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Journal

Marine Biology, 58(1)

Authors

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Publication Date

1980-10-01

Data Availability

The data associated with this publication are within the manuscript.

Peer reviewed

Observations on Behavior, Emergence and Reproduction of the Marine Midges *Pontomyia* (Diptera: Chironomidae)

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Abstract

Pontomyia is a genus of tiny flightless marine midges, with 4 described species, found on tropical or subtropical sea shores of the western Pacific Ocean. They are rarely noticed because of their small size (about 1.5 mm) and ephemeral adult life (1 to 3 h). They usually occur in association with seagrasses and seaweeds on which the larvae feed. The oar-like wings of adult males propel them over the water surface, but do not enable them to fly. Adult females are not only wingless but virtually legless. Emergence of the adults in the field may occur either during the day or at night. In a laboratory aquarium population of *P. cottoni* Womersley, maintained for about 18 months in a 12 h light–12 h dark cycle, males began to emerge at the end of the light period, whereas females emerged only after the onset of darkness. Field observations suggest that emergence times are probably influenced also by tides.

Introduction

Pontomyia is a genus of little-known marine midges. There are 4 known species: *P. natans* Edwards, *P. pacifica* Tokunaga, *P. oceana* Tokunaga and *P. cottoni* Womersley. A review of their distribution, biology and systematics, with a key to the species, has recently been published by Cheng and Hashimoto (1978). Since these midges are very small (adult males measure about 1.5 mm in length), have extremely short adult lives (lasting not more than 2 to 3 h), and occur only on certain tropical seashores, their biology has been little studied, except for an excellent and detailed study on the natural history and morphology of *P. pacifica* by Tokunaga (1932). Other work on these midges is limited to a few field observations (Buxton, 1926; Hashimoto, 1959; Marks, 1971). We present in this paper some information on the behavior of all 4 species of *Pontomyia* in the field, with

observations on emergence and reproduction. In addition, the behavior of *P. cottoni* was studied in the laboratory, with special attention to the influence of light-dark cycles on emergence.

Pontomyia spp. have so far been found only in shallow tropical and sub-tropical coastal waters in association with the following algae or higher marine plants: *Cladophora* sp. and *Sargassum* sp. associated with *P. natans* around Japan (Hashimoto, 1959); *Boodlea* sp. in shallow tide pools where *P. pacifica* was found (Tokunaga, 1932); and *Halophila* sp. with *P. cottoni* (Womersley, 1937). The type species, *P. natans*, was collected by towing a net at night over the seagrass *H. ovalis* (Buxton, 1926), but this midge may be found on other plants as well. Although we found *Halophila* spp. at Pulau Salu, Singapore, and Geoffrey Bay, Australia, at these sites the midges were more closely associated with intertidal algal mats on rocks than with the low-growing seagrass on sandy bottoms. The larvae probably live and feed among the tufted and filamentous algae. In our laboratory studies, although no *Halophila* sp. was provided in the aquarium, a stable population of *P. cottoni* was maintained for over 18 months.

According to the literature, *Pontomyia* adults generally emerge at night, more rarely in the daytime (see Cheng and Hashimoto, 1978). Our field observations suggest that the time of emergence is variable and may be determined by the tidal cycle. Although we were unable to carry out studies on times of emergence in the field, we were able to study the effect of light on the emergence of *P. cottoni* adults in experimental aquaria in the laboratory at the James Cook University, Australia.

Materials and Methods

Field observations were made on *Pontomyia natans* Edwards on several islets of the Enewetak Atoll (11° 30'N; 162° 15'E), Marshall Islands, on September 7–21, 1975; on *P. pacifica* Tokunaga at Pulau Salu (01°N;

