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BIOLOGY OF *HALOBATES* (HETEROPTERA: GERRIDAE)

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INTRODUCTION

Until about 10 years ago *Halobates* was probably known to only a handful of entomologists; outside this segment of the entomological world it was generally unknown. However, during the last 10 years there has been a great deal of research on various aspects of the biology of this unique insect genus. It has now become a well-known organism among marine biologists; ironically though, it is still not well-known among entomologists.

Insects are the most common of the metazoans, but it was generally thought that they are absent from the oceans, which cover some 75% of the earth's surface. We now know that insects in at least 14 orders, with some 1400 species, occur in various marine habitats (26), although in the open seas we find only members of the genus *Halobates*. These sea skaters, or ocean striders, are in the Family Gerridae of the Order Hemiptera and were discovered some 160 years ago by Eschscholtz (44). He included three species in his first description of the genus but said nothing about their biology. Between 1822 and 1883, when Buchanan-White described the *Halobates* collected during the *Challenger* Expedition, few papers were published on this genus. White (82) in 1883 listed 11 species, including 6 new ones, and provided a key to all described species. From then until 1961 a number of papers were published; many were descriptions of new species that were synonymized later, but some contained additional biological information. By far the most complete taxonomic treatment of *Halobates* was the review by Herring (53), who examined all available types described prior to 1960, synonymized many species, and described 14 new ones. He provided a key to all 38 species, maps showing the type locality or distribution of each of the non-endemic species, an annotated bibliography of earlier publications on the genus, and an account of some partial life history

studies that he carried out, together with notes from the literature. However, these insects remained more or less ignored by biologists for the next decade until interest was revived by Cheng (17). Since then, *Halobates* has become much better known to marine biologists and has been the subject of a variety of behavioral, biological, and biochemical studies. No attempt is made here to review the literature on *Halobates* prior to 1973, since it can be found in the earlier reviews of Herring (53) and Cheng (17). Instead, recent findings on this unique genus of insects are reviewed, with additional information from unpublished personal observations.

ORIGIN AND PHYLOGENY

There are no known fossils of *Halobates*. The family Gerridae dates back at least to the Oligocene (85). Most members of the family are pond skaters which commonly occur on the surfaces of freshwater streams or ponds. An excellent review of the world Gerridae was published in 1960 by Matsuda (60), and more recent studies on their phylogenetic relationships and zoogeography have been carried out by Calabrese (12, 13) and Andersen (4). *Halobates* is considered to be one of the more advanced members of the family. Although the majority of the Gerridae are freshwater inhabitants, there are a few genera besides *Halobates* that have representatives living in marine environments, e.g. *Rheumatobates*, *Asclepios*, *Stenobates*, *Rheumatometroides* (5). Of these, only *Asclepios* belongs to the same subfamily as *Halobates*, and it is the most likely ancestral form (53). Herring proposed that *Halobates* could have originated from an *Asclepios*-like ancestor in southeast Asia, since three of the four known species of *Asclepios* are found in that area (36, 53). Furthermore, at least 50% of the known coastal *Halobates* species occur in that area (see Figure 1), which is especially rich not only in Gerridae but also in other aquatic Heteroptera (33).

Circumstantial evidence from a recent study on the chromosomes of *Halobates* and *Asclepios* (64) lends support to Herring's hypothesis. For example, in all freshwater gerrids thus far investigated the chromosome numbers range from 19 to 23 (see 64). Newman & Cheng (64) found *Asclepios shiranui* to have 23 chromosomes, but in 4 *Halobates* species the number was 31, the highest recorded for any Gerridae. Since these insects have holocentric chromosomes, it is not unreasonable to postulate that breakages of such chromosomes may have given rise to the increased chromosome numbers found in the more advanced species (64).

GENERAL MORPHOLOGY

Unlike freshwater pond-striders, which may be either winged or wingless, all marine *Halobates* are permanently wingless. Wings, which are presumably useful for dispersal or migrations between discontinuous habitats, would be of

little use in the sea. The body of a sea skater is typically short and broad, and in the adult stage it may reach a maximum length of 6.5 mm and may be about 3.0 mm in width. The antennae are long and slender and are never modified. The front legs are short and used for grasping prey while feeding or for holding the female during mating; they are not used for locomotion, which is done principally by the long middle legs. The tibiae and tarsal segments of the middle legs are lined by long hydrofuge hairs, which may help in reducing friction between the legs and water surface, thereby allowing these insects to skate more effortlessly over the water surface (1). The hind legs, which are much shorter than the middle legs, are used more for steering than for propulsion. The hind tibiae and tarsal segments are also lined with hydrofuge hairs. The rostrum is 4-segmented and relatively short, not extending beyond the prosternum.

The nymphs are very similar to adults in external morphology, and there is no external sexual dimorphism until the last nymphal instar. Adult males, generally longer and thinner than females, have the last two or three abdominal segments modified to form the genitalia. Otherwise there are no structural differences between the sexes. Males of different species can be distinguished by differences in genitalia. Females, however, are very similar and difficult to identify. The abdominal tergum of most females is flexible, allowing for expansion during egg maturation; females that contain matured eggs may have a markedly humped abdomen (4).

LIFE HISTORY

There have been no complete life history studies on any species of *Halobates*. Some observations have been made on a few coastal and open-ocean species, and it is becoming clear that there are several consistent differences between the two groups.

The eggs of coastal *Halobates* are laid on substrates near shore. When brought to the laboratory and kept in an aquarium, *Halobates flaviventris* from Palau, West Caroline Islands, laid eggs glued to the container wall, 9 to 39 mm below the water level, in two distinct depth groups: one at 15–20 mm and the other at 35–40 mm below the water surface. There were no eggs at 0–9 mm or 20–31 mm depths. Of 59 eggs found, 21 were laid singly, 6 clusters were of 2 to 5 eggs, and 1 cluster had 16 eggs, probably all laid by a single female. Gravid *H. flaviventris* females dissected at Palau were found to contain from 2 to 20 fully matured, olive-green eggs (L. Cheng, unpublished data). Newly laid eggs are also olive green, but they turn bright orange in 2 to 3 days. As the embryo develops, the eyes become crimson, and dark grey pigmentation outlining the antennae, legs, rostrum, and the head and body segments can be seen clearly through the semitransparent chorion. Prior to hatching, the eggs are dark grey except for the eyes, which remain bright orange or crimson. In Palau, where the

seawater temperature in June 1981 was 29 to 30°C, the duration between egg laying and hatching was 17 days.

