

Pioneer Life of the Tadpole Shrimps, *Triops* Spp. (Notostraca: Triopsidae)¹

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(Received December 16, 1976)

Tadpole shrimps (*Triops* spp.) are aquatic animals which appear in paddy fields a few days after the flooding and ploughing. Their growth, oviposition, hatching of eggs, and the environmental conditions which stimulate egg hatching were analyzed especially in *T. granarius* and *T. longicaudatus* to test the hypothesis that tadpole shrimps are pioneer animals in a temporary water pool.

Many eggs hatched soon after submergence and developed rapidly to maturity. The shrimps began oviposition on the 10th day after submergence, while still growing in body size, and deposited many eggs in the soil during their short life span. The eggs hatched very heterogeneously and intermittently, and many eggs remained in the dormant state for a long period under constant water temperature. Desiccation of eggs was effective to promote subsequent hatching, and the rate of hatching fluctuated with the length of desiccation period. Total hatching was not achieved, however, even by repeated treatments of desiccation and submergence. Hatching of eggs was sensitive to light. These ecological characteristics are considered to be highly adaptive to an irregularly disturbed aquatic habitat.

INTRODUCTION

Tadpole shrimps, *Triops* spp., are aquatic crustaceans which appear in paddy fields a few days after flooding and ploughing. They control weeds by consuming the seedlings or uprooting them while scratching the soil surface in searching for food and egg-laying sites. Three species of tadpole shrimps distributed in Japan are the European, *Triops cancriformis*, the Asian, *T. granarius*, and the American tadpole shrimp, *T. longicaudatus*. The distribution of *T. cancriformis* is restricted within a narrow area in Sakata City, Yamagata Pref.² *T. granarius* and *T. longicaudatus* are distributed from the Kanto district to northern Kyushu (KATAYAMA, 1973; AKITA, 1976; MATSUNAKA, 1976).

The biology of *T. cancriformis* was analyzed by HEMPEL-ZAWITKOWSKA et al. (1967—1969). That of the other two species is not yet well analyzed although there have been several fragmental reports. Fundamental ecological study of these shrimps is

¹ Contribution from the Entomological Laboratory, College of Agriculture, Kyoto University. No. 453. This study was supported in part by grants from the Japanese Ministries of Education and Agriculture and Forestry.

² This species distributed in Sakata City was previously reported as *T. longicaudatus* by IGARASHI (1970, 1972) and KOKATA (1968).

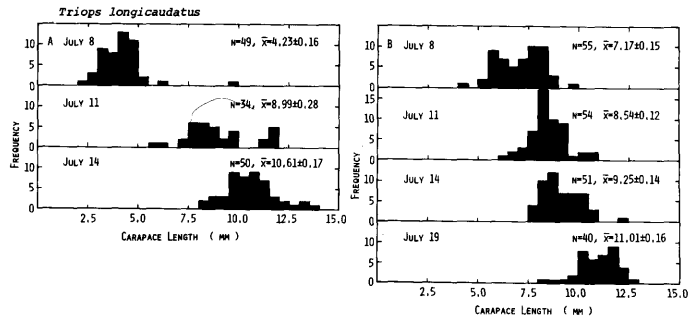


Fig. 1. Growth of tadpole shrimps in paddy fields. The program of cultivation was as follows:

Field	Flooding	Puddling	Transplanting of rice seedlings
A	July 1	July 2	July 3-5
B	June 29	June 30	July 3-5

essential for advancement of the biological control technique using them against weeds in paddy fields (KATAYAMA et al., 1974; MATSUNAKA, 1976; TAKAHASHI, 1977a). I attempted to examine the ecological characters of the shrimps in the laboratory as well as in the field. In this paper their growth, oviposition, hatching of eggs, and the environmental conditions which stimulate egg hatching were analyzed especially in *T. granarius* and *T. longicaudatus*.

BIOLOGY OF TADPOLE SHRIMPS

Growth of Triops in a paddy field and under laboratory conditions

For observation of the growth of the shrimps in a paddy field, samples of *T. longicaudatus* were collected from paddies in the College Farm, Kyoto University, Kyoto, after the flooding and rice transplantation in 1974. The dates of flooding, puddling, transplanting, and shrimp sampling in two paddies, A and B, are shown in Fig. 1. The shrimp samples were immersed in a storage solution (70% alcohol, 10% formalin, and 20% water). The carapace length, i.e., the length from the tip of the head to the end of the central line of the carapace, was measured as an index of growth in body size. The shrimps developed rapidly in both fields as shown in Fig. 1. In field A the average carapace length was 4.2 mm on the 7th day after flooding, growing rapidly to 9.0 mm on the 10th day. In field B, it was 7.2 mm on the 10th day and 8.5 mm on the 13th day. Oviposition began when the carapace length exceeded 7 mm; accordingly, it had probably begun by the 10th day after flooding. However, the speed of development differed between the two fields, probably owing to differences in population density and food conditions. On the other hand, the number of shrimps decreased rapidly and they disappeared from both fields within a month.

