Factors limiting the distribution of *Halobates* species

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Abstract

The open ocean is almost devoid of insects, except for members of the genus *Halobates*, first described in 1822. The *Challenger* expedition produced the first review on the genus but the next major review was not published until 1961. Until the late 1970s marine biologists paid very little attention to these unique insects. We now recognize 45 species in the genus, five being pelagic, the rest distributed in tropical nearshore habitats, often endemic to island groups. Since many remote tropical islands have rarely or never been visited by marine entomologists, it is likely that new species remain to be discovered.

The five pelagic *Halobates* species (*H. micans, H. germanus, H. sericeus, H. splendens* and *H. sobrinus*) are widely distributed in the World's oceans, roughly between latitudes 40°N and 40°S. All five species are found in the Pacific; the first two also occur in the Indian Ocean, but only one, *H. micans*, occurs in the Atlantic Ocean. The broad limits of distribution of the genus are probably determined by surface currents and sea-surface temperatures. Very few specimens have been collected outside the 20 °C or 21 °C isotherm. Within this warm water region, higher populations are generally found in areas where the surface water is warmer (above 24 °C). Specimens have also been collected further north than latitude 40°N, presumably having been carried by winds or currents beyond their normal distribution range.

Distribution ranges of all five species in the World's oceans are presented. In the Pacific Ocean, the ranges of the five ocean-skater species are discrete. There is some overlap in the distribution ranges, but areas where high population densities occur are quite separate. Although factors determining the broad geographical ranges of each species are likely to be mainly physical, e.g. temperature and surface currents, biological factors such as competition and food availability may also be involved.

Keywords: *Halobates*, distribution, marine insects, sea skater.

Introduction

Halobates is the only large genus of the water-strider family Gerridae found in marine environments. It was first described by an Estonian naturalist, J.F. Eschscholtz, in 1822, when three species were collected during the Russian circumnavigational *Rurik* expedition. The first review of this genus by White in 1883, following the *Challenger* expedition, recognized 11 known species, including six new ones. On the basis of records from earlier expeditions, White concluded that five species were found in the Atlantic although only one was restricted there, six were found in the Indian Ocean, of which only two were restricted, and nine were known from the Pacific Ocean. However, of the five species originally reported from the Atlantic Ocean (White, 1883), two were synonymised by Herring (*H. streatfieldanus* Templeton and *H. wüllerstorffi* Fraunfeld are both *H. micans*), and two others (*H. sericeus* and *H. flaviventris*) were mis-identifications, leaving only one species known from the Atlantic. When the second, major, review on *Halobates* was published in 1961 by Herring, a total of 38 species were known. Herring provided a key to all the species and also maps of the known distributions of many species. He divided the genus into two groups, an open-ocean and a coastal group. Several more species have been added since then. The genus now contains some 44 species, with seven belonging to the open-ocean group and the rest to the coastal group. However, about half of the species are known only from type specimens or locations (Cheng 1985). Undoubtedly more species remain to be described (Cheng & Holdway 1983) as more and more remote tropical islands are visited by biologists. Although Herring (1961, 1964) recognised seven species for his open-ocean group, two, *H. eschscholtzi* Herring and *H. trynae* Herring, are known only from the type specimens. The other five, *H. micans* Eschscholtz, *H. germanus* White, *H. sericeus* Eschscholtz, *H. sobrinus* Barber, and *H. splendens* Witlaczil, are widely distributed. In this paper only the distributions of these five pelagic species are considered.

Materials and methods

The data used in this study have been either gathered from the literature or based on specimens in my collection since 1970. The *Halobates* samples have either been collected during various oceanographic expeditions of the Scripps Institution of Oceanography, or have been given or loaned to me by colleagues in other institutions in Bermuda, Canada, China, France, Germany, India, Japan, Spain, the UK and the USA. In all, data from over 2000 samples collected by over 20 institutions, together with a few of the samples presented by individuals, have been used in compiling the distribution maps. In addition, locality data from the literature, chiefly those from Herring (1961), have been included.

Results

The distributions of the five pelagic *Halobates* species, compiled from known locality data, are presented in Figures 1-5.

