

トビヌメリの秋産卵期の開始・終了に対する水温および日長の影響

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著者	古川, 清 会田, 勝美 朱, 勇
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Effects of Water Temperature and Photoperiod on the Initiation and Termination of the Autumn Spawning Season in Tobinumeri-Dragonet *Repomucenus beniteguri*

Yong Zhu,*¹ Kiyoshi Furukawa,*¹ Katsumi Aida,*¹
and Isao Hanyu*¹

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In order to investigate the factors which initiate the autumn spawning, immature fish were reared under different conditions from August 15 to September 12. Spawning was observed from August 27 in the 12L12D/22-24°C group, and from August 30 in 15L9D/22-24°C group. However, much more eggs were obtained in the 12L12D group than that in the 15L9D group. No mature fish were found in the 15L9D/28-29°C group. These results indicate that the decrease in temperature is the main environmental cue that initiates the autumn spawning, and that short daylength accelerates gonadal maturation.

In order to investigate the factors which terminate the autumn spawning, mature fish were divided into 3 groups; reared under 1) temperature changed group (23°C→19°C→16°C→14°C→11°C; 13L11D), 2) natural temperature group (13L11D), 3) daylength changed group (13L→11L→9L→15L→11L; 22-24°C) in the autumn spawning season. In the temperature changed group, daily spawning continued until the temperature decreased to 14°C. In natural temperature group, daily spawning was observed above 13°C. In the daylength changed group, daily spawning was observed under 13L11D, 11L13D and 9L15D. Spawning, however, stopped under 15L9D, and resumed under 11L13D. The number of spawned eggs/fish increased with the decrease in daylength. These results indicate that the low temperature in early winter is the terminating cue of the autumn spawning season.

It is generally accepted that annual reproductive cycles in teleosts are regulated by the annual fluctuations of environmental factors, such as daylength and water temperature.¹⁾ It is emphasized that the effects of daylength and water temperature on the gonadal maturation are different in each seasonal spawner.²⁾ In spring spawners, such as goldfish *Carassius auratus* and akahiretabira-bitterling *Acheilognathus tabira*, increasing water temperature in spring initiates gonadal maturation, that in summer however, terminates gonadal maturation.^{3,4)} In spring-summer spawners, such as tairikubaratanago-bitterling *Rhodeus ocellatus ocellatus* and medaka *Oryzias latipes*, increasing water temperature in the spring initiates gonadal maturation; however, shortening daylength in autumn terminates gonadal maturation.⁵⁻⁷⁾ In summer spawners, such as kisu *Sillago japonica**² and urohaze-goby *Glossogobius olivaceus*,⁸⁾ increasing water tem-

perature in summer initiates gonadal maturation, and decreasing water temperature in autumn terminates it. In autumn spawners, such as zenitanago-bitterling *Pseudoperilampus typus* and kanehira-bitterling *Acheilognathus rhombea*, shortening daylength in autumn initiates gonadal maturation, however decreasing water temperature in winter terminates gonadal maturation.^{9,10)} In winter spawner, such as agohaze-goby *Chasmichthys dolichognathus*, decreasing water temperature in winter initiates gonadal maturation. However, increasing water temperature in spring terminates it.⁸⁾

Tobinumeri-dragonet has two spawning seasons, spring and autumn, within one year.^{11,12)} It is an interesting phenomenon, since seasonal breeders usually have a single breeding season in a year. It seems to be valuable to know how these two spawning seasons are formed. Therefore, the effects of water temperature and daylength on

*¹ Laboratory of Fish Physiology, Department of Fisheries, Faculty of Agriculture, University of Tokyo, Tokyo 113, Japan (朱 勇, 古川 清, 会田勝美, 羽生 功: 東京大学農学部水産学科魚類生理学研究室).

*² Furukawa *et al.*, unpublished data.

the initiation and termination of the autumn spawning season in the tobinumeri-dragonet were investigated in this study.

Materials and Methods

Experimental fish were obtained by angling from Lake Hamana, and transferred to the Fisheries Laboratory of the University of Tokyo, Maisaka, Shizuoka Prefecture. They were kept under natural conditions in an outdoor concrete pond (8×2×0.85 m) supplied with seawater and fed eel commercial paste at about 5% of body weight every day.