In a paddy field there are many factors which may modify the development and survival of the shrimps, such as a rise of water temperature, release of water, attacks by natural enemies, and chemical sprays. Development was therefore observed under controlled conditions. About 1 kg of paddy soil was submerged under about 3-cm depth of water in a 60 × 35 cm² pan, at room temperature of 23°C. The soil was taken

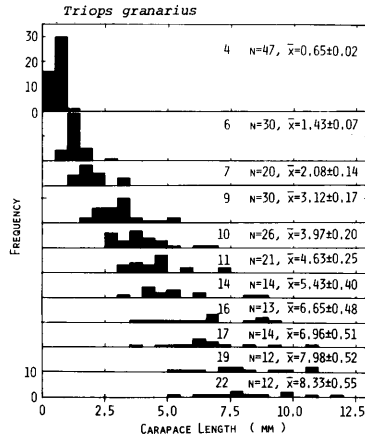


Fig. 2. Growth of carapace length in *T. granarius* at 20.5°C. $\bar{x} \pm S.E.$
The size of water pan was 60 × 35 cm² and the soil was submerged in water to 3-cm depth. Numerals in the figure indicate the days after water submergence.

from a field in Ibaraki City, Osaka Pref., inhabited by *T. granarius*. Water temperature was maintained a little lower at about 21°C during the experiment, owing to the evaporation of water. The room was illuminated by fluorescent lamps with a 16L-8D photoperiod. On the 4th day after submergence the young developed a carapace, and thereafter samples were taken for measurement of body size on the days shown in Fig. 2. The carapace length is easily measured with a binocular microscope after covering the body with a thin polyethylene film in a little water on a glass plate. After measurement the samples were returned to the pan.

The average carapace length grew rapidly in an S-shaped curve as shown in Figs. 2 and 4-A. The variation among individuals became larger with the increase of carapace length. *T. longicaudatus* and *T. cancriformis* reproduce unisexually by hermaphroditism, while *T. granarius* reproduces bisexually (LONGHURST, 1955). In this experiment, however, individuals were not sexed in measuring body size. Eggs appeared in the egg pouches of females when the carapace length exceeded about 7 mm.

The growth in body size of *T. granarius* was also examined by rearing in groups of 10 individuals without sexing in a large water pan or singly in a small water pan under two temperature conditions. The rearing conditions, i.e., water temperature and pan size, were as follows:

C-S: Water temperature was kept constant at about 21°C in a small water pan (26 × 20 = 520 cm²).

V-S: Water temperature was changed in a sine curve from 12 to 30°C, with an average of 21°C, in a small water pan.

C-L: Water temperature was kept constant at about 21°C in a large water pan (116 × 45 = 5220 cm²).

V-L: Water temperature was changed in a sine curve from 12 to 30°C, with an average of 21°C, in a large water pan.

The area of water surface per individual was the same (520 cm²) in all pans at the start of the experiment, but it increased with the death of individuals in the large pans.

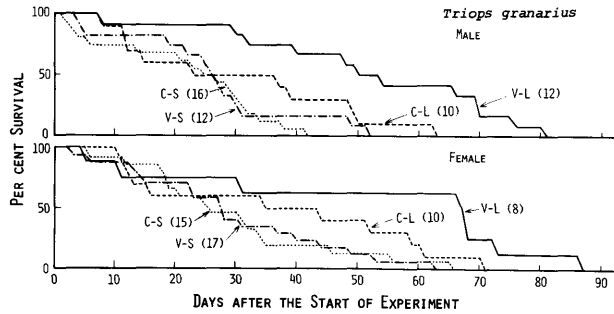


Fig. 3. Survivorship curves under constant or oscillating temperature and in a small or large water pan. The carapace length of individuals at the start of the experiment was about 5 mm. The number of individuals used is shown in parentheses. Temperature conditions in water were constant at 21°C (C) or oscillated between 12–30°C (V). Sizes of water pan were small (S, 26×20 cm²) or large (L, 116×45 cm²).

In these pans some fine soil (<60 mesh) was placed and the water depth was kept at about 2–3 cm. Fish powder and noodles were occasionally supplied as food. The room was illuminated with a 14L–10D photoperiod; under the oscillating temperature condition, the water temperature reached a maximum after 7 hours of illumination. At the start of the experiment individuals of uniform carapace length of about 5 mm were introduced into the water pans. During the observation they were sexed.

The survivorship curves of the shrimps under these conditions are shown in Fig. 3. In C-S and V-S pans, 50% mortality was observed after about 4 weeks in both sexes. On the other hand, in the larger pans (C-L and V-L) the longevity increased and also differed more markedly between the temperature conditions. Survival was better under oscillating temperature (two replicates of 10 unsexed individuals) than under constant temperature (two replicates of 10 unsexed individuals). The difference of survival between water pans of different sizes may be due to the difference in available area and of capacity for their habitat choice given the uneven distribution of food within a pan. In these experiments the longest survival was over 90 days from hatching.