103°51'E), Singapore, on August 10-11, 1976, and April 10-11, 1977; on *P. oceana* Tokunaga at Heron Island (23°27'S; 151°55'E), Australia, on May 13-16, 1976; and on *P. cottoni* Womersley at Geoffrey Bay, Magnetic Island (19°15'S; 146°45'E), Australia, in July-August 1976, September 1977 and January 1978. In addition, *P. cottoni* was studied in a laboratory population maintained on pieces of alga-covered coral skeleton collected in April 1976 from Geoffrey Bay on Magnetic Island. The midges were maintained in a 250-l glass aquarium with non-circulating, aerated seawater that remained close to ambient temperature (25° to 30°C). The water level was kept constant and no attempt was made to reproduce a tidal cycle. A regular 12 h dark-12 h light cycle was maintained throughout the period of study, with the light cycle corresponding to 04.00 to 16.00 hrs local time. At Townsville, the approximate times of sunset are 17.30 and 18.45 hrs in June and January, respectively. The light was provided by a bank of 6 (40 W) daylight fluorescent tubes and 6 (40 W) tungsten filament lamps 60 cm above the aquaria. Light intensity was $280 \mu\text{E m}^{-2} \text{sec}^{-1}$ at the water surface and $200 \mu\text{E m}^{-2} \text{sec}^{-1}$ at the bottom of the aquaria. Most of the observations on this laboratory culture were made in late July 1976 and from September 1977 through January 1978.

Results and Discussion

Field Observations

On several evenings at the Enewetak Atoll we observed numerous males of *Pontomyia natans* around the shores of Enewetak Islet, Medrin Islet, and Japtan Islet. They appeared just before sunset, evidently attracted by the white sides of our dinghy. The midges gave the impression of flying rapidly just above the surface of the water in arcs and figures-of-eight. However, when captured in a strainer (1 mm mesh) and transferred to a bucket of seawater, it became evident that they skittered rapidly on the water surface but never flew above it. Even so, aided chiefly by their incessant, rapid wing movements, the midges were able to ascend the sides of the bucket, as in nature they might climb over coastal rocks or rubble. For 2 to 3 h after sunset, these insects could easily be caught by attracting them to an electric light and netting them as described above. We observed these flies on 5 different evenings, 1 to 2 h after high tide (18.00 to 19.00 hrs, with ± 130 cm range), but not on several other evenings when the high tide occurred later (between 19.00 and 22.00 hrs) and when there was less tidal range (30 to 60 cm). No females were ever observed.

We first encountered these midges at Japtan on 7 September 1975 just before dusk, and continued to collect them until sunset (19.00 hrs). Although we sought them with flashlights, we did not see any midges after dark, nor during the daytime on the following day (when low tide occurred at about midnight). Unfor-

tunately, we were unable to visit the same islet on the following evening.

We continued our observations on the main islet, Enewetak, for 14 successive nights between 8 and 22 September, but during this period did not see any midges either during the day or at an electric light suspended beside the dock at night. However, on 18 September, at about 20.00 hrs, we observed large swarms attracted to our light; we caught over 100 males within 15 min. During the next 3 nights, we encountered similar swarms at the same locality. The insects remained in dense swarms for about 15 min, but then their numbers and activity fell off rapidly; we rarely saw any moving after one hour. Full moon occurred on 19 September and there was a considerable range (about 4 m) between the low and high tide levels. Low tide for this 4 d period was around 21.30 to 23.00 hrs. Since we have not been able to keep adult males in captivity alive and active for more than an hour or two, they could have begun to emerge no more than 2 to 3 h before we set up our light trap, i.e. 4 to 5 h before low tide.

At Pulau Salu, Singapore, adult males of *Pontomyia pacifica* were seen in dense swarms around boulders exposed at low tide. They behaved in much the same way as the males of *P. natans* observed at Enewetak. On both occasions when we saw swarms of male midges, they were active 2 or 3 h before an afternoon low tide. Unfortunately, we were unable to carry out regular observations on *P. pacifica* in Singapore.

At Heron Island, both dead males and females of *Pontomyia oceana* were found washed ashore in the mornings; hundreds were found in a few cupfuls of beach foam. We did not see any live midges at low tide during the day (15.00 to 17.00 hrs), and the weather was too rough to permit light trapping at low tide at night.

Laboratory Observations

In the aquarium, males of *Pontomyia cottoni* skittered on the water surface almost incessantly, just like those observed in the field. It was extremely difficult to determine the path pattern due to their very fast movements, estimated to exceed 15 cm s^{-1} . Each midge typically traveled in a zig-zag, never in a straight line. They occasionally stopped suddenly for some seconds, but commenced skating again on the slightest disturbance. Pupae of both sexes actively swam to the water surface just before emergence. We did not observe females being helped out of their pupal skins by the males (as described for *Clunio marinus* by Neumann, 1976), but such behavior might occur in *Pontomyia* spp. Adult females of *P. cottoni*, which are wingless and have extremely short legs, floated passively on the water surface until found by males. Mating took place soon after a male encountered a female, usually within 60 s of her emergence. The male and female copulated posterior to posterior, and he dragged her behind him for a few minutes while they remained in copula. Males



Fig. 1. *Pontomyia cottoni*. Portion of egg coil, showing eggs encased within a jelly coat; scale line is 200 μm long

appeared to be strongly attracted to freshly emerged females, even those already copulating. However, after a female was released by a male she seemed unattractive to other males, even when they contacted her by chance.