Halobates micans is the only species found in all three major oceans, and is the only species found in the Atlantic Ocean. Its distribution in the Atlantic is roughly between latitudes 40°N and 40°S. However, there is a conspicuous gap in the SE Atlantic between 20° and 40°S and east of 30°W in longitude (Figure 1). Although the south Atlantic is less well sampled than the north, the evident absence of *Halobates* in this area is probably real (Cheng & Schulenberger 1980). In the Pacific this species occupies a zone roughly between 20°N and 20°S, except in the western Pacific, where it extends further north to the coasts of Japan and south towards Queensland, Australia. In the Indian Ocean it is found from the continental edge to 10°S, except in the western half where it extends along the coast of Africa to almost 40°S.

Halobates sericeus is found only in the Pacific Ocean (Figure 2). It is absent from a zone about 5 degrees north or south of the equator, and has an amphi-tropical distribution, more extensive in the north than in the south. It is almost completely absent from a large area off the coast of South America (see Figure 2).

Halobates germanus is found in both the Pacific and the Indian Oceans (Figure 3). It is absent in the eastern Pacific and has a distribution more extended in the south than north of the equator. It appears to follow more closely the coasts of islands, being found closer to shore than *H. micans*. It has been found in large numbers in the Red Sea (Cheng & Holdway 1983) and is the only pelagic species found there. It occurs also in the Gulf of Oman and may have penetrated the Persian Gulf, but we have no collections from that area. Although the Mediterranean Sea has been sampled extensively, no *Halobates* has yet been reported there.

Halobates sobrinus occupies a rather limited area off the coast of Mexico and central America (Figure 4). The south-western limits of distribution of this species are quite well established, based on collections made on the EASTROPAC expedition, where an area extending from the coast of America to 125°W and between latitudes 20°N and 20°S was sampled on a seasonal basis for a period of 15 months (Cheng & Schulenberger 1980). Additional samples from other cruises have extended the northern boundary of this species into the Gulf of California.

Halobates splendens is the rarest of the pelagic species. In no samples in the EASTROPAC survey have we obtained more than 10 specimens (Cheng & Schulenberger 1980). It occurs off the coast of South America and appears to have a northern limit at 10°N (Figure 5). It extends much further out to sea than *H. sobrinus*. Although in my collection the westernmost sample was taken at about 125°, Savilov (1967) reported collecting this species at a single station at 140°W, near the northern Marquesas Islands. My samples from that area were all identified as *H. hawaiiensis*, a species of the same size as *H. splendens* and rather similar in male genitalia morphology (Herring 1961). Until more samples become available, a conservative distribution range for *H. splendens* is given here.

Discussion

Ocean-skaters are totally wingless and thus cannot fly. They do not dive either, although if they are pushed under water they are able to swim and must eventually break surface if they are not to drown. They therefore live in a strictly two-dimensional environment at the sea–air interface, seemingly without any other physical barriers. Theoretically it would be possible for ocean-skaters of any species to move to any corners of the World Ocean, but evidently they do not do so. What factors limit the distributions of the various species? The most likely ones are physical and biological; chemical factors are probably of negligible importance, although local oil-spills and other agents that may alter the surface tension or surface-film properties of the sea must adversely affect the survival of these ocean-surface insects. Evolutionary considerations may also be of some significance.

The most important physical factors are temperature and surface currents, perhaps also surface winds. Data from several expeditions have shown that ocean-skaters are either absent or very rare when sea surface temperatures fall below 20 °C (Savilov 1967, Scheltema 1968, Sagaydachnyy 1975, Cheng & Schulenberger 1980, Cheng & Schulz-Baldes 1981, John 1982). At higher temperatures, not only are the frequencies of occurrences increased, but also the populations densities (Cheng & Schulenberger 1980, Cheng & Schulz-Baldes 1981). Although we do not know how temperature affects the physiology and reproduction of the different species, in the Pacific Ocean *H. micans* is restricted to the warmer, tropical waters, whilst *H. sericeus* is found in the cooler parts. The separation of these two species may also be main-