The growth curve of the carapace length is shown in Figs. 4-B and 5. The curves are similar between the different temperature and rearing conditions (group or isolation). Steady growth continued, with frequent ecdyses, until death. The largest individual observed in C-L pan also grew steadily as shown by the points connected with a dotted line in Fig. 4-B.

Oviposition with aging in T. longicaudatus

Metanauplii of *T. longicaudatus* hatched under laboratory conditions were reared at a water temperature of 21–22°C in a water pan (163×81.5 cm²) with some fine soil. Fish powder and dried noodles were supplied as food. On the 10th day there were 43 individuals in the pan, and a few carried some eggs in their egg pouches. A sample of 10 individuals was drawn from the pan; their average carapace length was 6.7 mm. They were kept singly in vials for 24 hours for oviposition. The vials, 11 cm in diameter and 7 cm in depth, contained about 2.5-cm depth of fine soil sieved by a 60-mesh net and about 3-cm depth of water. The eggs deposited by any individual

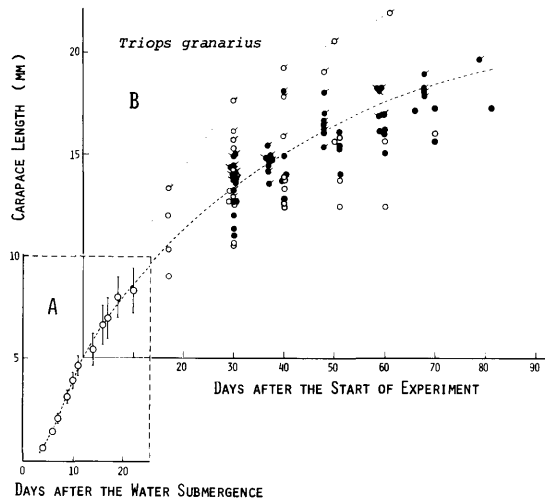


Fig. 4. Growth of carapace length in *T. granarius* under constant and oscillating temperatures in a large pan.

A: The results shown in Fig. 2 are redrawn with the 95% fiducial interval of the average which is indicated by the vertical bars.

B: The carapace length of individuals used at the start of the experiment was about 5 mm. Males (♂), females (♀).

Water temperature was constant at 21°C (○) or oscillated between 12–30°C (●). Size of water pan was 116×45 cm² and water depth was 2–3 cm.

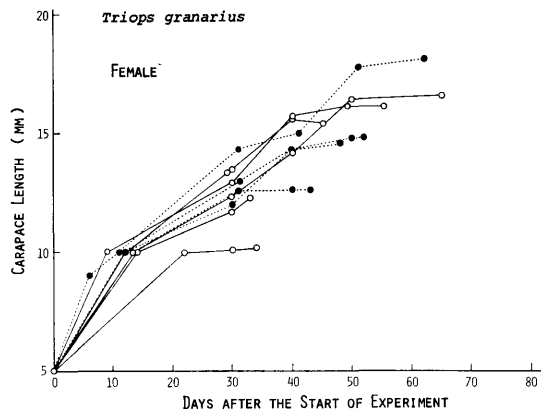


Fig. 5. Growth of carapace length under constant or oscillating temperature in a small pan. The carapace length of individuals used at the start of the experiment was about 5 mm. Water temperature was constant at 21°C (○) or oscillated between 12–30°C (●). Size of water pan was 26×20 cm² and water depth was 2–3 cm.

which survived for 24 hours were sifted out from the soil by a 48-mesh net in running water, and counted. The sampling was repeated thereafter to observe the changes in daily oviposition. The changes in the number of shrimps ($1x$ -curve), in the carapace

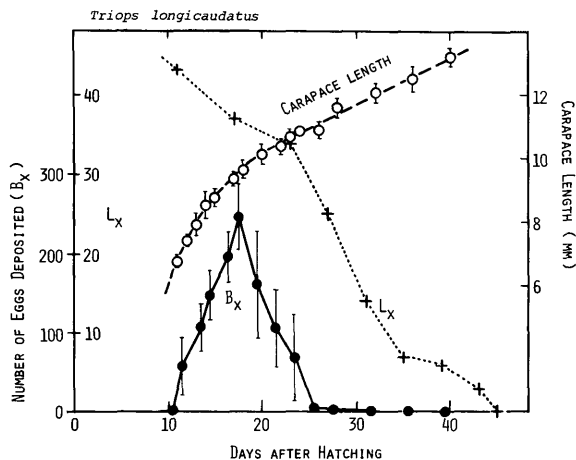


Fig. 6. The survivorship curve (L_x), the fecundity curve (B_x), and the growth of carapace length in *T. longicaudatus* reared at the constant water temperature of 21-22°C. The vertical bar shows the 95% fiducial interval of the average.

length, and in the number of eggs deposited per individual within 24 hours (b_x -curve) are shown in Fig. 6.

