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DAILY MOVEMENTS OF DESERT PUPFISH, *CYPRINODON MACULARIUS,* IN SHORE POOLS OF THE SALTON SEA, CALIFORNIA

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Introduction

The desert pupfish, *Cyprinodon macularius* Baird and Girard, is a small teleost (usual length 20-30 mm) widely distributed in the Colorado River Basin. Its normal habitat is desert springs and drainages, but it has established itself in the Salton Sea and associated shore pools (Miller 1943).

I frequently visited the shore pools during 1954 and 1955 in order to gather data for another problem. Causal observations of the pupfish revealed that they moved into and out of the shallow areas with some degree of predictability. Because of this the distribution of the fish at different times of the day was observed more carefully. At the same time changes in the water temperature were recorded.

The objective of this paper is to describe the movements of the pupfish in relation to the rapid and extensive temperature changes which characterize the shore pools of the Salton Sea.

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SHORE POOLS

Description

The Salton Sea is a large saline lake lying 235 feet below sea level in the Colorado Desert of Southern California. It was formed in 1905-1907 by escaped irrigation water from the Colorado River, which flooded the dry Salton Sink (Sykes 1937, Hubbs and Miller 1948). Because of the irregular supply of waste irrigation water the level of the sea is variable.

Except for the southern end, the Salton Sea is ringed by shore pools 5 to 15 meters wide and from 20 to 200 meters long. Some pools form interconnecting series extending for as much as a kilometer along the shore. Most of the pools are characterized by arms about a meter in width, 10 cm or less in depth at their deepest points, and extending 2 to 5 meters into the surrounding desert (Figure 1).

FIG. 1. Shore pool on eastern shore of Salton Sea. Sea is to right of sandbar.

The pools are usually deepest just inside the sand bar which separates them from the sea. Thus the inside face of this bar is quite steep but most of the bottom of the pool, which is soft mud from fine desert soil, slopes gently towards the landward side.

The pools are usually cut off from the sea but some times open into it, especially during the winter when the level of the sea rises. Nonetheless, the water level of larger pools remains fairly constant. Evidence of the sea washing over the bar is often noted.

Salinity

The salinity of isolated shore pools reached higher values than the sea, as might be expected. The maximum recorded salinity of a large shore pool was Δ_0 −3.36°C (approximately 62‰). Substantial salinity differences were found between adjacent pools, even when contiguous (Table I), although no differences were detected within individual pools.

TABLE I. Salinities in °C freezing point depression as determined with a conductivity bridge. Pool #1 was adjacent to pool #2

Date (1954)	Pool #1	Pool #2	Sea	Sandbar	Interpool Channel
5/29	−1.71	—	−1.63	open	open
6/15	−1.99	−2.26	—	closed	open
7/ 3	−2.42	−2.54	−1.59	closed	open
7/16	−1.70	−1.69	−1.56	closed	open
8/ 6	−1.59	−1.46	−1.38	open	open
9/11	−1.87	−1.68	−1.32	closed	closed
10/10	−2.66	−2.64	−1.66	closed	closed
10/31	−2.55	−2.78	−1.64	closed	closed
11/14	−2.40	−2.54	−1.64	closed	closed
12/ 5	−2.08	−2.32	−1.52	closed	closed

The relative concentrations of most of the constituent salts of the Salton Sea are similar to those in the ocean. However, there are some pronounced differences, particularly with regard to the sulfate, calcium, and potassium ions (Carpelan 1954[1]).

Oxygen

The amount of oxygen dissolved in the water along the bottom of the shore pools was not determined. However, Carpelan (1953) has studied the oxygen content of the water of the Salton Sea. His data from the shallowest station, 1.5 meters deep, are of special interest here because this situation is comparable to that found in the shore pools. Daily noctural minima and diurnal maxima were reported. On one day, during September, the oxygen content over the bottom increased from 1.7 ml/l at 0500 to 4.8 ml/l at 1700. These should be nearly minimal values, because of the high water temperatures (28.4°C and 32.7°C).

pH

The pH of shore pool water was not studied. Carpelan (1955) has shown that the pH of the Salton Sea undergoes a daily diurnal increase and nocturnal decrease. In April the pH over the bottom, 3 meters deep, was as follows: 8.39 at 0600, 8.40 at 1200, 8.60 at 1800, and 8.47 at 2400.

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[1] Carpelan's data are from mimeographed reports with limited circulation. These reports have been incorporated into one manuscript and will be published soon.