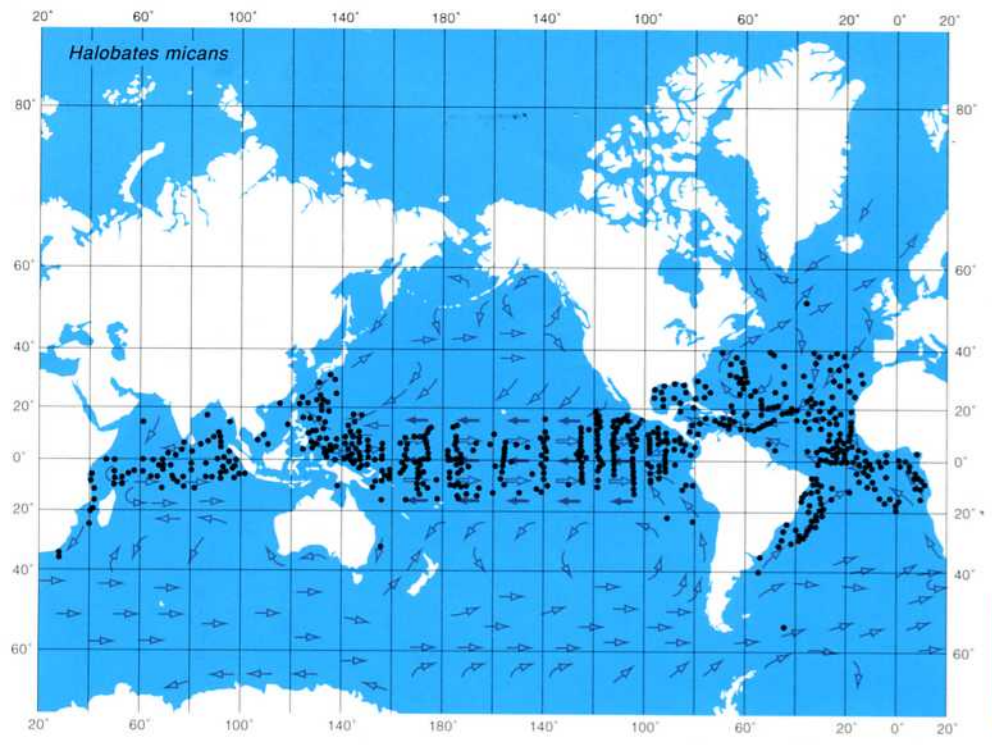


Figure 1.
World distribution of *Halobates micans*.

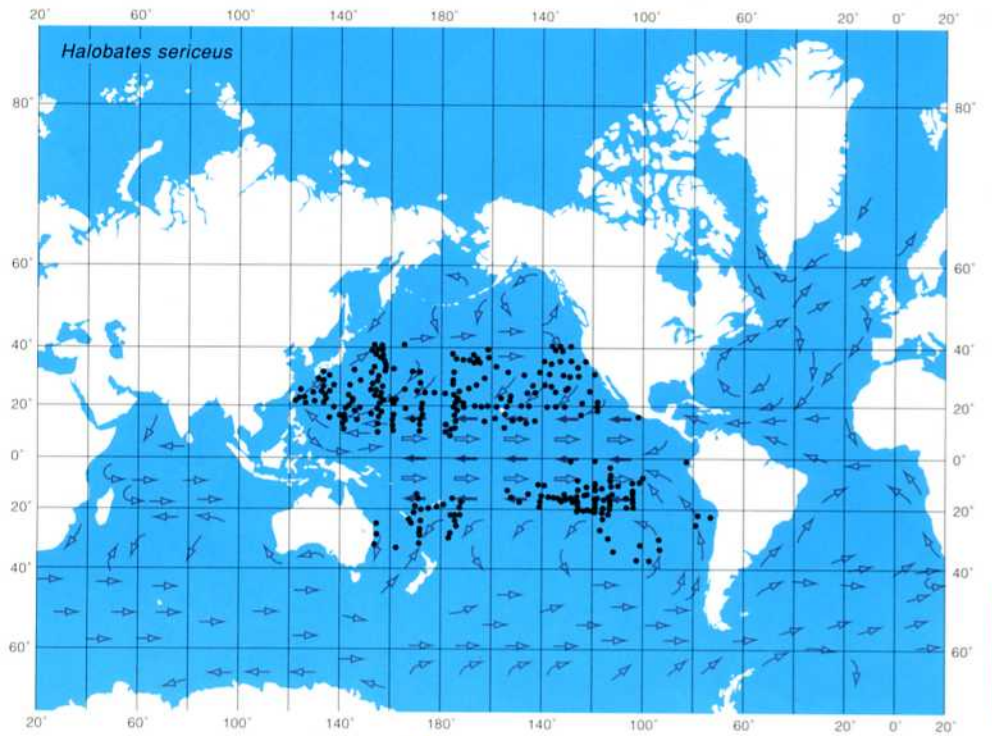
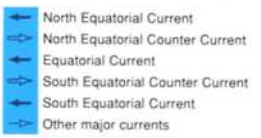