In the open ocean the eggs are laid on floating substrates: feathers, small pieces of wood, mollusk shells, seeds, tar lumps, insect carcasses, etc. I have found two fourth-instar nymphs of *H. micans*, from the Atlantic Ocean, bearing eggs on the dorsal surfaces. The development of the embryos of *H. sobrinus* is similar to that observed for *H. flaviventris*, although in a batch of *H. sobrinus* eggs collected near La Paz, Baja California, in November 1974 and studied in the laboratory, development took much longer. In that sample several hundred eggs had been laid all over a tar lump approximately 1.5 cm across; in some places they were two or even three egg-layers deep. The eggs hatched (up to 50 per day) sporadically over a period of 30 days, suggesting that embryo development might take up to one month at 20°C. In about 90% of the developing embryos, the ventral surface faced upwards, with the crimson eyes and the neatly folded antennae and legs clearly visible through the translucent chorion. Some 10% of the eggs were slightly turned to one side, with only one eye visible from the top. When the embryo was ready to hatch, the abdomen contracted 6 to 7 times at approximately 2-sec intervals. A slit was then made with the chitinized egg burster, and the head emerged followed by the abdomen. The legs were then pulled out, leaving the embryonic skin behind. The entire process took about 3 min.

Egg hatch was followed at 2-hr intervals for 2 days. Less than 10% hatched during each of the periods of 0–4 hr and 12–18 hr. The majority (51%) hatched between 4 and 10 hr, and about 20% hatched between 20 and 22 hr. Since newly hatched nymphs are more susceptible to predation, the timing of egg hatch might be an important factor in reducing nymphal mortality.

Despite diligent searches carried out in the field on many occasions, I have not found any eggs on coastal rocks or on submerged mangrove branches or roots. This is unexpected since nearshore *Halobates* presumably oviposit on such substrates.

Newly hatched nymphs of *Halobates* measure about 1 mm in body length. The cuticles, initially pale, become tanned within an hour or two, and the young insects are able to move about in a jerky fashion soon after hatching. Attempts to feed newly hatched nymphs of *H. sobrinus* in the laboratory have not been successful; in one rearing study they all died within five days of hatching. The young nymphs occasionally preyed on one another, but they did not feed on any marine organism or on freshly killed *Drosophila* offered to them, although older nymphs (from third instar onwards) and adults readily take such food organisms. How first instar nymphs survive in the open ocean is still a mystery. They may be able to utilize nutrients from the organic-rich surface film, but this has not been substantiated.

Development and molting of third to fifth instar nymphs have been observed

in *H. mariannarum* (24). Although it was not possible to follow any single nymph through the developmental period, by collecting and examining the molts it was possible to estimate that each nymphal stadium lasted 12–14 days. This is similar to the observations of Herring (53) on *H. hawaiiensis*: 8–10 days for the earlier instars; 10–12 days for later instars. He, too, was unable to follow the nymphs through a complete cycle.

In my laboratory population of *H. mariannarum*, molting occurred only between 0530 and 1100 hr, mostly before 0800 hr. Individuals ready to molt stopped feeding and appeared sluggish. Newly molted nymphs were very pale yellow or almost white, but tanning began almost immediately. Within one hour most insects had turned light brown, and within three hours they had attained normal coloration. Some one to two hours after the molt they began to feed.

Assuming that each nymphal stadium takes 12–14 days, the total developmental period from eggs to adult may last from 60 to 70 days. The most important factor for embryonic and nymphal development is probably temperature, as in the case of various freshwater gerrids studied (15, 77), although we have still no data for *Halobates*. Other information on eggs and nymphal development was published by Herring (53) and Selvakumar (74).

TAXONOMY

The taxonomy of *Halobates* was fully reviewed by Herring in his 1961 (53) monograph. Thirty-eight species were included in his key, which is at present the only workable key for the genus. Since this publication, six new species have been added: *H. trynae* from the Bay of Bengal (54), *H. esakii* from Brunei (61), *H. melleus* from the Sudan coast of the Red Sea (59), *H. mangrovensis* from the Gulf of Aqaba and the Gulf of Zulu on the Red Sea (70), *H. acherontis* from Darwin, Australia (66), and *H. herringi* from North Queensland, Australia (67).

Table 1 lists all the known *Halobates* species together with their broad ranges of distribution or type localities. Herring (53) recognized two basic groups of *Halobates*, the open-ocean and the near-shore or coastal group. The former includes seven species. However, since *H. eschscholtzi* and *H. trynae* are known only from their type locations, these two species are excluded from further considerations of open-ocean *Halobates* in this review.

The basic taxonomic characters distinguishing *Halobates* species are structures of the male genitalia; there are few specific differences in color pattern and few modifications on any of the appendages. When only females are available, lengths of various appendages may be used, but taxonomic uncertainties generally remain. For the five oceanic species, however, there is a satisfactory working key, even if only females are available (22). Nymphs can

Table 1 List of *Halobates* species described prior to 1982, with their known distribution