Temperature

A remarkable feature of the physical ecology of the Salton Sea is the extreme annual range of temperature. In 1954-1955 the temperature of the open water ranged from 10°C to 36°C. Lowest winter and highest summer monthly means were 12°C and 34°C respectively (Carpelan 1956).

The daily temperature range of the Salton Sea is 2°C to 3°C (Carpelan 1956) except along the shore. In the shore pools the daily temperature change far exceeds that of the sea. The temperature of the shallower pools may undergo a daily change of 15°C or 20°C in either summer or winter. The area of most uniform temperature in the pools, *i.e.* the deepest holes, may range over 10°C to 15°C on a hot day (or as little as 5°C on a cool winter day).

The Salton Sea buffers the temperature changes of the air over it. The daily range of air temperature 1 meter over the surface of the pools was usually less than 10°C, although the daily range in the adjacent desert (R. B. Cowles, personal communication) might be 20°C or more.

The most striking aspect of the thermal situation in the shore pools is the difference in rate of temperature change in various regions (Figure 2). The rate of change over the bottom is clearly depth dependent; the deeper the water the slower the change, and consequently, the smaller the daily amplitude. The pools are nearly uniform in temperature for a short period each morning and each evening. This pattern of temperature change is characteristic of both summer and winter.

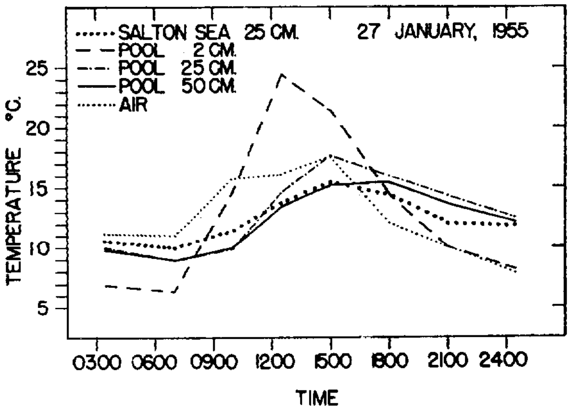

Fig. 2. Water temperatures recorded just over bottom at each depth. Air temperature taken 1 m over surface of water.

Thermal stratification is usually absent throughout most of the pools. The shore pools which were observed regularly showed a vertical thermal gradient only adjacent to the face of the steep sandbar. Even under favorable conditions, the differences between bottom and surface water temperatures were commonly less than 2°C. On the other hand, a well developed vertical gradient was observed in one atypical pool which was deeper than most (just over 1 meter), turbid, and highly saline (62‰). High sand dunes protected it from wind. At 0930 the water temperature was 28.6°C at a depth of 1 meter and 30.6°C at the surface. At 1145 the temperatures were 29.0°C and 34.5°C respectively. Similar stratification has been noted in other small pools and ponds (Vass and Sachlan 1955, Young and Zimmerman 1956).

Fauna

The macroscopic fauna of the shore pools is limited to a few species. The pupfish is frequently the dominant vertebrate. Another cyprinodontiform fish, *Gambusia a. affinis* (Baird and Girard), is common in the larger, and particularly in the more brackish pools. A goby, *Gillichthys mirabilis* Cooper, and less often a sciaenid, *Bairdiella icistius* (Jordan and Gilbert) are found in the deeper pools.

The macroscopic invertebrate fauna is dominated by three species: The hemipteran *Trichocorixa reticulatus* (Guerin), the polychaete *Neanthes succinea* (Frey and Leuckart) and the barnacle *Balanus amphitrite* Darwin. Free living benthic nematodes probably of the genus *Spirophorella,* heliid and ephydrid larvae, and a harpacticoid copepod, are also present.

OBSERVATIONS

Methods

The fish were observed systematically on 3 different occasions. In each instance the sun shone brightly throughout the day and a 5-10 mile per hour wind blew during the morning and again during the evening, but did not hinder observations. On each occasion the bottoms of the pools were visible everywhere in the afternoon. Visibility was limited to a depth of 35-40 cm during the morning.

At night the fish were located by flashlight. Their distribution at this time was confirmed by taking successive seine hauls over a standard distance (5 meters) at various depths.