Figure 2.
World distribution of *Halobates sericeus*.



tained by the North and South Equatorial Currents (Herring 1961, Cheng & Schulenberger 1980) (Figures 1 & 2). The patterns of distribution of the other three species, *H. germanus*, *H. sobrinus* and *H. splendens*, do not appear to be so clearly limited by surface currents.

Biological factors limiting distribution include predators, food, and competition between closely related species for food or habitat. The only known important predators of oceanic *Halobates* are two species of sea birds, the Blue-grey Noddy (*Procelsterna cerulea*), and the Bonin Petrel (*Pterodroma hypoleuca*) (Cheng & Harrison 1983). Although several other seabirds are also known occasionally to take *Halobates*, these insects have not been found to be important items of their diet. Surface-feeding fishes are also likely predators but there are very few relevant data. It

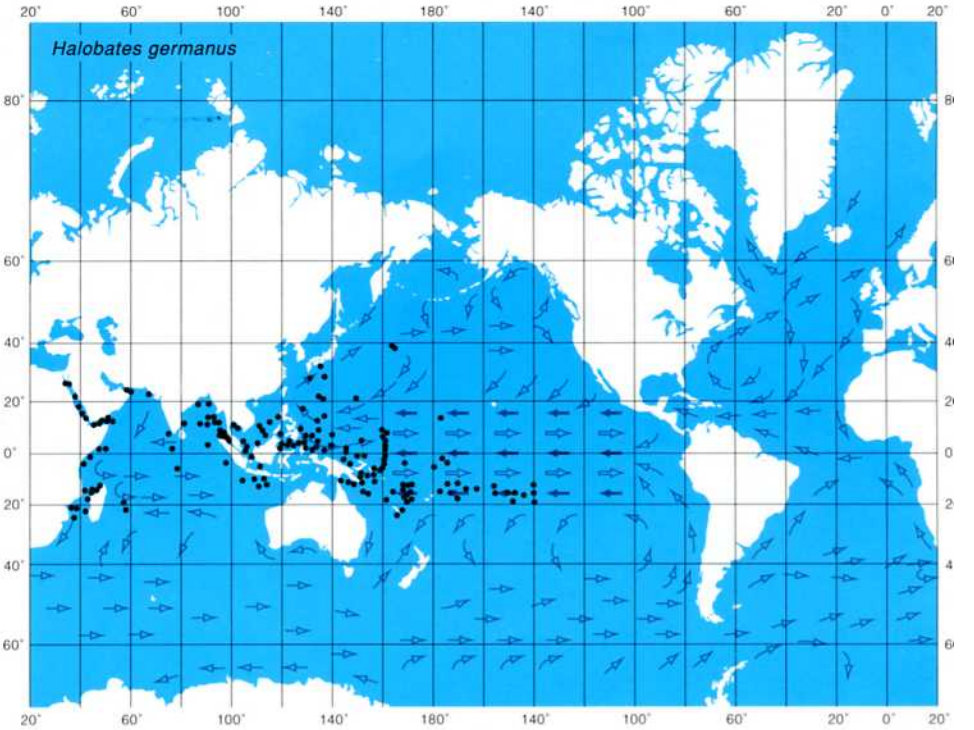
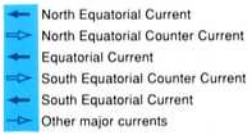


Figure 3.
World distribution of *Halobates germanus*.