Species	Known distribution
1. <i>H. alluaudi</i> Bergroth	Seychelles; Mahe I.; Praslin I.
2. <i>H. browni</i> Herring	Kolombangara I.; British Solomons
3. <i>H. bryani</i> Herring	Fiji I.; Matuku I.
4. <i>H. calyptus</i> Herring	Philippines; New Guinea
5. <i>H. darwini</i> Herring	Australia
6. <i>H. eschscholtzi</i> Herring ^a	Zanzibar
7. <i>H. fijiensis</i> Herring	Fiji I.
8. <i>H. flaviventris</i> Eschscholtz	Indian Ocean; Pacific Ocean
9. <i>H. formidabilis</i> Distant	Andaman Sea; Bay of Bengal
10. <i>H. galatea</i> Herring	Arabian Sea
11. <i>H. germanus</i> White ^a	Indian Ocean; Pacific Ocean
12. <i>H. hawaiiensis</i> Usinger	Hawaii; Marquesas; Society I.; Tahiti; Tuamotu
13. <i>H. hayanus</i> White	Red Sea; New Guinea; Indonesia; Malaysia; Australia
14. <i>H. japonicus</i> Esaki	Japan
15. <i>H. katherinae</i> Herring	New Caledonia
16. <i>H. kelleni</i> Herring	Samoa
17. <i>H. kudrini</i> Nasanov	New Caledonia
18. <i>H. maculatus</i> Schadow	Solomon; New Guinea
19. <i>H. mariannarum</i> Esaki	Marianas; Guam; Caroline I.; Marshall I.
20. <i>H. matsumarai</i> Esaki	Japan; Formosa; Korea; China
21. <i>H. micans</i> Eschscholtz ^a	Atlantic Ocean; Indian Ocean; Pacific Ocean
22. <i>H. mjobergi</i> Hale	Australia
23. <i>H. nereis</i> Herring	Palau; New Guinea
24. <i>H. panope</i> Herring	New Caledonia
25. <i>H. peronis</i> Herring	Solomon I.; ¹ New Guinea; Philippines
26. <i>H. poseidon</i> Herring	Kenya
27. <i>H. princeps</i> White	Celebes; Malaysia; New Guinea; Palau; Moluccas; Java
28. <i>H. proavus</i> White	Moluccas; New Hebrides; Java; Philippines; Solo- mon I.; Malaysia; Nicobar I.
29. <i>H. regalis</i> Carpenter	Torres Straits
30. <i>H. robustus</i> Barber	Galápagos Islands
31. <i>H. salotae</i> Herring	Tonga
32. <i>H. sericeus</i> Eschsholtz ^a	Pacific Ocean
33. <i>H. sexualis</i> Distant	Malaysia
34. <i>H. sobrinus</i> White ^a	North and Central America
35. <i>H. splendens</i> Witlaczil ^a	South America
36. <i>H. tethys</i> Herring	Mauritius
37. <i>H. trynae</i> Herring ^a	Bay of Bengal
38. <i>H. whiteleggei</i> Skuse	Australia

Table 1 (continued)

Species	Known distribution
39. <i>H. zephyrus</i> Herring	Australia
40. <i>H. mangrovensis</i> Schmidt and Müller	Red Sea
41. <i>H. melleus</i> Linnavuori	Red Sea (Sudan)
42. <i>H. esakii</i> Miyamoto	Brunei
43. <i>H. acherontis</i> Polhemus and Cheng	Darwin, Australia
44. <i>H. herringi</i> Polhemus	Queensland, Australia

* Open-ocean species.

generally be identified only in association with adults. The developmental stages of nymphs can be assigned by comparing segment lengths of various appendages. Tables of nymphal measurements are available only for *H. micans*, *H. robustus*, and *H. mariannarum* (24, 38).

ECOLOGY

Habitat

All *Halobates* species have been found in marine habitats except for *H. acherontis*, which was recently described from the Daly River in Northern Territory, Australia (66). (However, although the specimens of this species were collected several kilometers upstream from the river mouth, no salinity measurements were taken.) Of the 44 species now known, only 5 live on the open ocean; the others are known solely from type localities or near coasts. Near-shore species of *Halobates* seem to prefer coastal areas fringed with mangrove, where they may occur in densities reaching 120 m^{-2} (8) and can be easily caught with a pond net or a plastic strainer. The adults are usually found in the more open areas away from the mangroves, whereas the nymphs, especially those of the first two instars, are more or less confined to shallow waters among the roots where they might be more protected from predators. I have seen extremely dense patches of young nymphs among aerial roots of mangroves in Fiji (*H. fijiensis*), Guam and Ponape (*H. mariannarum*), and the Galápagos (*H. robustus*). In coastal areas without mangroves, young nymphs are often found close to overhanging branches or rocks, e.g. *H. maculatus* in the Solomons and *H. nereis* in Palau, while adults and older nymphs ply more open waters.

Near-shore *Halobates* are rarely found along exposed coasts, e.g. on Rorotonga in the Cook Islands, unless mangrove or coastal vegetation is present. If there are islands with mangrove or other vegetation, some of the adult insects may wander from them to feed along more exposed sections along the coasts,

e.g. among the rock islands in Palau. Breeding populations appear to be more closely associated with vegetated coastal habitats, including bays, lagoons, and river mouths.

The five open-ocean *Halobates* species are usually caught by towing a neuston net over the ocean surface (10). They are seldom found close to shore except after storms. I have found hundreds of still living specimens of *H. germanus* stranded among wrack on Mana Island, Fiji, following an onshore wind storm. Another species, *H. micans*, was found under similar conditions on the Cayman Islands, in the Caribbean, and on the island of Moen in the Truk Lagoon, Caroline Islands (western Pacific).

Although the open ocean surface appears to be a habitat without physical boundaries, *Halobates* tends to concentrate in patches. Physical oceanographic properties that may limit or control the occurrences of ocean skaters in such areas are discussed in the next section.

Distribution

The type locations of the 39 coastal *Halobates* species (including *H. eschscholtzi* and *H. trynae*) are shown in Figure 1. The great majority of the species are found in the Indo-Malaysian and Australasian region, which is probably the center of evolution of the genus. Not a single coastal species has been found in the Atlantic Ocean. Although many of the coastal species are known only from their original type locations (see Table 1), we cannot safely conclude that they are truly endemic, since sea skaters may occur around remote islands seldom visited by marine biologists and, even more rarely, by entomologists (23, 37, 39). Certain species found around islands in areas for which there is considerable collecting information may indeed be endemic (e.g. *H. robustus* in the Galápagos Islands). A few of the coastal species are very widely distributed, e.g. *H. flaviventris*, *hayanus*, *mariannarum*, but each is confined to some well-established geographic area where it could easily have spread from island to island by following oceanic currents. The distribution pattern of *H. hawaiiensis* is not so easily explained. This species has been reported from the Hawaiian Islands, situated around 20°N, and also from a group of islands (Tahiti, etc.) located around 20°S (see Table 1). Specimens from Hawaii and Tahiti are apparently indistinguishable. It would be interesting to find out whether they could interbreed, actually or potentially, since the island groups are about 5000 km apart and there are now no known ocean-surface current systems connecting them. The populations of *H. hawaiiensis* may be remnants of a more widely distributed species as in the case of certain barnacle species (W. A. Newman, personal communication).