The carapace length increased steadily with the same trend as shown in Fig. 4. The number of eggs increased rapidly with increase in carapace length until the 18th day after hatching, but then decreased steeply to nearly zero on the 28th day. After the 30th day no eggs were produced even though there were many surviving individuals and their carapace length continued to increase. This trend of the b_x -curve was also observed under field conditions and oviposition was found to cease after about 20 days (TAKAHASHI, unpublished). The eggs deposited under laboratory conditions seemed a little feeble but were viable. The total number of eggs deposited during a life span is estimated at about 1850. The maximum number of eggs deposited within 24 hours was 246, when the average carapace length was 9.7 mm, but it was 430 in the individuals collected from the field, with a carapace length of 13.2 mm. Accordingly, an individual produces several thousands of eggs in one generation. Some artificial measures employed in the field to lengthen the life span of the shrimps may be effective for weed control, but egg production by the old shrimps cannot be expected.

Duration of egg stage after oviposition, under constant water temperature

The hatching of eggs was observed from the time of their deposition, under constant water temperature. Some individuals of *T. granarius* collected at Nishinomiya City, Hyogo Pref., deposited eggs within 24 hours on July 11th and 12th. The eggs were kept in water vials, 12 cm in diameter and 3-4 cm in water depth. The water temperature was controlled at 19°C under photoperiod of 16L-8D. The daily trend of hatching is shown in Fig. 7. Hatching began on the 8th day after oviposition and continued intermittently and with marked fluctuation. On the 112th day in Group A and on the 125th day in Group B, half of the eggs remained unhatched.

Similar trends of egg hatching were also observed in *T. longicaudatus* (TAKAHASHI,

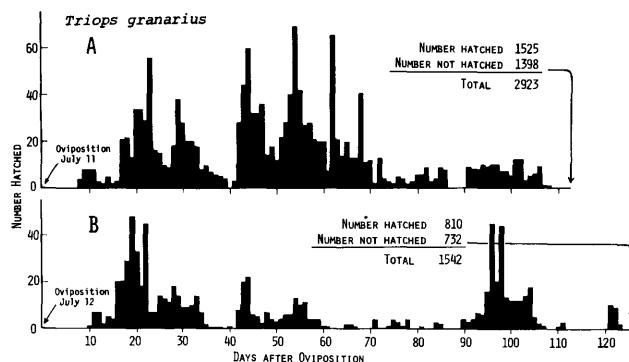


Fig. 7. Sequence of egg hatching at water temperature of 19°C after oviposition.

unpublished). In this experiment it was observed that some changes in water conditions, such as renewal or stirring of the water, may stimulate egg hatching.

Environmental conditions which stimulate egg hatching

The above-mentioned results show that *Triops* eggs hatch not simultaneously but heterogeneously when kept under constant water conditions. Various environmental conditions were examined for possible stimulation of hatching, such as the effects of low temperature, previous desiccation of eggs, and illumination.

The *T. longicaudatus* eggs used in these experiments were collected from paddy fields in the College Farm on August 13th. They were shifted from the soil by 28- and 48-mesh sieves in running water, as the egg diameter was about 0.4 mm, then picked from the sieved debris under a binocular microscope and kept in water at 28°C until October. In the case of *T. granarius* some individuals were collected at Nishinomiya City and their progeny were reared in a plastic-covered green house from September to November. Their eggs were collected from the soil between Nov. 20th and Dec. 6th, and some were kept in water at 28°C. Eggs of *T. cancriformis* were collected in Sakata City and the resultant metanauplii were reared in the laboratory at 25°C to obtain their eggs.

For examination of hatchability after desiccation, the eggs were dried for a certain period in a tragacanth gum solution on paper. The percentage of hatching was examined by submerging the dried eggs in water at 19°C. The eggs were kept beneath a stainless steel wire net in a water vial, 11 cm in diameter and 5 cm in water depth, to prevent their floating. After the low temperature treatment or water submergence the number of hatched metanauplii was counted daily for 4—14 days. The unhatched eggs were then treated with a 10% antiformin solution (sodium hypochlorite solution), to remove the outer egg covering and to confirm their survival (KOKATA, 1968). One hundred eggs were used for each treatment, but they included dead eggs. The sum total of the hatched eggs and the live unhatched eggs was not less than 85. The standard lighting condition was 16L-8D.

a) *Effects of low temperature*

The *T. longicaudatus* eggs kept in water at 28°C were transferred to water at 5°C for various periods from 0 to 62 days and then returned to 19°C. Their hatching was