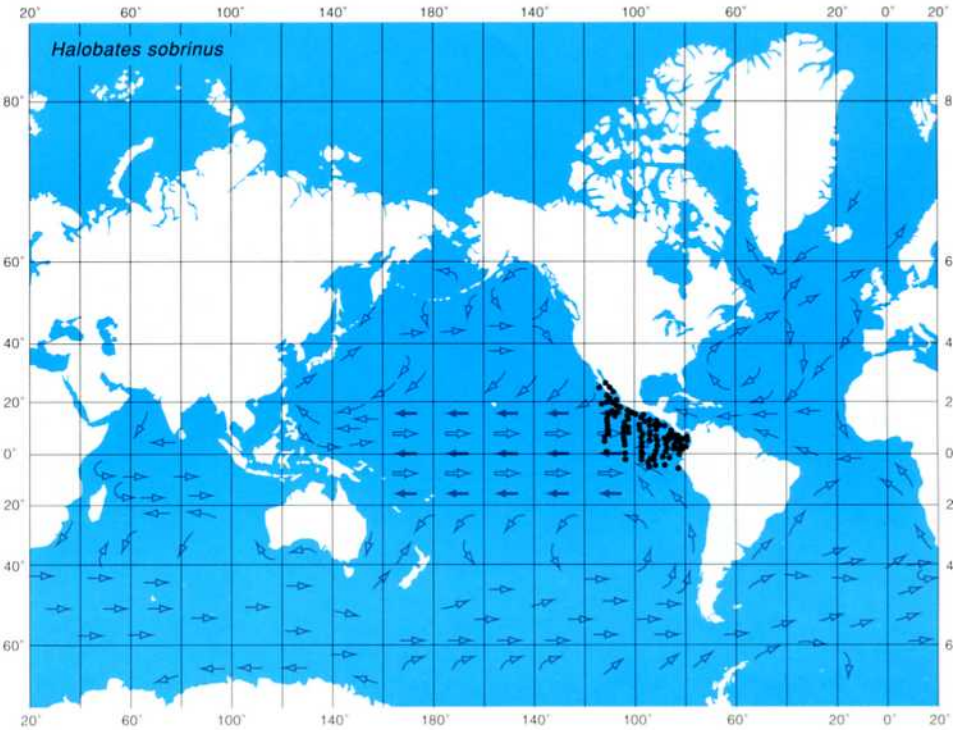
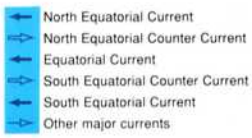


Figure 4.
World distribution of *Halobates sobrinus*.



seems unlikely that the distribution patterns of pelagic *Halobates* would be determined by predators.

Halobates themselves are predators; they capture prey organisms at the sea-surface and suck their body contents (Cheng 1974). Oceanic *Halobates* store lipids in the form of triglycerides, which can presumably be metabolised when there is food shortage, enabling the insects to survive periods of starvation for up to two weeks (Lee & Cheng 1974): Sagaydachnyy (1975) suggested that the distribution of *H. germanus* in the Indian Ocean could be limited by food, but he presented no evidence for this.

Another limiting factor may be oviposition substrata (Sagaydachnyy 1975, Andersen & Polhemus 1976). Eggs of *Halobates* have been found on all sorts of flotsam