The distributions of the five oceanic *Halobates* species are now well established (17, 20, 25, 37, 42). They are all in tropical or subtropical waters where the winter temperature does not fall much below 15°C (Figure 2). Their

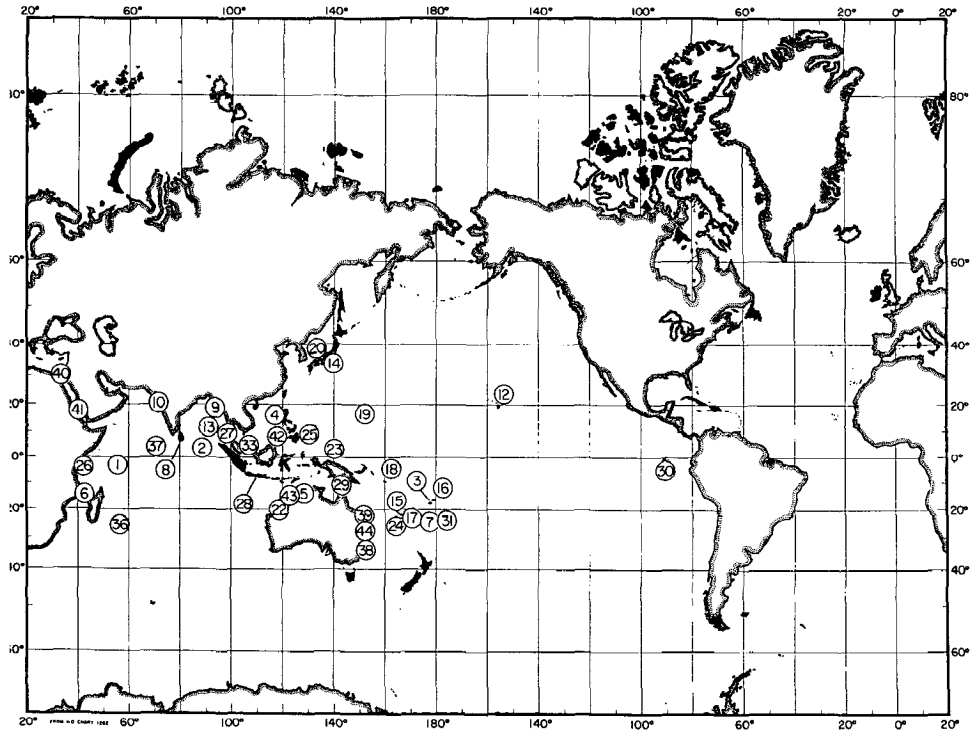


Figure 1 Type locations of coastal *Halobates* spp (including *H. eschscholtzi* and *H. trynae*). Species numbers given in Table 1.

occurrence and abundance on any given water mass is apparently controlled by surface water temperatures (40, 42). The optimum temperature range for 4 eastern Pacific species is 24–28°C (42).

Halobates micans is the only cosmopolitan species found in all three major oceans (Figure 2). In the Pacific and Indian oceans its range is generally confined to a zone between about 20°N and 20°S, but it expands to 40°N to 40°S in the Atlantic Ocean. In the western Pacific Ocean this species may extend northward beyond 20°N towards Japan, possibly being carried there by the Kuroshio Current; there is a similar southern extension in the western Indian Ocean attributable to the Angulhas Current (Figure 2). The unequal distribution of this species in the North and South Atlantic presumably is also caused by surface current systems. The species is more or less evenly distributed in the northern section but is almost completely absent from the subtropical South Atlantic (42). The northern extension is probably influenced by seasonal warming of surface water (57).

The other four species of ocean skaters are all found in the Pacific Ocean, but they have very different distribution patterns (see Figure 2). *H. sericeus* is the

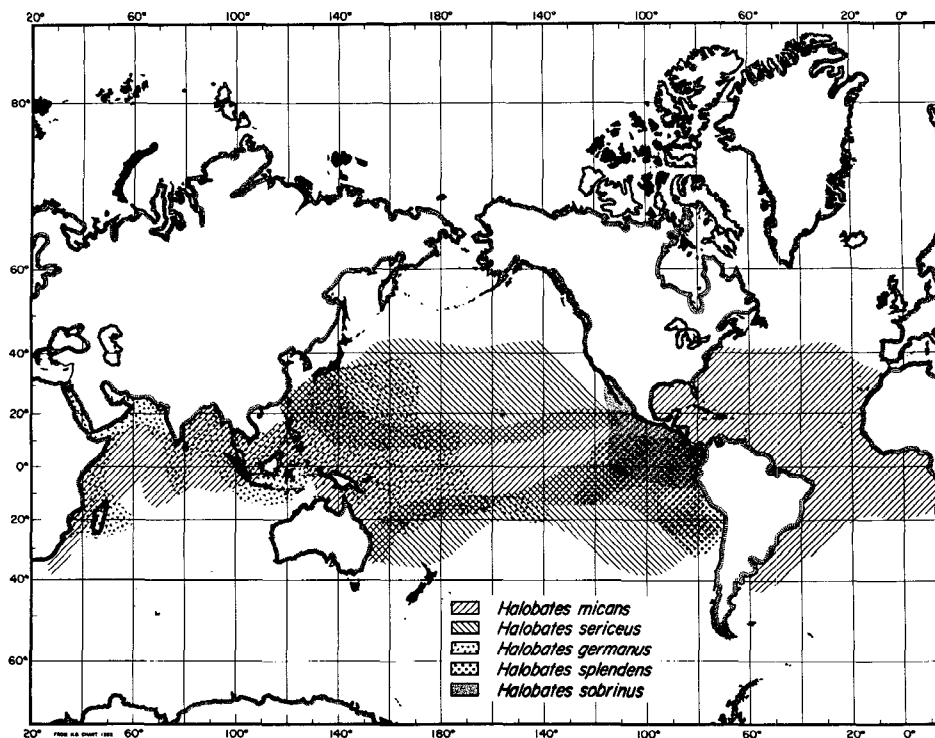


Figure 2 Ranges of distribution of the five major oceanic *Halobates* spp.

most widespread, with a bipolar distribution rather like those of certain zooplankton organisms with planktonic larvae in the water column (9, 68). It is rather unusual for a surface-dwelling pleustonic organism to show such a discontinuous distribution. The absence of *H. sericeus* between about 12°N and 12°S (established by an abundance of negative data; 42) may be due to competition with *H. micans*. Although specimens of both species may occur together in some locations, there is no overlap in their ranges in areas where they occur in high densities (Figure 3; 42). *H. sobrinus* and *H. splendens* are rather more restricted in their distributions, and they tend to be more coastal than *H. micans* or *H. sericeus*.