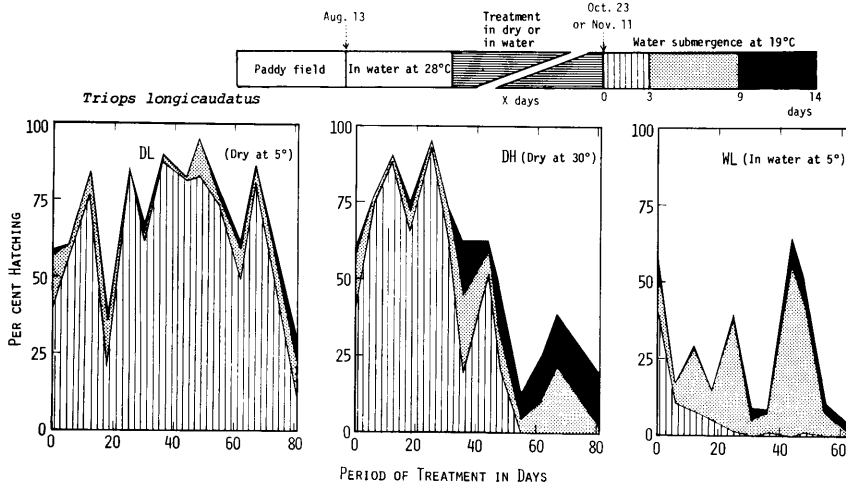


Fig. 8. Effects of durations of desiccation and low temperature on egg hatching in *T. longicaudatus*. The programs of treatment of eggs are shown above.

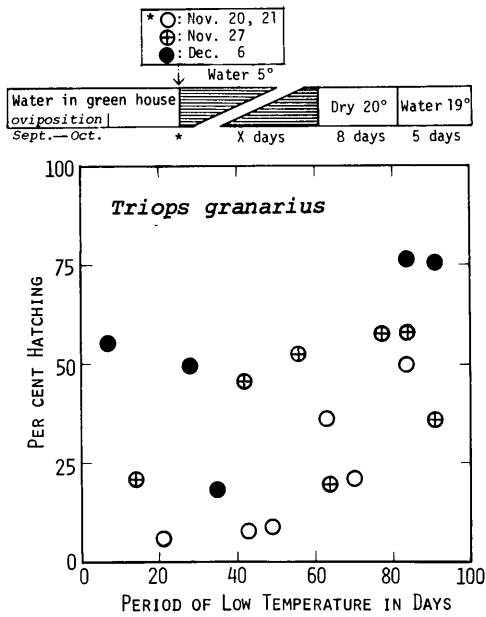


Fig. 9. Effects of duration of low temperature on egg hatching in *T. granarius*. The program of treatment of eggs is shown above.

observed for 2 weeks; the resulting hatching percentage is shown in Fig. 8-WL. The exposure to low temperature was not very effective in raising the percentage: only some of the eggs hatched gradually during about 10 days.

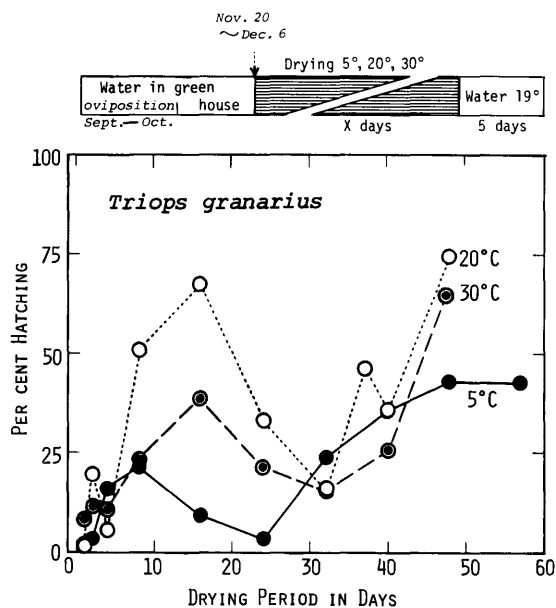


Fig. 10. Effects of duration of desiccation on egg hatching in *T. granarius*. The program of treatment of eggs is shown above.

T. granarius eggs were kept for various periods at 5°C, dried for 8 days at 20°C and then submerged in water of 19°C for 5 days. The result was also inconclusive (Fig. 9) but, roughly speaking, the percentage seemed to increase with the length of the low-temperature treatment.

b) *Effects of desiccation*

T. longicaudatus eggs kept at 28°C were dried for various periods from 0 to 81 days at 5°C or 30°C and 70% R. H. After this desiccation they were submerged in water of 19°C and their hatching was observed for 2 weeks. The hatching percentage varied with the length of drying period as shown in Figs. 8-DL and DH. The percentage increased with the increase of drying period under both temperature conditions, but decreased and became irregular when the drying period exceeded 70 days at 5°C or 30 days at 30°C.

T. granarius eggs were dried at 5, 20 and 30°C for various periods and submerged in water of 19°C. The percentage of hatching was examined for 5 days, with results as shown in Fig. 10. The curves differ with the temperature conditions at the time of desiccation, but the trends of fluctuation are similar. The percentage increased with the increase of drying period to a peak at 10 to 16 days of desiccation, but it decreased to a minimum at 24 days in the 5°C drying or 32 days in the 20 and 30°C dryings, and then increased again with further increase of the drying period.