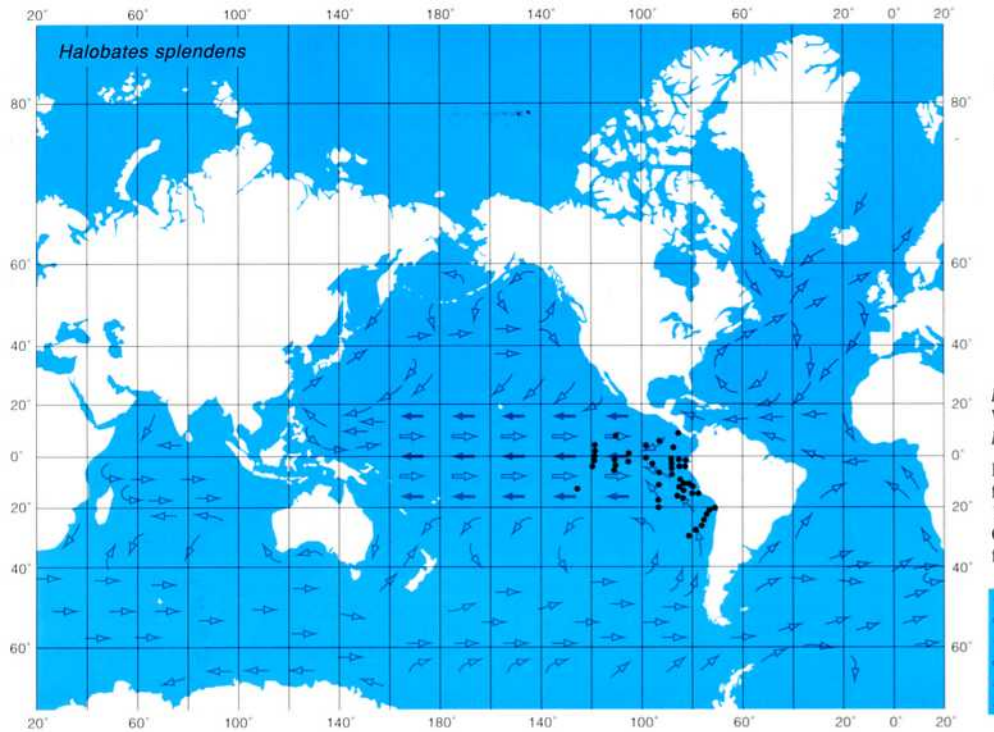


Figure 5.
World distribution of *Halobates splendens*.

Figures 1, 2, 4 and 5 updated from Cheng & Schulenberger 1980. Figure 3 updated from Cheng 1973. Surface currents from McLellan 1965.

such as pieces of algae, plastic, wood, cork, mollusk shells, seabird feathers, tarlumps, seeds and even bodies (presumably dead) of other *Halobates* and seabirds (Lundbeck 1914, Delsman 1926, Cheng 1974, Andersen & Polhemus 1976). However, no quantitative studies are available to indicate that their paucity limits *Halobates* egg production. Stoner & Humphries (1985) did not find any correlation between the abundance of *Halobates* and *Sargassum* in the Northwest Atlantic. Another limiting factor is the finding of mates. Although individual *Halobates* may be brought into close proximity by surface currents and/or winds, how they eventually meet and mate is not known. Mates could possibly be located by sight, by propagation of ripples, as employed by some freshwater gerrids (Wilcox 1972), or by surface pheromones (Birch *et al.* 1979).

One of the most interesting and unexplained features of the distribution of *Halobates* is the complete absence of coastal species in the Atlantic, where only one pelagic species is found. One might speculate that *H. micans* is the oldest of the pelagic species, which had evolved from some brackish-water ancestor in the southeast Asian or Indo-Malaysian region (see Cheng 1989), and reached the Atlantic before the last closure of the Isthmus of Panama, some 3 million years ago. Conversely one might speculate that more species of *Halobates* had been present in the Atlantic but that they were completely exterminated during the Ice Ages. Changing seawater temperatures during the last Ice Age which ended some 20 000 years ago are believed to have caused the disappearance of certain animals such as coral-inhabiting barnacles (Ross & Newman 1973) and corals (Wells 1957) in the Atlantic Ocean. This is nevertheless not likely to be the case for *Halobates*, since, unlike corals and barnacles which are sedentary, these insects can move freely without meeting physical barriers to areas where seawater temperatures may be more suitable for their survival and reproduction. It seems much more likely that *Halobates micans* colonised the Atlantic Ocean either from the Pacific, via the Isthmus of Panama before it closed, or from the Indian Ocean around the Cape of Good Hope (Jaczewski 1972). Samples of *H. micans* have never been collected in the Panama Canal but some have been collected near the Cape of Good Hope from both coasts (see Figure 1). Although present-day surface currents do not seem to facilitate the dispersal of surface pleuston animals from the Indian Ocean to the Atlantic, such a dispersal event with a single gravid female need occur only once. Whether, nowadays Indian and Atlantic Ocean *H. micans* populations still inter-breed is not known. A third possibility is that *Halobates* is a relatively new genus originating in the Pacific region, and that *H. micans* was introduced to the Atlantic in historic times as eggs attached to vessels of early explorers (as suggested to me by J.T. Carlton). However, none of these speculations has any scientific support. It is necessary for us to gather more information on the temperature tolerances of the

different species; the degrees of relatedness of the five pelagic species to one another and to certain nearshore species, the evolutionary age of the genus, etc. Until such information becomes available we can only reiterate that, by and large, the distributions of the open-ocean *Halobates* species are determined by the interactions of surface currents and winds. Within these broad limits, the patterns of distribution of the various species may be established by their differential tolerances to temperature and, to a lesser degree, by the availability of oviposition substrates or food, though evidence for the latter possibilities is still lacking.

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