The same two shore pools on the west side of the sea were observed on each occasion. Each was approximately 15 by 50 meters with a maximum depth of about 60 cm. The pools were visited every 3 hours for a 24-hour period. The number and sizes of the pupfish were estimated and the temperature of the water was recorded at each place where they were sighted. In most instances fish smaller than 10 mm in length were not considered, nor were large territorial males. The water temperature just over the bottom was noted at several fixed stations of different depths. The air temperature 1 meter over the water was also taken.

Results

The first series of observations was made in August, 1954, commencing just before local apparent sunrise (Figure 3). No fish were seen at dawn so they must have been at a depth greater than 35 cm, *i.e.*, in the warmest water. At 0900 the temperature of the pools was almost uniformly 27.5°C and pupfish appeared at the intermediate depth of 25 cm. Although many adults were observed, none were found in shallower water. At noon, however, the bulk of the population was concentrated in very shallow, warm water. When the temperature of the water of the shallows rose above 36.5°C (1500) the fish moved to the deeper water (more than 40 cm deep) where they were concentrated between the temperatures of 35.5°C and 36.5°C. When the shallows cooled to a temperature of 36.0°C the pupfish moved back into this area. At this time (1800) the pools were again nearly uniform in temperature.

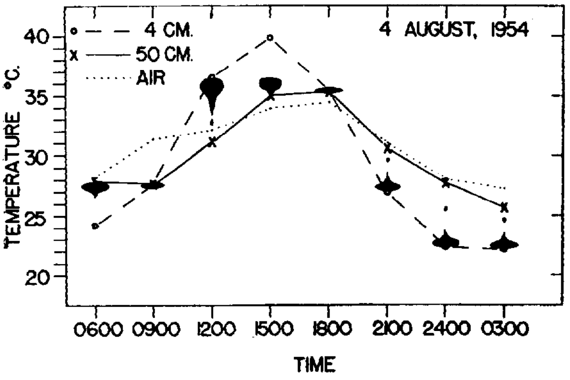

FIG. 3. Water temperatures recorded just over bottom. Width of black models represents relative abundance of pupfish.

After sunset, careful searching with a flashlight revealed that most of the pupfish were inactive on the bottom at a depth of less than 5 cm. This observation was confirmed by sampling with a fine mesh seine at depths of 40, 25, 15, and 5 cm. The numbers of fish taken were 3, 0, 2, and 78, respectively. The 3 pupfish taken at 40 cm were large territorial males in breeding color.

In summary, the fish occupy the coldest and most rapidly cooling areas of the pools at night. At dawn they move into the deepest and warmest areas. As the morning progresses, the adult pupfish slowly work their way into the shallows and remain there until this area is excessively heated. Then they retreat into deeper water, avoiding temperatures above 36.5°C. As the water in the shallows cools, the pupfish move back again, presumably following the 36.5°C maximum. Observations made during a 24 hour period on the same pools a month later conformed to the same pattern.

The pattern of movement during the winter was somewhat different from that noted during the summer (Figure 4). The morning movement of fish into the shallow areas was considerably delayed. The pupfish did not congregate in the shallows until mid-afternoon. By this time the temperature of the shallows had passed its maximum and was rapidly falling. In contrast to their behavior during hot weather, the fish spent the entire morning in the deeper water and the afternoon and night in the shallows. There was no withdrawal from high temperatures during the mid-afternoon.

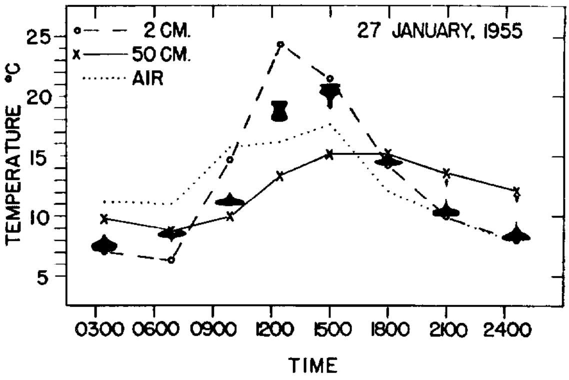

FIG. 4. Water temperatures recorded just over bottom. Width of black models represents relative abundance of pupfish.

It should be noted that there is a striking similarity between the temperature versus time curves of the summer and winter, except that the winter curve has shifted downward approximately 15.0°C. Further, the difference between temperature maxima of deep and shallow water is more pronounced in the winter.