In order to elucidate the initiation cue of autumn spawning, experiment 1 was started prior to the autumn spawning season. Immature fish which were caught in spring and summer were randomly divided into four groups. The fish (25 females and 25 males for each) was transferred to experimental tanks (2×1×0.8 m) on August 15

and reared from August 22 under 1) 15L9D/28–29°C, 2) 15L9D/22–24°C, or 3) 12L12D/22–24°C till September 12. Another group was reared in a outdoor tank (8×2 m) under conditions of natural daylength and natural temperature (NL/NT). Spawning eggs were collected and the total egg volume was measured during the experimental period except NL/NT group. Ten females and 10 males were sampled from each group on September 3 and September 12. After anesthetizing the fish with 0.01% tricaine methanesulfonate solution, their body weight and gonad weight were measured. Gonadosomatic index (GSI: gonad weight×100/body weight) was calculated. The gonads were fixed with Bouin's solution for histological observation.

In order to understand the termination cue of autumn spawning, experiment 2 was undertaken in the autumn spawning season. Fish which were caught in spring and summer matured in autumn. They were randomly divided into

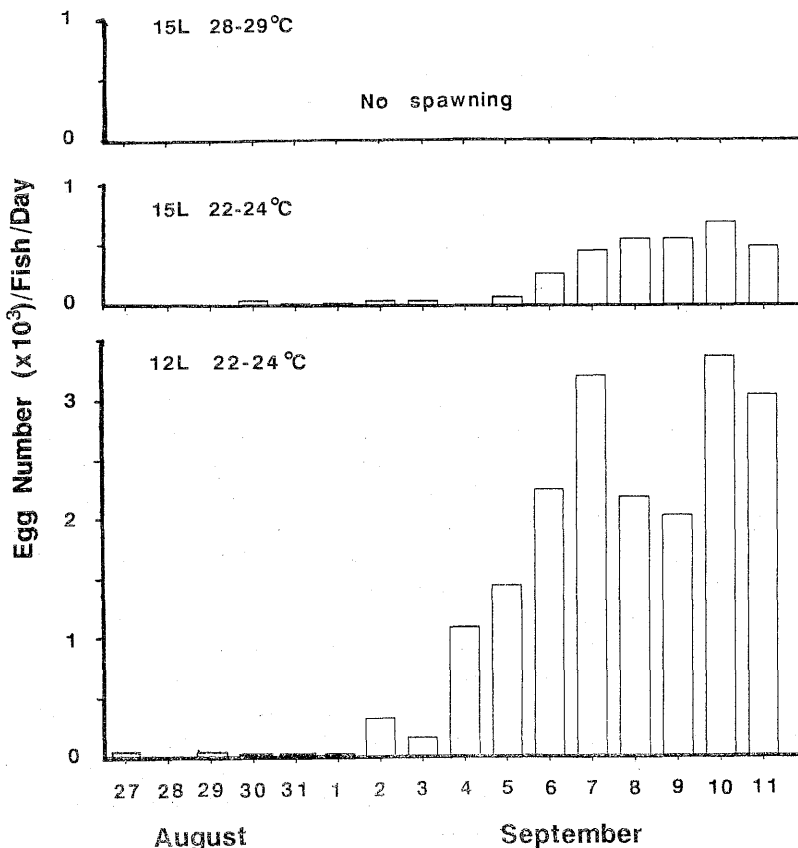


Fig. 1. Effects of daylength and water temperature in the initiation of autumn spawning. Each column indicates the number of eggs spawned/female/day. The number of eggs was not recorded in the NL/NT group.

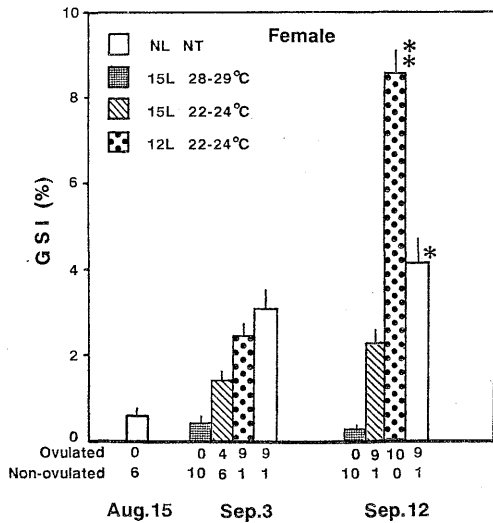


Fig. 2. Effects of daylength and water temperature on the initiation of ovarian maturation in autumn. Columns and bars indicate the mean \pm SE. The number of fish ovulated and non-ovulated are indicated under the column. NT, natural temperature. NL, natural daylength. Statistical analysis was undertaken using Kruskal-Wallis and Dunn's methods. * and ** indicate significant differences at $p < 0.05$ and $p < 0.01$, respectively, when compared to the initial GSI on August 15.