A few (0.5 to 5) minutes after mating, the female raised the tip of the abdomen and extruded a strand of eggs on to the posterior dorsal segments of her abdomen. The abdominal tip was then flipped down to the water surface and the strand-like egg coil was released below the surface film. The egg jelly quickly swelled as the coil sank and adhered to the first solid object encountered. Presumably, in nature, the egg coils sink to the algal mat on a coral rock substrate where the larvae, when hatched, might find food and shelter. Sinking rates of between 160 and 190 mm min^{-1} were observed. In the aquarium, the eggs, each encased in a thick gelatinous coat, were laid in coils about 300 to 350 μm wide and up to 2.5 cm in length. Each egg was elliptical ($115 \times 230 \mu\text{m}$), positioned with its long axis perpendicular to the coil wall, about half an egg width from its nearest neighbor (Fig. 1). If the female was knocked over by a passing male during the extrusion of the egg mass, the jelly swelled rapidly upon wetting, restricting oviposition of more eggs. This may account for the variable lengths of the egg strands, which contained from 50 to 200 eggs.

Females kept separate from males, and thus unmated, did not lay any eggs, and died on the surface within 3 h. A virgin female could be readily identified by her large girth, attributable to unlaid eggs. When the ratio of males to females was experimentally reduced to one-half, all the females eventually laid eggs, indicating that males may copulate more than once. Each female laid only one egg strand. The viability of eggs produced under these conditions was not determined.

For *Pontomyia cottoni*, the interval from oviposition to hatching was 3.8 d at 24° to 25°C , 5.9 d at 20°C and 9.5 d at 15°C . At 15°C , many eggs failed to develop beyond early embryonic stages. The earliest appearances of segmentation, cephalization and paired eyespots were three conspicuous events occurring sequentially during egg development. When the eggs were kept at 24° to 25°C these three stages were reached at 0.8, 1.1 and 1.8 d, respectively, after oviposition. An average of 4.2% of the eggs in a single strand (of 32 strands studied) did not complete development, usually arresting after the segmentation stage but before the eyespot stage.

Coral surfaces which were left until covered with an algal film were used to start new cultures of *Pontomyia cottoni* by transplantation of freshly laid egg strands. An analysis of subsequent adult emergence showed that at 24° to 25°C development from egg to adult took 19 to 25 d (mean, 21 d). It is possible that in nature, where food may be limiting, generation times could be considerably longer. No accurate information on the mortality of larvae was obtained, but, if one assumes a mean egg count of 100 per strand and counts the total number of adults emerged, the mean mortality could be as high as 70% in freshly started cultures. In long-established cultures, mortalities were as high as 96%, survivorship presumably being reduced by predation by polychaetes and amphipods also present in the tanks.

In all cultures of *Pontomyia cottoni*, the ratio of males to females was greater than unity. Mean monthly sex ratios of specimens collected over the month ranged from 1.35 to 2.35. In one well-established culture, followed for 92 d, daily emergences ranged from 19 to 58. From a total of 3,570 adults that emerged, 2,241 were males, giving a total sex ratio of 1.69. The daily

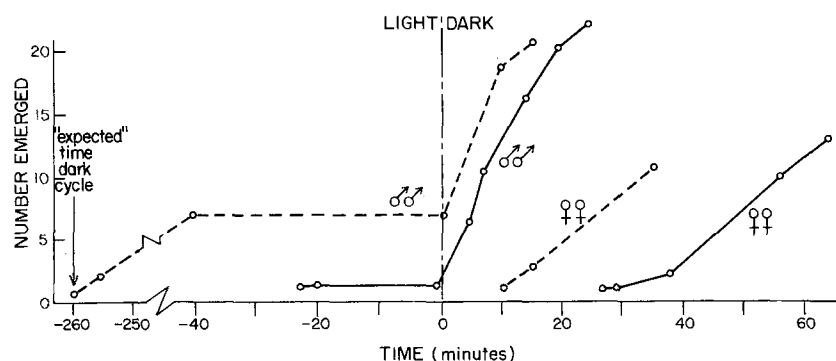


Fig. 2. *Pontomyia cottoni*. Numbers of males and females emerging in laboratory culture on a 12 h dark-12 h light cycle (solid lines). Dashed lines connect points for adults emerging from pupae subjected to a 4.3 h delay in the onset of the dark period

ratios ranged from 3.0 to 0.56; on only 9 d did the ratio fall below unity. A χ^2 test and a run-analysis showed significant differences ($P < 0.01$) among the daily sex ratios, but revealed no regular trends in cycling or sequences.