From these results it is suspected that the eggs of *T. longicaudatus* may show a fluctuating trend of egg hatching similar to that of *T. granarius* when the desiccation period becomes much longer. Egg hatching was examined by IGARASHI (1970) in *T. cancriformis*. In eggs collected from paddies in Sakata City at various times of the year, he observed a similar trend in their hatching ability.

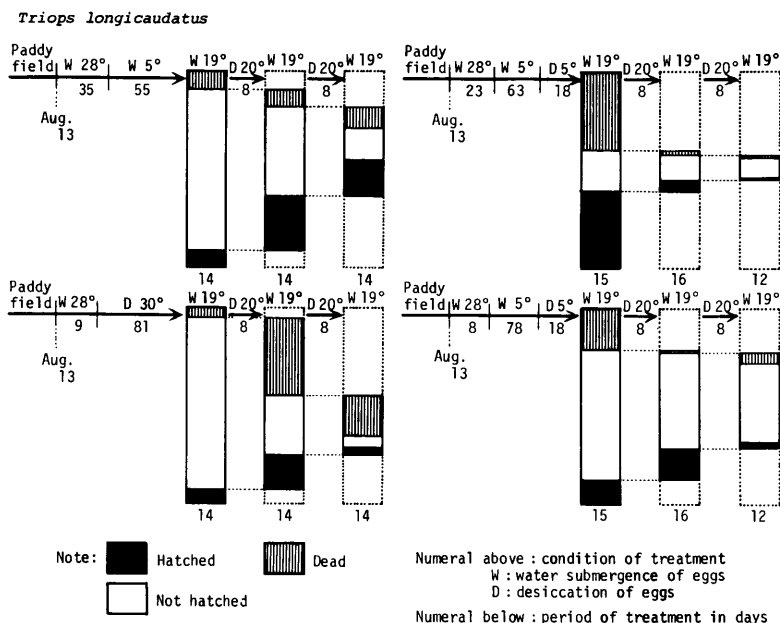


Fig. 11. Effects of repeated desiccation and water submergence on egg hatching in *T. longicaudatus*. The programs of treatment of eggs and the percentage of hatching when submerged in water are shown diagrammatically.

c) *Effects of repeated desiccation on hatchability*

In none of the experiments mentioned above was 100% hatching achieved. The unhatched eggs were tested for viability by repeated desiccation and water submergence, besides the antiformin treatment as a test of their survival. HEMPEL-ZAWITKOWSKA (1967) stated that the unhatched eggs proceeded to hatch after repeated desiccation in *T. cancriformis*. Some of the unhatched *T. longicaudatus* eggs in the above experiments were dried for 8 days at 20°C and resubmerged in water of 19°C for 14 days. Some eggs hatched in this period but others still remained unhatched, as shown in Fig. 11. Hatching was again examined after further desiccation and submergence, but 100% hatching could not be accomplished by these repeated treatments.

The treatment of eggs with antiformin solution to remove the outer covering was reported by KOKATA (1968), who mentioned that in *T. cancriformis* the naked eggs were killed. I examined the viability of naked eggs in three species of *Triops* and found that many eggs hatched within a few days after the antiformin treatment. Some naked eggs were placed in tragacanth gum solution on a paper and dried for 7 days. Of 100 naked eggs of *T. granarius*, 52 hatched out within 8 days of water submergence and 44 remained alive but unhatched. When they were again desiccated and submerged in water, 18 eggs hatched out of 35 eggs treated. When desiccated the naked eggs became like deflated rubber balls, but they could hatch normally. There is a report that the osmotic pressure of the ambient water has an influence on egg hatching in *T. cancriformis* (HEMPEL-ZAWITKOWSKA, 1969). The osmotic pressure may affect eggs through their inner egg shell, because the outer egg covering has less influence on the