The remaining open-ocean species, *H. germanus*, is found both in the Pacific and Indian oceans, where, like *H. splendens* and *H. sobrinus*, it seems to follow the coasts of the continents and islands (Figure 2). During the circumnavigational cruise of "Operation Drake" (37), *H. germanus* was collected at several stations. Its population densities (as expressed by number of insects caught per standard 30-min tow; 37) were much higher in the Java Sea and Red Sea (respectively 46.2 and 27.3) than in the Pacific Ocean proper (2.6), but no specimen was caught in the open stretch of the Indian Ocean (37).

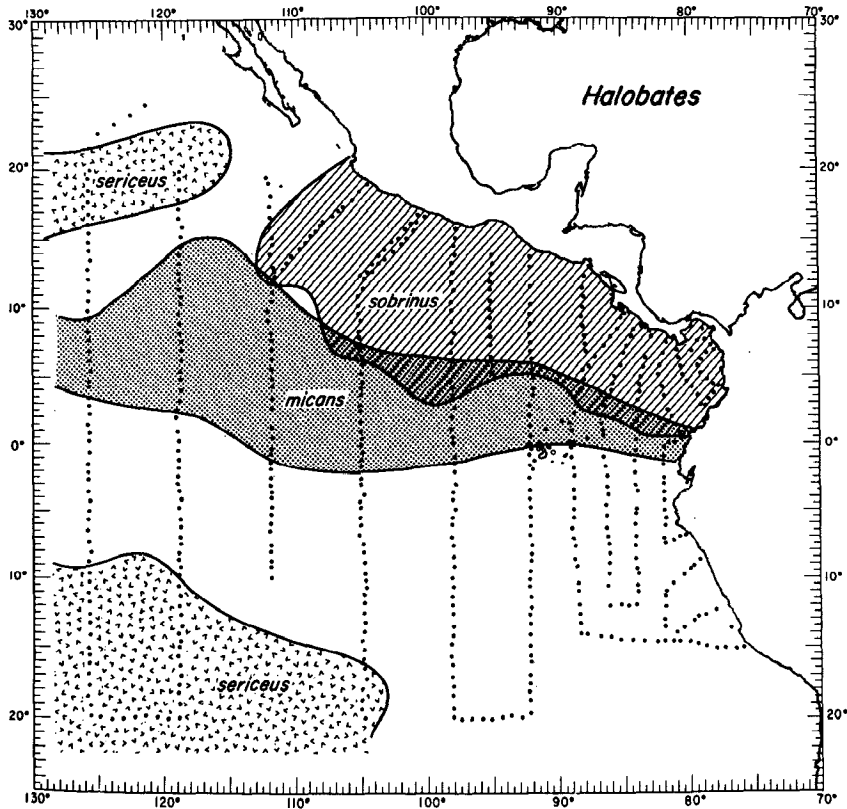


Figure 3 Areas of high population densities of three *Halobates* spp. in the eastern tropical Pacific Ocean (42).

Similar observations have been reported by Sagaydachnyy (69), who suspects that *H. germanus* may have different food preferences from *H. micans*, which could account for its somewhat more coastal habitat.

Food

Sea skaters are predaceous. They have typical hemipteran sucking mouthparts where the mandibular stylets have toothed ends used for cutting and the maxillary stylets are held together by fine ridges to form the feeding tubes (20). When the insects are not feeding, the stylets are retracted into the short rostrum. The diet of *Halobates* is varied. In general, near-shore species feed on land insects trapped at the water surface (46), which can be rather abundant offshore (29, 30), but open-ocean species feed on various zooplanktonic organisms (20) as well as on floating insects. Cannibalism has been observed, both in the field and in the laboratory, among pelagic as well as nearshore sea skaters. Adults

and older nymphs may feed on younger nymphs, but adults have never been seen to feed on one another. In the Galápagos, Foster & Treherne (46) found that 15% of the prey of *H. robustus* were specimens of their own kind. I have never observed or been able to induce any *Halobates* to dive either for food or for anything else. Foster & Treherne (46) found the same was true for *H. robustus*. Sea skaters probably detect food either by sight (dead prey) or by sensory detection of ripples created by prey struggling at the water surface, as has been observed in freshwater Gerrids by Murphey (62). Although I have found that *H. sobrinus* and *H. sericeus* prefer living, struggling fruit flies to immobile ones, Foster & Treherne (46) reported that coastal *H. robustus* avoided struggling prey. If the prey is small, it is generally grasped by the sea skater's front legs and held completely free from contact with the water surface (Figure 4 and 5), presumably so that there are no ripples from a struggling prey to attract attention from other potential predators. When the prey is large and too heavy to lift, such as a small fish, I have seen three to four sea skaters feeding simultaneously on the same animal. Other information on feeding behavior can be found in the paper by Foster & Treherne (46). Feeding time obviously depends on the relative sizes of the prey and the consumer, as shown for the freshwater *Gerris* (56). A laboratory-reared fruit fly, *Drosophila melanogaster*, can be sucked "dry" by an adult *Halobates* in less than 20 min. In my experience, one or two flies per day suffice for each adult *H. mariannarum*. The feeding processes in *Halobates* are presumably similar to those of other freshwater Gerrids (14), where a digestive enzyme is secreted and pumped into the prey's body to fluidize the muscles and other body contents. The liquid food is then sucked up through the food canal.

Predators

Surface-feeding seabirds are the most important predators of pelagic *Halobates* spp. (20, 35). Remains of *H. micans* have been found in guts of the bridled tern (*Sterna anaethetus*) in the Seychelles (43; L. Cheng, unpublished data). Although *H. sericeus* was found in the regurgitates of 9 out of 18 bird species studied in the Northwestern Hawaiian Islands (35), this food item is important in the diet of only four species: the blue-gray noddy (*Procelsterna cerulea*), the Bonin petrel (*Pterodroma hypoleuca*), the gray-backed tern (*Sterna lunata*), and Bulwer's petrel (*Bulweria bulwerii*). The blue-gray noddy and the phoenix petrel (*Pterodroma alba*) had been earlier reported to take considerable numbers of ocean skaters (6, 20), but in those studies sample sizes were too small for quantitative assessments. In a more recent study, Cheng & Harrison (35) found *H. sericeus* in 153 out of 627 (24.4%) regurgitates from the four major bird predators listed above. For the most important predator, *Procelsterna cerulea*, some 81% of the sampled birds had fed on *Halobates*, and the average number of insects per food sample was 30. This diminutive bird,

