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1 **Different degrees of lunar synchronization of ovary development between two**
2 **morphs of a Tanganyikan cichlid fish**

3

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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