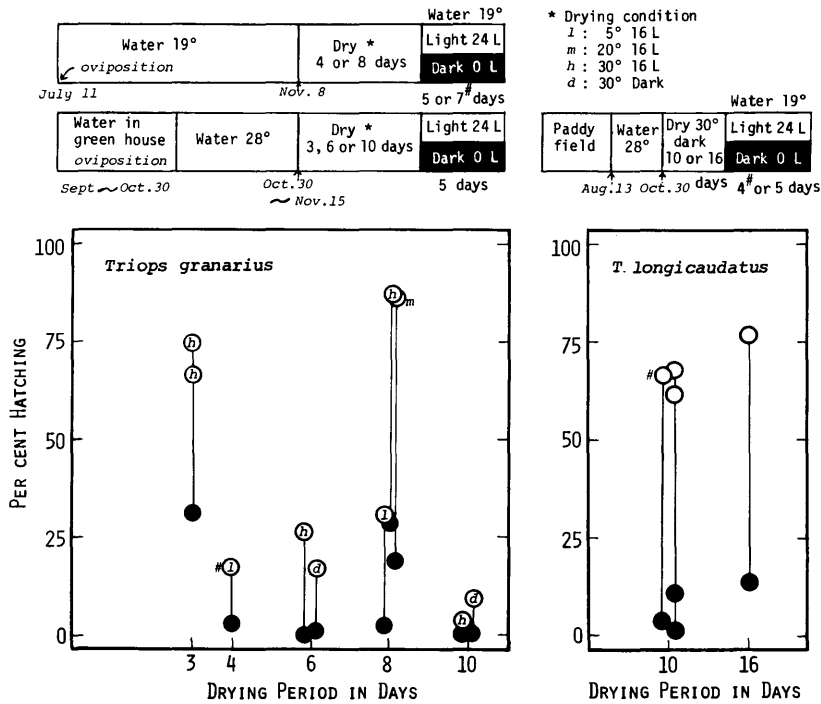


Fig. 12. Egg hatching under the conditions of total light (24L-0D; ○) and total darkness (0L-24D; ●) in *T. granarius* and *T. longicaudatus*. The programs of treatment of eggs are shown above.

heterogeneous egg hatching.

The naked eggs were colored milk-white in *T. longicaudatus* and orange-yellow in *T. granarius*. They were pale lilac in *T. cancriformis*, though KOKATA (1968) stated that they were white. But, in other experiments some eggs of these three species were milk-white. The reason for these color differences has not yet been established.

d) Photosensitivity in egg hatching

In a previous paper I reported on the effect of photoperiod on the egg hatching in *T. granarius*. Under shorter day length, i.e., less than 4 hours of illumination (4L-20D), hatching was significantly suppressed, as also under total darkness (0L-24D) (TAKAHASHI, 1975). Hatching of the eggs of the three species was examined under constant light (24L-0D) and darkness (0L-24D). Eggs of *T. longicaudatus* and *T. granarius* which had been kept in water at 19°C and 28°C were dried for 3 to 16 days, then submerged in water at 19°C for 4 to 7 days. The percentage of hatching was as shown in Fig. 12, where the partner treatments of light and dark conditions are connected by a line. Eggs of *T. cancriformis* which had been kept in water at 21 or 28°C for 90 days after oviposition were dried at 23°C in the air for 10 days. Their hatching was examined in water of 19°C for 5 days; the results are shown in Table 1.

The percentage of hatching was significantly higher in the light condition than in total darkness in every case. In *T. cancriformis* no eggs hatched in darkness, and

Table 1. THE EGG HATCHING IN *T. cancriformis* UNDER TOTAL LIGHT (24L-0D) AND DARK (0L-24D) CONDITIONS

Conditions of treatment				Number hatched	Number not hatched	Number dead	Total
Storage of eggs		Drying	Hatching				
in the soil for 7 days	in water for 90 days	in the air for 10 days	in water for 5 days				
21°C	21°C	23°C	19°C Light	50	6	3	59
			19°C Dark	0	56	3	59
21°C	28°C	23°C	19°C Light	42	11	5	58
			19°C Dark	0	57	3	60

the difference seems to be much clearer in *T. longicaudatus* than in *T. granarius*.

DISCUSSION

There are a number of reports concerned with the biology of tadpole shrimps (LONGHURST, 1955; HEMPEL-ZAWITKOWSKA, 1967, 1969; HEMPEL-ZAWITKOWSKA and KLEKOWSKI, 1968; KOKATA, 1968; IGARASHI, 1970; KATAYAMA, 1973; AKITA, 1976). However, they are rather descriptive of each ecological characteristic of the shrimps, and previous experiments were conducted mostly on *T. cancriformis* and only fragmentally on the other two species. Their ecological characteristics can be summarized as follows: the eggs of tadpole shrimps have a high persistency in the dormant state under severe dry, cold, and hot conditions; their eggs are sensitive to osmotic pressure in hatching; they begin to develop rapidly soon after submergence in water, but their hatching occurs heterogeneously; their nutritional requirements are wide, forming an omnivorous food habit; their growing and reproductive stages are greatly overlapped; they have a high reproductive power producing many eggs; and some strains reproduce unisexually.

A review of their characters suggested that tadpole shrimps have quite similar ecological characters to those of annual weeds in paddy fields. The effect of illumination on egg hatching was examined to compare the characters of *T. granarius* eggs to those of the seeds of annual weeds, whose germination is sensitive to light (TAKAHASHI, 1975). To confirm the hypothesis that they are pioneer animals in temporal water pools (TAKAHASHI, 1977), more reliable data on the ecological characters of *Triops* are necessary.

The results of the present experiments with *T. granarius* and *T. longicaudatus* coincide with those obtained previously on *T. cancriformis* and support the above-mentioned hypothesis. Many of the shrimp eggs hatch soon after the flooding of paddies and develop rapidly to maturity (Fig. 1) in an abruptly formed habitat, which is temporarily created without any forewarning by rainfall or flooding. They begin deposition of eggs as early as the 10th day, when they are still very small in body size, and continue oviposition until their mid-age. Though their life span is short under field conditions, they deposit many eggs in the soil before death. The shrimps have an omnivorous

food habit, feeding on many kinds of living and dead organisms in their habitat. Their maximum body size and longevity vary greatly with their environmental conditions. In *T. cancriformis* body size is negatively correlated with the number of individuals in a paddy (IGARASHI, personal communication). This result suggests that their development is highly determined by the amount of food preserved in the habitat and the population density. They do not have a character to prevent over exploitation of food in advance by self-regulation of population density. Accordingly, they are subject to competition for food with a high mortality and a reduced body size under over-crowded conditions.