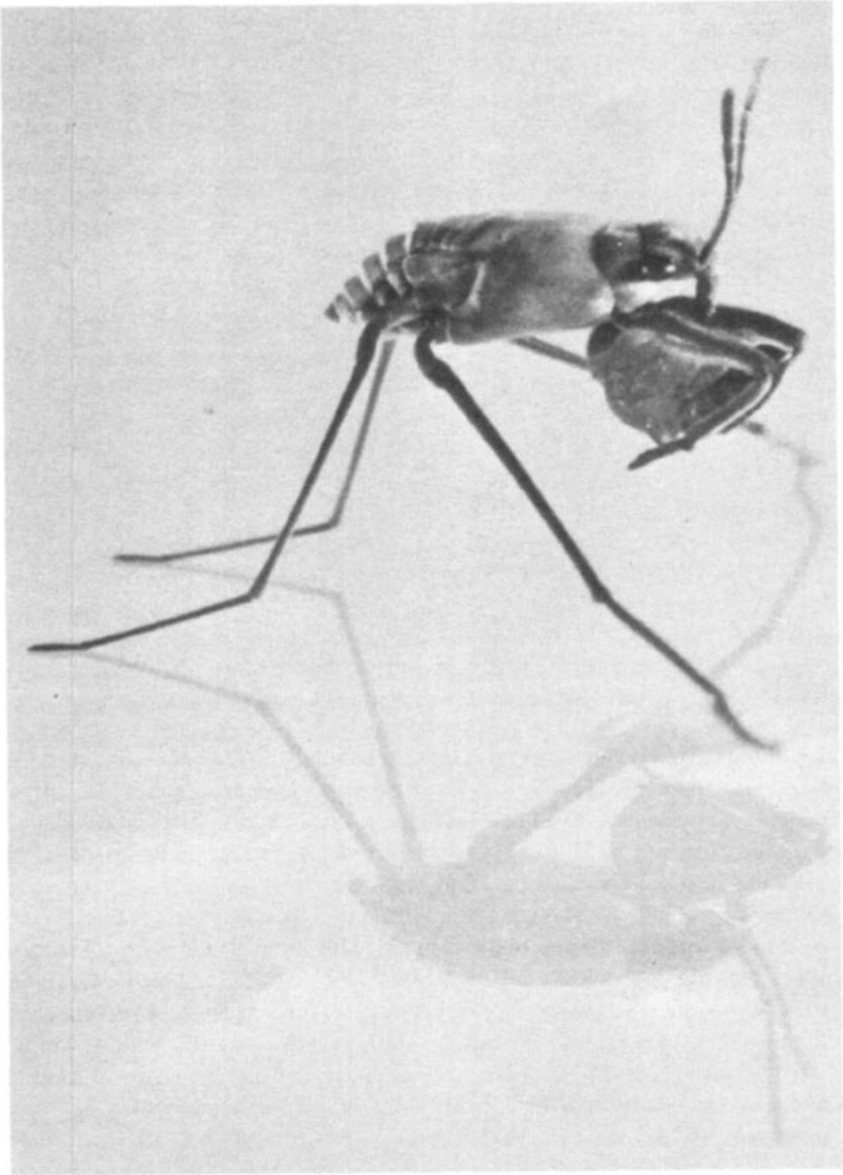


Figure 4 *Halobates sericeus* female feeding on de-winged fruit fly.

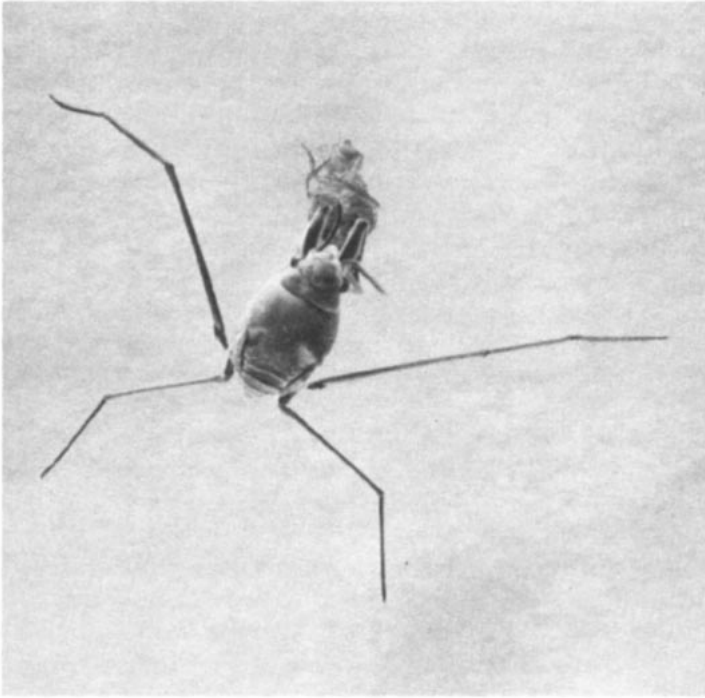


Figure 5 Top view of living *Halobates sericeus* female feeding on a de-winged fruit fly.

weighing only about 50 gm, can at times feed solely on *Halobates* and no doubt is a very important predator on sea skaters in the open ocean. [The energy content of *H. flaviventris* adults was found to be 5.8 kcal g^{-1} dry wt (L. Cheng, C. S. Harrison and T. N. Pettit, unpublished data), a value similar to that of the plant bug *Philanaenus* (Jassidae) and within the range given for several invertebrates (76, p. 360).] Although around the Hawaiian islands the coastal species *H. hawaiiensis* can often be found in appreciable numbers (35), we did not find specimens of this species in any of the 1500 bird stomach samples we examined (35). We do not know whether pelagic birds also feed on coastal *Halobates* spp. In the Galápagos Islands predation on *H. robustus* by the yellow warbler (*Dendroica petachia*), small fish (*Sardinops sagax* and a species of mullet), and on one occasion a lava lizard (*Tropidurus albemarlensis*) has been observed (46, 81).