The following observation, made during the month of January, is cited here because of its relevance to the problem of fish distribution relative to water temperature. At 1000, pupfish were observed in the pool along the sandbar in water 7 cm deep; the bottom temperature was 11.4°C. On the landward side the bottom temperature at a similar depth was 14.0°C and no fish were present there. They were found on the landward side, however, at the greater depth of 15-25 cm where the temperatures were 11.9°C and 10.8°C. Thus the fish on the landward side were found only at depths 2 to 3 times as great as those along the sandbar, but at almost identical temperatures.

A series of observations was also made in August, on a school of pupfish isolated in a small (2.5 m x 35 cm x 7 cm deep), wave-built pool situated in a sandbar between the sea and the pools. A small pile of twigs, partly covered by moist sand, extended over, and slightly into, the water providing shade from the intense desert sun. Although the shaded area was less than 100 sq cm, the temperature of this area during the heat of the day remained 2°C lower than that of the water in direct sunlight (Figure 5).

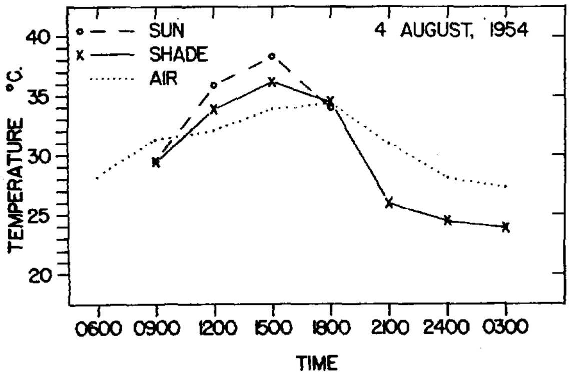

FIG. 5. Temperatures of sunlit and shaded water in a small, isolated pool.

Pupfish, trapped in the small pool, foraged actively over the bottom at 1200 when the water temperature was 35.9°C. At 1500, however, the entire population of the pool retired to the shade (36.2°C) and was relatively inactive. The sunlit water was at 38.3°C. At 1800 the pupfish were again in the sun working over the bottom but the temperature of the sunlit water had dropped to 34.8°C. These pupfish apparently avoided water warmer than 36.0°C.

DISCUSSION

The thermal ecology of the desert fishes of the genus *Cyprinodon* has long attracted attention because these small fishes are found in many of the hot springs throughout the Great Basin and its associated drainages (Hubbs and Miller 1948, Miller 1948). Nonetheless, the paradox exists that few data are available concerning the thermal tolerance of these fishes and even less concerning their distribution within the hot springs (Miller 1948, 1949).

Each hot spring supplies a relatively stable thermal gradient between the source and its progressively cooler stream. In a hot spring with a substantial flow, pupfish should be able to maintain themselves in an optimal water temperature by selecting the proper place in the temperature gradient. Indeed, Miller (1948) observed that the bulk of the population of *Cyprinodon nevadensis* Eigenmann and Eigenmann, in South Tecopa Hot Springs, was concentrated at 36°C or below, although a few stragglers were seen in water as warm as 40°C.

Pupfish often occur in pools which are not supplied by hot springs, such as those along the shores of the Salton Sea. In these instances the temperature situation is dynamic in that some parts of the pools heat or cool at a greater rate than others. The pupfish of these pools could be expected to move about in such a manner as to keep themselves in a suitable temperature and to reduce the temperature changes which they might otherwise experience.

The behavior of terrestrial reptiles, faced with a situation in which the temperature is highly variable, appears to be directed toward maintaining a particular body temperature by seeking out the appropriate thermal microhabitat (Cowles and Bogert 1944, Bogert 1949, Norris 1953). Among Amphibia, adult *Hyla regilla* Baird and Girard move to and from the water in response to changes of environmental temperatures, and the tadpoles of this species congregate in the warmest part of a pond (Brattstrom and Warren 1955).

Behavioral responses of fishes to temperature changes in the field, other than seasonal movements, have seldom been recorded. Schools of *Jenkinsia lamprotaenia* (Gosse) in a quasi-natural situation were observed to restrict their movements so as to avoid water warmer than 30°C (Breder 1951). Regular diurnal patterns of movements, usually based on catch records, have been cited for some lake fishes. Schools of fish have been reported moving into shallow regions during the night and retiring to deeper water during the day, or vice versa (Carlander and Cleary 1949, Scott 1955, Hasler 1956).

Desert pupfish show daily patterns of movements in the shore pools of the Salton Sea. These movements are related to the constantly changing physical characteristics of the pools.