The eggs started to hatch on the 8th day after oviposition under laboratory conditions. However, the eggs hatched very heterogeneously and intermittently under constant water temperature (Fig. 7), especially at higher temperatures (TAKAHASHI, unpublished). Many eggs remained for a long period in the dormant state. This heterogeneous hatching was not improved by low-temperature treatment (Fig. 8). Desiccation of eggs, however, was effective to raise the percentage of hatching on subsequent submergence in water, many eggs hatching within a few days (Figs. 8—10), though the percentage of hatching varied with the length of the previous desiccation period. Attempts were made to stimulate hatching of the unhatched eggs by repeated desiccation and submergence, but 100% hatching was not achieved (Fig. 11). This character is very advantageous to maintain population abundance under the great fluctuation of environment between favourable and unfavourable conditions (TAKAHASHI, 1977). Hatching of eggs of the three species was markedly prevented under total darkness and stimulated by illumination (Fig. 12). This character is also adaptive to promote development when the habitat is abruptly created and the eggs are floated over the soil by puddling while other eggs remain in dormant state in the soil.

These ecological characteristics which are demonstrated in the three species of *Triops* are considered to be highly adaptive to the irregularly disturbed aquatic environment and tadpole shrimps can be regarded as pioneer animals in temporal water pools under arid conditions.

ACKNOWLEDGMENTS

I would like to express my deep thanks for kind advice to Mr. H. KATAYAMA, Kyodo Scientific and Agricultural Research Laboratory, Dr. S. MATSUNAKA, National Institute of Agricultural Sciences, and Prof. K. UEKI, Kyoto University.

REFERENCES

- AKITA, M. (1976) Classification of Japanese tadpole shrimps. *Zool. Mag.* **85**: 237-247.
- HEMPEL-ZAWITKOWSKA, J. (1967) Natural history of *Triops cancriformis* (Bosc.). *Zool. Poloniae* **17**: 173-239.
- HEMPEL-ZAWITKOWSKA, J. (1969) Hatchability of eggs of *Triops cancriformis* (Bosc.) in solution of chlorides and sulfates. *Pol. Arch. Hydrobiol.* **16**: 105-114.
- HEMPEL-ZAWITKOWSKA, J. and R. Z. KLEKOWSKI (1968) The influence of desiccation at different air humidities on hatchability of *Triops cancriformis* (Bosc.) eggs. *Pol. Arch. Hydrobiol.* **15**: 183-189.
- IGARASHI, K. (1970) Ecological studies on *Triops longicaudatus* (Notostraca) inhabiting Shonai district, Japan. 2. *J. Yamagata Agric. Forest. Soc.* **27**: 34-39 (In Japanese with English summary).

- IGARASHI, K. (1972) Changes with time in the populations of *Triops longicaudatus* (LECONTE) in two Japanese rice fields. 1. *J. Yamagata Agric. Forest. Soc.* **29**: 13-19 (In Japanese with English summary).
- KATAYAMA, H. (1973) The species of *Triops* and their distribution in Osaka district. *Nature Study* **19**: 62-67. (In Japanese).
- KATAYAMA, H., K. UEKI, M. SOGA, and H. MATSUMOTO (1974) Studies on effect of tadpole shrimp on biological control of weeds in paddy field 1. Field experiment on effect *Triops granarius* (LUCAS). *Weed Research, Japan* **17**: 55-59. (In Japanese with English summary).
- KOKATA, Y. (1968) On the development of the tadpole shrimps. *The Heredity, Tokyo* **22** (4): 72-74 (In Japanese).
- LONGHURST, A. R. (1955) A review of the Notostraca. *Bull. Brit. Mus. (Nat. Hist.) Zool.* **3**: 3-57.
- MATSUNAKA, S. (1976) Tadpole shrimp: a biological tool of weed control in transplanted rice fields. *Proc. 5th Asian-Pacific Weed Sci. Soc. Conf., Tokyo* **1975**, 439-443.
- TAKAHASHI, F. (1975) Effect of light on the hatching of eggs in *Triops granarius* (Notostraca: Triopsidae). *Environ. Control in Biol.* **13**: 29-33. (In Japanese with English summary).
- TAKAHASHI, F. (1977) Generation carryover of a fraction of population members as an animal adaptation to unstable environmental conditions. *Res. Popul. Ecol.* **18**: 235-242.
- TAKAHASHI, F. (1977a) *Triops* spp. (Notostraca: Triopsidae) for the biological control agents of weeds in rice paddies in Japan. *Entomophaga* **22**: (in press).