Food-Chain Relationships

Halobates spp., whether coastal or pelagic, belong to the marine pleuston community (21). Although animals in this two-dimensional environment are confined to the sea surface, they interact with organisms that generally live

above or below them. Pelagic ocean skaters feed on zooplankton trapped at the sea surface. In areas where population densities of insects are high (up to $1 \times 10^4 \text{ km}^{-2}$; 42), they must remove a considerable number of prey organisms. However, since ocean skaters are fluid-feeders, it has not yet proved possible to study their diets by examining their gut contents or to estimate the impact of ocean skaters on the population of any zooplankton organisms. Eventually we should be able to develop immunological (45) or electrophoretic (51) methods suitable for such analyses. Coastal *Halobates* species probably feed largely on land insects that have been blown or washed out to sea or have fallen to the water surface from overhanging vegetation; unlike their open-ocean cousins, they have not been observed to take marine organisms. *Halobates* may fall prey to fish or seabirds and thereby contribute in some way to the recycling of nutrients in the marine environment, but it will be many years before we have enough quantitative data for estimating their trophic relationships in the pelus-ton (21).

Certain organic compounds and heavy metals are known to be concentrated at the sea-surface film, but their concentrations in the film are technically difficult to measure (52). *Halobates* species, which live at the sea-air interface in the open ocean, have been found to accumulate some of the heavy metals. Since they presumably obtain such metals either through bioaccumulation up the food chain or by drinking surface-film water, they could conceivably be used as indicators of heavy-metal pollution in the open ocean. It may be significant that bioaccumulation of some of the heavy metals, and of chlorinated hydrocarbons, was found only in pelagic *Halobates*, not in near-shore gerrids.

For example, Cheng & Bidleman (28) found that total DDT concentrations in *H. sobrinus* were 5–10 times higher than in specimens of the near-shore *Rheumatobates aestuarius* collected from the vicinity. The higher DDT concentration in *Halobates* was attributed to a diet of marine zooplankton organisms, which are themselves predators. *Rheumatobates*, on the other hand, feeding mainly on terrestrial insects, many of which may be phytophagous, would be less likely to concentrate DDT.

The contents of heavy metals, such as cadmium (Cd), copper (Cu), iron (Fe), lead (Pb), nickel (Ni), and zinc (Zn), have been measured in several species of both pelagic and near-shore *Halobates* [e.g. by Cheng et al (27); Cheng et al (34)]. In general, the trace-element contents in sea skaters are within the ranges or slightly higher than those reported for other marine invertebrates (27). However, the Cd concentrations tend to be much higher, by a factor of 10 or more, than the highest values obtained for zooplankton samples. Since Cd is toxic to humans and other animals (49) and has been extensively investigated in the marine environment, we pursued studies on the uptake and accumulation of this trace element in captive sea skaters (71, 73), its concentration in natural

populations (24, 27, 34, 72), and its possible transfer to the avian predators of these marine insects (11, 41). We found that, on the whole, coastal *Halobates* contained less than 5 ppm (dry wt) of Cd in their bodies, whereas open-ocean species may contain up to 300 ppm. Although this element can be taken up from their prey, much of the Cd found in ocean skaters is probably obtained from the surface film by drinking (34). Some of the dietary Cd may be excreted or stored in the cuticle; a fraction undoubtedly remains in the tissues. What effect it may have on the biology or physiology of ocean skaters has not yet been investigated. Cheng et al (41) have found that the blue-gray noddy (*Procelsterna cerulea*), the most important avian predator of *H. sericeus*, has proportionately more Cd in its feathers than do three other related birds from the same habitat, suggesting that this metal can be transferred from ocean skaters up the food chain to its predators.

Behavior

Halobates are strongly attracted to light at night. How this type of phototactic behavior evolved is not easy to understand. In the open sea there are no naturally occurring light-emitting pleuston organisms that might serve as food. Nevertheless, in areas where sea skaters occur but may be difficult to catch in daytime because of their extreme agility, it is often easy to capture them by using a light lure after dark. In coastal areas where fishermen practice night fishing, their lights often attract large numbers of land insects as well as various planktonic organisms and fish, providing a rich food source for *Halobates*. Sea skaters have well developed eyes, which they use for hunting and in avoiding or escaping from predators. They can see well not only in daylight but also on bright moonlit nights, as evidenced by net-avoidance studies based on net catch data (18, 32). Since it is almost impossible to carry out behavioral studies of pelagic *Halobates* in the field and we have not yet been able to provide suitable laboratory conditions for rearing open-ocean species, information on their behavior is limited mainly to short-term observations carried out at sea or to indirect deductions based on population analyses of preserved samples.

However, in several locations around the world, high densities of *Halobates* populations are known to occur near shores where experimental studies can be carried out with relative ease. Several interesting field studies have been carried out at the Galápagos Islands, where *H. robustus* is found in great abundance (7, 8). Insects of this species often form dense aggregates close to the edges of mangrove thickets or coastal lava rocks. The patches of highest density consist of mating pairs of adults (up to 120 m^{-2}); mixtures of adults *in copula* and older nymphs tend to be less dense (8). The least dense aggregates are composed of mixed populations of mating adults, single adults, and older nymphs (third to fifth instar). Young first to second instar nymphs, almost never found in such

aggregates, normally occur in dense patches of their own age group among mangrove roots, where they may avoid cannibalism by older siblings.

Flotillas of *H. robustus* maintain stations in areas with fringing mangrove along rocky shores, where they tend to maintain relatively constant positions throughout tidal cycles. Where the mangrove trees are close to shore areas exposed at low tide, the flotillas remain aggregated, but they move to pools and remain there until the tide returns; then they move back to their original positions in relation to the mangrove edge. The remarkable ability of *Halobates* aggregations to maintain or resume stations in this way is probably achieved by some sort of orientation by the individual insects to topophysical features such as mangrove roots or rocky shore lines (8). The cohesion of such flotillas is probably attributable to gregarious behavior. The functional significance of aggregations in *H. robustus* was studied by Foster & Treherne (46–48), who considered that such aggregates may reduce susceptibility to predators. They found that the approach of a predator or model would cause individuals at the periphery to change their speed and direction of movement, thereby increasing encounter rates among individuals of the flotilla and perhaps confusing the predator and avoiding predation. Furthermore, the number of encounters was found to depend on group size: avoidance behavior in a large aggregate can be achieved by minimal visual stimulation at maximal predator approach (79). Since Treherne & Foster (80) observed in the field that the transmission of avoidance behavior through the flotilla greatly exceeded the speed of an approaching predator model, they called it the Trafalgar Effect. This behavior enables the insects to initiate avoidance behavior even before the approaching predator is seen. Besides aiding predator avoidance, *H. robustus* aggregates also serve as arenas for mate finding and selection (48). Single males form small aggregates, which attract females (and other males); as the size of the flotilla increases, the proportion of insects *in copula* also increases. Foster & Treherne (48) found *H. robustus* pairs remaining *in copula* for up to 47 hr. This is consistent with my own unpublished observations of *H. flaviventris* in Palau and *H. mariannarum* in Guam. Presumably such prolonged copulation reduces competition among sperm of competing males (see 3, 65). Mate finding and copulation may be similarly facilitated by group formation in other species of *Halobates*.