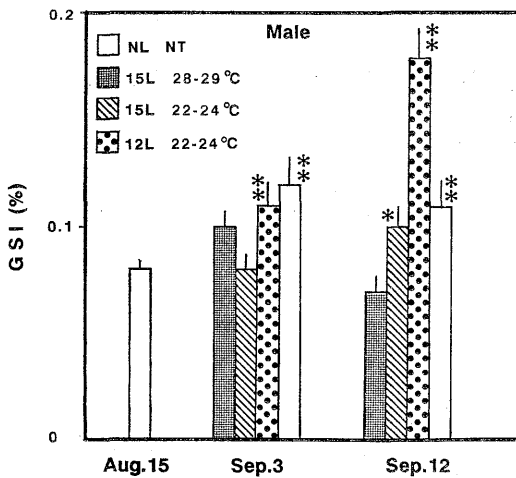


Fig. 3. Effects of daylength and water temperature on the initiation of testicular maturation in autumn. Columns and bars indicate the mean \pm SE. NT, natural temperature. NL, natural daylength. Statistical analysis was undertaken using the multiple range test of Duncan. * and ** indicate significant differences at $p < 0.05$ and $p < 0.01$, respectively, when compared to the initial GSI on August 15.

three groups, 1) temperature changed group (25 females and 22 males: Fig. 4), 2) natural temperature group (25 females and 22 males: Fig. 5) and 3) daylength changed group (25 females and 25 males: Fig. 6). They were transferred into each concrete tank ($3 \times 1.5 \times 0.9$ m). During the experimental period, the photoperiod was maintained at 13L11D in the temperature changed and natural temperature groups, and water temperature was maintained at 20–22°C in the daylength changed group. In the temperature changed group, water temperature was maintained above 23°C from September 21 to October 2, decreased to 19°C on October 3, to 16°C on October 10, to 14°C on October 23 and to 11°C on November 10, and then increased to 20°C on December 7. In the daylength changed group, the daylength was maintained 13L from August 27 to November 14, shortened to 11L on November 15, to 9L on November 23. The daylength was increased to 15L on October 8, and then shortened to 11L on October 23. The spawning time was monitored and the total egg

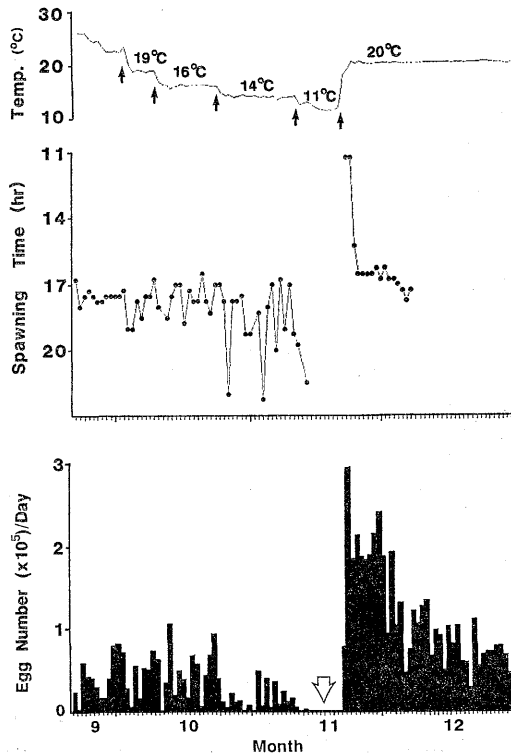


Fig. 4. Effects of temperature (Temp.) on the termination of the autumn spawning under 13L11D. Large arrow indicates the period when the fish were not spawning. Small arrows indicate temperature changes.

volume was measured during the experimental period. The number of eggs spawned was calculated from the total egg volume (4146 eggs/ml).

