  $156$ ,  $P = 0.367$ ; lunar-cyclic model versus non-cyclic model:  $F = 6.32$ ,  $df = 2$   
146 and  $157$ ,  $P = 0.002$ ; this result was also supported by analyses using  $\log(I_G)$ ].  $I_G$  peaked  
147 prior to the full moon (13 days). In the dwarf morph, some females collected during the



148 second quarter of the lunar cycle (7–15 days) possessed higher  $I_G$  than females collected  
149 during the fourth quarter (22–0 days), like the normal morph (Fig. 2B). However, the  
150 difference of  $I_G$  among sampling days was not significant (Kruskal-Wallis:  $\chi^2 = 15.6$ , df  
151 = 18,  $P = 0.618$ ) and  $I_G$  did not significantly fit the full and lunar-cyclic models [full  
152 model versus lunar-cyclic model:  $F = 1.81$ , df = 1 and 170,  $P = 0.180$ ; lunar-cyclic  
153 model versus non-cyclic model:  $F = 2.38$ , df = 2 and 171,  $P = 0.096$ ; this result was also  
154 supported by analyses using  $\log(I_G)$ ]. This result suggests that the ovary development of  
155 the dwarf morph was not synchronized with the lunar cycle, or that the degree of lunar  
156 synchronization of ovary development was lower than the detection level of the present  
157 test.

158

159

## 160 **Discussion**

161

162 The present study revealed that 1) the ovary development of the normal morph was  
163 significantly synchronized with the lunar cycle, and 2) the ovary development of the  
164 dwarf morph was not significantly synchronized with the lunar cycle ( $P = 0.096$ ), or at  
165 least the cycle was less pronounced compared to the normal morph. The ovary  
166 development of the normal morph peaked during the second quarter of the lunar cycle,  
167 suggesting high activity of reproduction during this period, in accord with the findings  
168 for nine other substrate-brooding species of Tanganyikan cichlids (Nakai et al., 1990;  
169 Rossiter, 1991). Three possible explanations have been proposed for the lunar cyclic  
170 spawning of the Tanganyikan substrate brooders, and two of these explanations are  
171 applicable to the normal morph.

172           The first applicable explanation is synchronization of the vulnerable stages of  
173 the brood (egg and yolk-sac stages) with a period when nocturnal predators are not  
174 active (Rossiter, 1991). The bagrid catfish is one of the main predators in the lake (Fryer  
175 and Iles, 1972). Small bagrid catfishes (*Phyllonemus* spp. and young of *Chrysichthys*  
176 spp.) are ubiquitous in rocky shorelines, which are the main habitat of the normal morph.  
177 Predation by these catfishes will critically affect the survival of the broods of the normal  
178 morph. Young of the normal morph hatch out about 3 days after spawning (Kato et al.,  
179 2005), and therefore the vulnerable stages of the brood occur around the full moon,  
180 which accords with a period when bagrid catfishes are not active (McKay, 1983;  
181 Rossiter, 1991).

182           The second applicable explanation is synchronization of the vulnerable stages  
183 of the brood with a period when the nocturnal parental guarding is effective (Nakai et al.,  
184 1990; Rossiter, 1991). The parents of the normal morph attack and repel the brood  
185 predators when they approach (Mboko and Kohda, 1999). The ambient light during the  
186 full moon may assist the parents in visual detection at night, and in repelling  
187 approaching nocturnal brood predators, for example, spiny eels (Ochi et al., 1999).

188           The other proposed explanation for lunar cyclic spawning, namely, that  
189 spawning prior to the full moon improves the survival of young dispersing under the  
190 cover of darkness (Nakai et al., 1990), is unlikely in the normal morph. The young of  
191 some substrate-brooding species leave the spawning nest immediately after they  
192 complete yolk absorption. The period of yolk absorption is about 2 weeks (Kuwamura,  
193 1997), resulting in the dispersal of the young during dark nights during the fourth  
194 quarter and new moon (Nakai et al., 1990). However, the young of the normal morph  
195 remain in the spawning nest for more than 1 month after yolk absorption (Mboko and

196 Kohda, 1999). The timing of dispersal of the free-swimming young of the normal  
197 morph may be decided by some environmental cue.

198           As discussed above, the lunar cyclic spawning of the normal morph may  
199 improve the survival of the brood by synchronizing the vulnerable stages of the brood  
200 with the period when the nocturnal brood predators (bagrid catfish) are not active and  
201 the nocturnal parental guarding is effective. On the other hand, the dwarf morph did not  
202 show clear lunar synchronization of ovary development. The dwarf morph uses empty  
203 snail shells as spawning nests in shell beds. The eggs and yolk-sac larvae were always  
204 found with a female close to the end of the hole within a shell ( $N = 12$ , observed in  
205 November of 2005 and October to November of 2007 by the author), suggesting that  
206 females spawn and care for the brood there. The end of the hole is very small and is  
207 invisible from the outside. The predators would probably have trouble finding and  
208 accessing the brood. Spawning nests within empty shells, therefore, will be very  
209 effective for preventing predation on the vulnerable brood of the dwarf morph, and  
210 therefore lunar cyclic spawning may be dispensable for predator avoidance. Release  
211 from the limitation of the spawning timing may reduce the degree of lunar  
212 synchronization of the reproduction of the dwarf morph.

213           Different degrees of lunar synchronization in spawning have been reported  
214 among eight species of Tanganyikan substrate-brooding cichlids, and these variations  
215 were suggested to be related to the spawning sites (Nakai et al., 1990). The present  
216 statistical test of the lunar synchronization using a cosine-curve function supports this  
217 suggestion. However, this explanation for the different degrees of lunar synchronization  
218 is based on circumstantial evidence, and other explanations remain possible. In fact,  
219 females of *Lamprologus callipterus* and *Altolamprologus compressiceps* use shells as

220 spawning sites like the dwarf morph of *T. temporalis*, but show lunar spawning (Nakai  
221 et al., 1990). Other factors, such as spawning position within the shells, may also play a  
222 role. The present study was conducted from the end of dry season to the beginning of  
223 rainy season covering two lunar cycles. More analyses of other life-history traits and  
224 replicates in another season will be needed to reveal the mechanism and the adaptive  
225 significance of the lunar synchronization.

226 Lunar cyclic spawning is a well-documented feature in marine organisms  
227 (Leatherland et al., 1992; Hernández-León, 2008). More detailed analyses of the normal  
228 and dwarf morphs of *T. temporalis* will help to clarify the mechanism and evolution of  
229 this phenomenon.

230

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239

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278 **Figure legends**

279

280 **Fig. 1** Relationship between the ovary weight and body weight in the normal (solid  
281 circles;  $N = 173$ ) and dwarf (open circles;  $N = 174$ ) morphs. Regression lines and  
282 functions in the graph are of the mature individuals of the normal ( $N = 160$ ) and dwarf  
283 ( $N = 174$ ) morphs (see text)

284

285 **Fig. 2** Periodic change of ovary development during the study period. The normal  
286 morph showed a significant lunar cyclic pattern (**A**;  $N = 160$ ), whereas non-significant  
287 cyclic pattern was seen in the dwarf morph (**B**;  $N = 174$ ) (see text). A line in the graph  
288 and a function above the graph are of the selected model in each morph

289