Oxygen content of the water might be considered an ecologically limiting factor in the daily movement of the pupfish and reduced oxygen tension has been shown by Fry (1937) to be an important factor initiating vertical migration in the cisco, *Leucichthys artedi* (LeSueur). However, the oxygen tension in the pool water is probably higher at all times than the values quoted for Carpelan's shallow water station. His station was in deeper water and somewhat protected from wind. Even on windless nights the cooling surface layers of shallow pools would sink, enriching the oxygen content of the water. Further, behavioral evidence indicates that the oxygen tension is rarely a limiting factor. Pupfish spend the nights in shallows during both summer and winter. Large males are sometimes taken in deeper water on the warmest of nights when the oxygen tension should be minimal. In addition, the fish move into the deeper water at dawn, when its oxygen tension is probably lowest, and into the shallows during the late afternoon when the oxygen tension of the deeper water should be greatest.

The pH of the water is an even poorer candidate for the factor restricting the movements of the pupfish. Local pH differences, of the magnitude that a fish could be expected to respond to, probably do not occur. The over-all change in pH in the shallow water of the Salton Sea proper is small (Carpelan 1955). Further, Creaser (1930) has shown that pH is probably the factor in the environment which least limits the distribution of the brook trout.

The movements of pupfish were clearly independent of salinity. Within each observed pool no over-all or local changes were recorded during the course of a day. Slight differences between contiguous pools have been noted above.

The euryhalinity of cyprinodontiform fishes is impressive. In the two pools studied, maximum salinities were 46°/₀₀ and 52°/₀₀. Many small pools along the shore which contain pupfish dry up completely during summer and fall. Pupfish were found in one pool the salinity of which was 68°/₀₀. Cowles (1934) has commented on the salinity tolerances of pupfish in the Salton Sea. These fish are also found in fresh water irrigation ditches which enter the Salton Sea. Simpson and Gunter (1956) have recorded *Cyprinodon variegatus* Lacepede in salinities of 1.8°/₀₀ to 142.4°/₀₀, but they were most abundant in 30°/₀ to 37°/₀₀. Two other Cyprinodontidae, *Aphanius fasciatus* (Valenciennes) and *Aphanius sophiae* (Heckel), have been recorded at high salinities in the Near East (Fox 1926, Steinitz 1951). Herre (1929) reported the occurrence of a cyprinodontiform fish, *Mollienisia latipinna* LeSueur, at salinities as high as 87°/₀₀. It would be surprising if the movements of the pupfish were restricted by small salinity differences.

There is one factor in the physical ecology of the pools which may play an important part in the movement of the pupfish but which has not been analyzed. This is light intensity. Although the pools are shallow, the difference in the amount of light impinging on the bottom in the shallow and in the deep water at different times of the day was apparent to the eye of the observer. The over-all change in illumination between night and day might play a role in the movements of fishes (Kawamoto and Konishi 1955, Hasler 1956a, 1956b, Herter 1953). A further complicating factor is that fish may respond differently to light when exposed to water of different temperatures (Andrews 1952).

We are left, then, to a consideration of water temperature as a primary limiting factor in the physical ecology of the pools. The most obvious manner in which temperature limited the movements of pupfish, at least during the summer, was shown in their avoidance of shallow areas when the temperature there exceeded 36°-37°C. Numerous summer recordings, in addition to those cited in the observation section, showed a consistent avoidance of temperatures above 36°-37°C. *Cyprinodon nevadensis,* for the most part, avoids temperatures over 36°C (Miller 1948). I have never observed *C. macularius* in water warmer than 37°C when cooler water was available. When trapped in small pools along the shore, they have been seen in water as warm as 38.7°C. Pupfish at temperatures just above 36°C show no apparent distress except that they forage continuously. These data were collected on summer days of average heat. During the hottest days of the summer pupfish in small pools must endure temperatures of at least 40°C.

Brues (1928) suggested that 40°C is close to the maximum temperature at which aquatic vertebrates can sustain life. He reported the cyprinid fish *Notropis lutrensis* (Baird and Girard), living in spring water at 39.5°C. A few stragglers of *Cyprinodon nevadensis* were seen in water as warm as 40°C. All records of *Cyprinodon* surviving at temperatures over 40°C have been regarded as doubtful (Miller 1948, 1949). The maximum temperature to which young goldfish, *Carassius auratus* (L.), can be acclimated is slightly over 40°C (Fry, Brett and Clawson 1942). Bailey (1955) reported a heavy kill of several species of fishes in a shallow pond when it reached 38°C while the cyprinodontiform and centrarchid fishes survived.