Results

Experiment 1

First spawning was observed on August 27 in the 12L12D/22–24°C group, and on August 30 in the 15L9D/22–24°C group. Thereafter, spawning occurred every day except August 28 (12L12D/22–24°C group), and September 4 (15L9D/22–24°C group). No spawning was observed in the 15L9D/28–29°C group. The number of eggs spawned/female was approximately three times higher in the 12L12D/22–24°C group than that in the 15L9D/22–24°C group (Fig. 1). The GSI of female exposed to 15L9D/28–29°C showed a small decrease, while the GSI of female exposed to 15L9D/22–24°C, 12L12D/22–24°C or NL/NT showed a rapid increase, and reached from 0.6% to 1.4%, 2.5%, 3.1% on September 3, and 2.3%, 8.7%, 4.2% on September 12, respectively (Fig. 2). The number of ovulated females were 0, 4, 9, 9 on September 3, and 0, 9, 10, 9 on Sep-

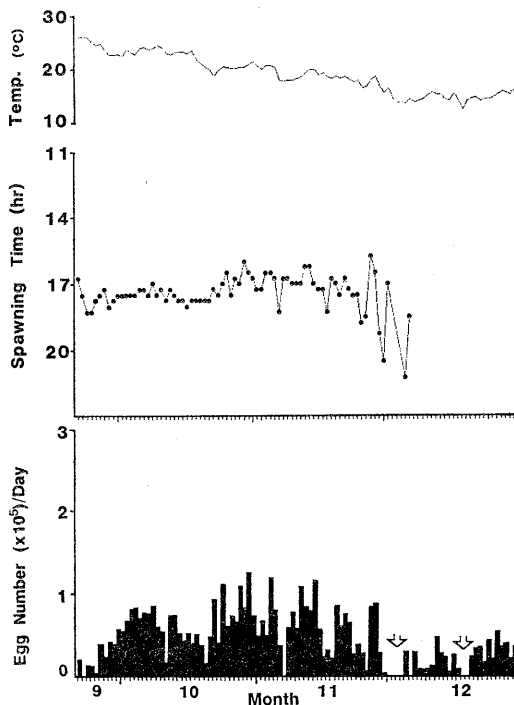


Fig. 5. Effects of natural temperature (Temp.) on the termination of the autumn spawning under 13L11D. Arrows indicate the period when the fish were not spawning.

tember 12 in the 15L9D/28–29°C, 15L9D/22–24°C, 12L12D/22–24°C and NL/NT groups, respectively (Fig. 2). The oocytes were at the peri-nucleolus stage in the 15L9D/28–29°C group. Some atertic oocytes were observed in the 15L9D/22–24°C group, whereas the oocytes developed normally in the 12L12D/22–24°C and NL/NT groups.

GSI in the male groups unchanged on September 3 (Fig. 3). The GSI value was highest in 12L12D/22–24°C group on September 12. The GSI value in the 15L9D/22–24°C group was lower than that in the NL/NT group on September 12. Almost all fish survived until the end of the experiment.

Experiment 2

In the temperature changed group, daily spawning continued until the temperature decreased to 16°C. The egg number decreased at 14°C and spawning stopped at 11°C. Thereafter, the temperature was raised to 20°C. The fish resumed spawning soon and spawned a larger number of eggs (Fig. 4). In the natural temperature group, daily spawning was observed above 13°C, and stopped below 12°C. Spawning, however, stopped for 3 days when the temperature decreased

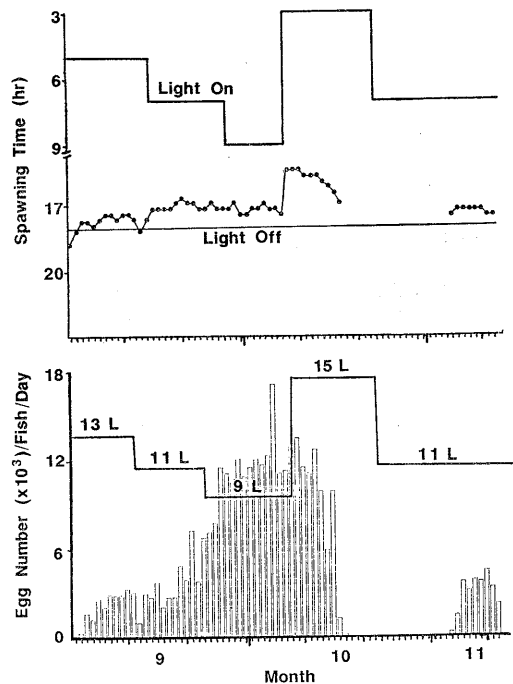


Fig. 6. Effects of photoperiod on the termination of the autumn spawning under 20–22°C.

rapidly from 16°C to 13°C (Fig. 5). In the daylength changed group, spawning occurred every day under the conditions of 13L, 11L, and 9L. The egg number increased with the decrease in daylength. Spawning stopped 10 days after the increase in daylength from 9L to 15L. Spawning resumed two weeks after the decrease in the daylength from 15L to 11L (Fig. 6).