During the periods of our observation, adult midges emerged soon after the commencement of the dark period, the males usually appearing within the first 30 min and the females during the next 30 min. When all emerged adults were removed 2 h after the onset of darkness, no more flies appeared until the end of the light period. The earliest males, but apparently no females, emerged 20 to 30 min before the lights were turned off (Fig. 2).

To further test the effect of light on emergence, the dark period was delayed by 4.3 h. As shown in Fig. 2, males began to emerge before the initiation of the advanced dark period. Observations were continued for 7 d before the dark period in the cycle was returned to "normal". The "usual" emergence pattern was re-established by the second day. Compared with a normal emergence sequence, the delayed onset of darkness promoted emergences of males, but not of females. The emergence of the females appeared to be more rigidly controlled by light, although it did show a significant advance of 20 min in the first emergence. Whether adults of *Pontomyia cottoni* in the field normally emerge after sundown is not known; we observed them only once at night at Geoffrey Bay.

We do not know what influences the emergence times of *Pontomyia* spp. in nature, although daylight and tides are probably important determining factors. The precise period in the tidal cycle when marine midges emerge is probably not as important for *Pontomyia* spp. as for certain other intertidal chironomids, e.g. *Clunio marinus* (see Hashimoto, 1976; Neumann, 1976), which must emerge just before or at low tide so that the adults can mate and lay eggs before the larval habitats (intertidal rocks) are covered by water. *Pontomyia* spp., however, does not depend on exposed rock surfaces for mating and egg-laying, since copulation occurs on the water surface, the eggs are adapted for being laid on water, and the larvae can develop in habitats permanently submerged.

Although it may not be too important for *Pontomyia* spp. to synchronize emergence with the tidal cycle, the

emergence times of the males and females must be synchronized since the adults live for only about an hour or two. Other important factors for ensuring their successful mating and reproduction are probably warm air and limited wave action. It is presumably more difficult for the males to locate and mate with the females if the water surface is agitated.

Males emerge at dusk or at night. They do not feed at all, but remain very active throughout their brief ephemeral adult life. When they are moving, the front legs and antennae are extended on both sides of the head and are not in contact with the water surface. The adult males are very thin and light; for example, the dry weight of a *Pontomyia natans* from Enewetak was 30 μg , and that of a *P. cottoni* from Townsville was only 23 μg . While the insect is in motion, the sole points of contact with the water surface are probably the skate-like claws at the tip of each hind tarsus (Cheng and Hashimoto, 1978). The insect is evidently propelled by the action of its wings alone, which enable it to skate on the water surface, though not to take off and fly.

Although the females have extremely reduced eyes, consisting of only 4 to 8 rudimentary facets (Cheng and Hashimoto, 1978), the males, which are strongly attracted to light, have well developed eyes; these presumably aid in the location of mates. Moreover, the relatively large maxillary palps of the male, which may be pheromone sensing organs, are possibly also involved in the mating process. It is conceivable that the females produce a 2-dimensional pheromone that is dispersed over the water surface, and that the males use sense organs on the legs or palps for detecting it and thus locating the passive females, but such a system has yet to be demonstrated.

Acknowledgements. We thank Dr. Hashimoto, Shizuoka University, Japan, for confirming the identification of the various *Pontomyia* species, Dr. R. A. Lewin for assistance in the field, and Dr. Z. Florian of James Cook University for assistance with photomicrography. L. C. acknowledges a grant from the Mid-Pacific Marine Laboratory, University of Hawaii, for research carried out at Enewetak Atoll, and the Roche Research Institute for Marine Pharmacology, Australia, for providing facilities at Heron Island.

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Date of final manuscript acceptance: May 30, 1980.
Communicated by N. D. Holland, La Jolla