The role of temperature in limiting the movements of pupfish, beyond the fact that they avoid water warmer than 36°-37°C, is not altogether apparent. Clearly the fish do not move so as to maintain themselves in a constant water temperature in the late afternoon and at night. They move into deeper, warmer water in the morning but seem quite sensitive to still warmer water, especially in the winter. This is best illustrated by the

January observation of pupfish at quite different depths on opposite sides of the pool but at the same water temperature. Morning sensitivity to warm, shallow water is seen to a lesser degree in the summer. In spite of their avoidance of shallow areas in the morning one gets the distinct impression that pupfish "prefer" the shallowest areas of the pools.

It is extremely doubtful that any single physical property of the habitat could be invoked to account for the daily, predictable, patterns of movement of the pupfish. It is more likely that a delicate balance exists between the physical environment and higher behavioral patterns of the pupfish such as microhabitat preference, schooling or foraging. Water temperature, and perhaps light intensity, probably are important as factors restricting, but not directing the movements of pupfish.

SUMMARY

1. Shallow pools are a regular feature of the shore line of the Salton Sea. The desert pupfish is abundant in these pools.
2. The temperature of the water of the shore pools changes rapidly. The shallow water heats and cools faster than the deep water. For a short period during each morning and each evening the pools are rather uniform in temperature.
3. The pupfish spend the nights in the shallowest, coolest areas of the pools. At dawn they move into the warmest, deepest areas. Later in the morning, during the summer, they work their way into the shallow parts of the pools. Then they retreat from the shallows when the water temperature there exceeds 36°-37°C. They return to the shallows when the water cools to 36°-37°C or below. During the winter the pupfish do not move into the shallows until mid-afternoon and they remain there into the night.

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ON FLUCTUATIONS IN POPULATION DENSITY OF THE RICE STEM BORER *CHILO SUPPRESSALIS*[1]

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1

Economic entomologists are well aware that the population density of insect pests fluctuates from generation to generation with a wide range of amplitude, the outbreak periods occurring at intervals of several years. However, with regard to none of the species which vary greatly in abundance can we say why they vary or forecast with any certainty the size or the time of occurrence of the population peak. There are a number of rival theories as to the basic causes underlying population fluctuation. Various workers have stressed the importance of weather, natural enemies, overcrowding and so on to the exclusion of other factors.

In Japan the rice stem borer *Chilo suppressalis* is one of the most serious pests of the rice plant in paddy fields and fluctuates in number from year to year. Population fluctuation is especially violent in the south-western part of the country, where most heavy damage to rice is experienced. Accordingly, for a long time much attention has been devoted to the problems caused by this pest in order to predict the outbreak year. Harukawa *et al.* (1935) observed the fluctuation in larval density of the rice stem borer in paddy fields for six years in relation to changes in climatic conditions, the abundance of natural enemies and other ecological factors, but were not then in a position to conclude that this fluctuation is determined solely by weather conditions. They felt that they should study the inter-relations of those organisms which are part of the environmental complex of the rice stem borer more thoroughly. Since that work was published, however, the idea of climatic predominancy has prevailed and extensive studies have been carried out, such as those of Fukaya (1950) and Ishikura (1951), which were based upon long-term data provided by light trap collections and in which it has been emphasized that climate is the main regulating factor, with fungus disease acting subordinately. Recently Ishikura (1951), after surveying the data from light trap collections, pointed out that a gradational outbreak is common in the population fluctuation of the rice stem borer. This point of view regarding outbreaks was then thoroughly analyzed by Miyasita (1955). These works were very important in clarifying the problem but many points remained to be solved.

The present work is rather critical of the prevailing idea of climatic predominancy and approaches the problem from the opposite viewpoint in population ecology. Using the data available from long-term light trap collections and from a census of larval density made in several successive years, we examine the periodicity in population fluctuation, the life table in the gradation year and the change in reproductive rate in each generation.

2

Since the adult moth of this borer is strongly phototactic, a record of annual catch by light trap has long been accumulating at each prefectural experiment station in different districts of Japan. These records have been made available through the extensive publications of Ishikura (1946) and Fukaya and Nakatsuka (1955), who collected these data for the prediction of the outbreak year. In the present paper some of these data are used, excluding those records of capture which are either too short to treat statistically or which show some years of interruption.

The actual number of living moths or the popu-

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