Although the spawning time fluctuated largely just after temperature was changed in turn (23°C→19°C→16°C→14°C) in the temperature changed group, the spawning time returned to the former level soon. The spawning time was almost constant in the natural temperature group. In the daylength changed group, the spawning time showed small changes when the time of lights-on was changed (0500 h (13L)→0700 h (11L)→0900 h (9L), the time of lights-off was constant at 1800 h). Although the spawning time advanced 2 hours when the time of lights-on was changed from 0900 h to 0300 h (15L), it returned gradually to the former level. Thereafter, spawning stopped under 15L. Spawning resumed under the daylength of 11L (photophase: 0700–1800 h). The spawning time was similar to the former level. Almost all fish survived until the end of experiment.

Discussion

Experiment 1 has revealed that the ovary matures under 22–24°C regardless of photoperiod. The number of eggs spawned was much larger in the 12L12D group than in the 15L9D group. However, gonadal maturation was inhibited in the fish exposed to 15L9D/28–29°C. The results were consistent with the results obtained in previous experiments,^{11,12} in that the gonad recovered rapidly in September, when both water temperature and daylength decreased to appropriate levels. The higher temperatures in summer are probably a major factor inhibiting gonadal maturation.

The results of the second experiment indicate that low water temperature and long daylength inhibit spawning in autumn, whereas shortening daylength accelerates vitellogenesis and spawning. Although long daylength terminated spawning, it is not a termination factor of the autumn spawning season, because natural daylength gradually decreases in autumn. Therefore, it is clear that the low water temperature in early winter is the terminating factor of the autumn spawning season.

The initiating and terminating factors of the reproductive season have been studied mostly in freshwater teleosts. The initiating factors have been found to be either temperature or photoperiod or a combination of both. For example, the rising temperature has been demonstrated to be the initiating factor in akahiretabira-bitterling,⁴⁾ tairikubaratanago-bitterling,⁶⁾ *Gasterosteus aculeatus*,¹³⁾ and medaka.⁷⁾ Both warm temperature and long photoperiod, however, are required in *Notemigonus crysoleucas*.¹⁴⁾ On the other hand, decreasing temperature in autumn and winter initiates gonadal recrudescence and maturation in green sunfish *Lepomis cyanellus*.¹⁵⁾ Gonadal maturation in zenitanago-bitterling and kanehira-bitterling is initiated by the shortening daylength in autumn.^{9,10)} In salmonids which spawn in autumn and early winter, gonadal recrudescence is often favored by the short and decreasing photoperiod.¹⁾

In contrast, the terminating factor of the spawning season for the medaka and tairikubaratanago-bitterling is the decreasing daylength in autumn.^{6,7,16–19)} Whereas in summer, high temperature induces gonadal regression in spring spawning species, such as honmoroko *Gnathopogon caeruleus*,^{19,20)} akahiretabira-bitterling,⁴⁾ green sunfish *Lepomis cyanellus*,¹⁵⁾ and longjaw goby *Gillichthys mirabilis*.²¹⁾ Low temperature in late autumn terminates the autumn spawning in the fish such as zenitanago-bitterling⁹⁾ and kanehira-bitterling.¹⁰⁾ The existence of endogenous factors which induce gonadal regression has also been suggested for several teleosts.^{1,7)}

In this investigation, it has been ascertained that the tobinumeri-dragonet belongs to short day spawners. However, about a half of the fish which belongs to larger fish group spawns in spring. The reason why these fish can spawn in spring is still unknown. Photoperiodism of this species may disappear in spring as in spring spawning cyprinid species, such as akahiretabira- and tairikubaratanago-bitterlings and medaka. Environmental regulation of the spring spawning in the tobinumeri-dragonet should be investigated in future.

In the tobinumeri-dragonet, spawning occurs during 1600 to 2000 h everyday, [suggesting the existence of cues which determine spawning time. The spawning time, however, was not influenced by the levels of water temperature and the time of lights-on. Since the photoperiod is known as a major factor which

determines spawning time in the goldfish, common carp and kisu, further investigation on the effects of photoperiod on the spawning time will be conducted in next studies.

In conclusion, the decreasing water temperature is the main environmental cue which initiates the autumn-spawning, short daylength accelerates the gonadal maturation, and the low water temperature in early winter is the major factor for the termination of autumn-spawning.

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