In the freshwater gerrid *Rhagadotarsus kraepelini*, Wilcox (83, 84) found that males can attract females by producing surface ripples or wave signals. Although this sort of system could be expected to work well on still surfaces of ponds or lakes relatively protected from winds, it is difficult to visualize such a system operating efficiently on the open ocean except during exceptionally calm spells. If pelagic species of *Halobates* depend on this system for mate finding, one would expect to find a correlation between their reproduction and

doldrum conditions. However, analyses of field collections so far have not shown any clear indication of seasonality (19, 24).

Special Adaptations

As mentioned earlier, *Halobates* is the only insect genus living on the open ocean; it is also the only marine invertebrate actually feeding at the sea-air interface. What special adaptations enable it to occupy such a specialized and often hostile environment? And how does it interact with various biological, physical, and chemical factors peculiar to the sea-air interface? These are some of the problems we have to solve if we are to understand the biology of this unusual insect. So far we have only limited information on some of the adaptations of pelagic *Halobates* to its special habitat, since there are obvious difficulties involved in conducting research on the open ocean. Of necessity, most of the relevant information has been obtained from specially preserved specimens and from studies on coastal species.

Life at the sea-air interface is in some ways simple, but in others it must be remarkably complicated. In this essentially two-dimensional environment the survival of the animal is predicated largely on its ability to minimize accidental submergence and to avoid drowning. *Halobates* does this by enclosing itself in what is analogous to a water-repellent envelope. For example, the body and legs of pelagic *Halobates* are covered by a layer of hydrofuge microtrichia in addition to the macro-hair coat (2, 16). In *H. germanus* the hook-shaped microtrichia are about 1.5 μm high, 1.0 μm wide across the top, 0.5 μm wide at the base, and spaced 1.5 μm apart, while the average inter-cap distance is about 0.5 μm . Their density was found to be in the range of $6-7 \times 10^5 \text{ mm}^{-2}$ for *H. flaviventris* and $1.2 \times 10^6 \text{ mm}^{-2}$ for *H. germanus* (2). In such an arrangement, a layer of air trapped among the hairs surrounding the insect gives it buoyancy and enables it to pop up to the sea surface like an air bubble if it is accidentally submerged. In the freshwater gerrid *Ventidius* the microtrichia are peg-like (16). According to Thorpe & Crisp (78), hook-shaped microtrichia provide a much more efficient plastron than peg-like ones.

To test the efficiency of the air-retaining plastron of *Halobates*, I carried out some experiments at the marine laboratory in Palau, West Caroline Islands, in 1981 and 1982, using the coastal species *H. flaviventris*. Specimens were forced to remain submerged in boiled seawater (containing 3.5 ppm O_2) and in unboiled seawater (containing 7.4 ppm O_2). Within 5 minutes the specimens in the boiled water exhibited signs of paralysis, with their middle and hind legs extended backwards (Figure 6). Live *Halobates* hold their legs flexed in a characteristic skating position (see Figure 5). In unboiled seawater, paralysis set in only after 30 min (L. Cheng, unpublished data). If specimens were removed from the experimental vessels shortly after paralysis was observed (within 2-3 mins), then dried and returned to the surface of seawater, they soon

recovered and within a few minutes began to skate normally. If, however, insects in boiled seawater were left to drown, they sank within 40 min. If then taken out and dried, even though they might still be alive, they never regained normal movement, as the legs had evidently suffered permanent impairment. On the other hand, after being held under unboiled seawater, even after a 2-hr submergence, most (8 out of 12 specimens) remained afloat and appeared to be alive. Thus the microtrichia layer on *H. flaviventris* held sufficient air to allow the insect to survive under water for at least 2 hr at 31.5°C, whereas in boiled seawater the oxygen was quickly depleted to lethal levels. Individuals of the oceanic *H. sericeus*, which occurs in much cooler waters (23°C), were able to remain submerged for up to 16 hr without suffering any apparent ill effects (L. Cheng, unpublished data).

Apart from being able to avoid drowning, sea skaters must be capable of maintaining their body fluids at an osmolarity considerably below that of the seawater (freezing-point depression $\Delta = -1.86^\circ\text{C}$). The osmotic pressure of the hemolymph of *H. sobrinus* was found to be 523.6 m osmol l^{-1} ($-0.974 \Delta^\circ\text{C}$) (E. B. Edney and L. Cheng, unpublished data), which is not very different

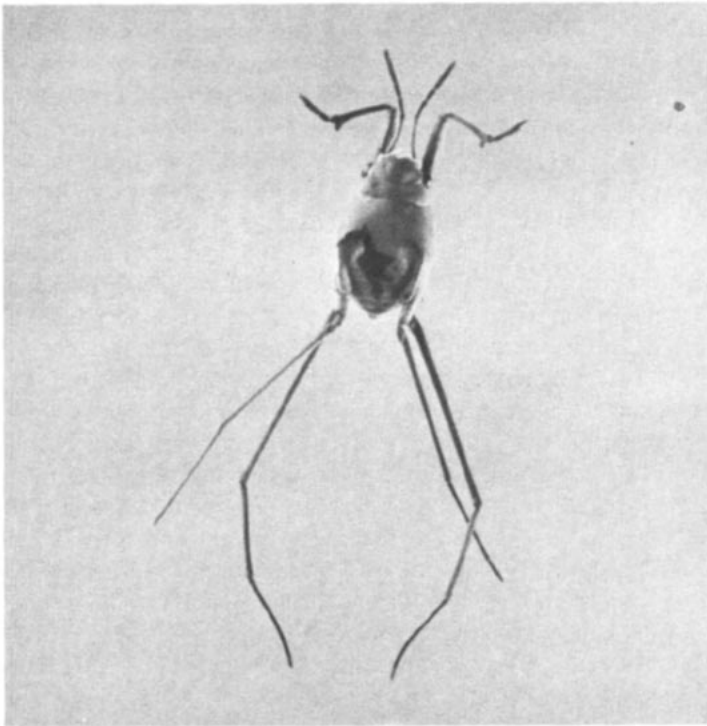


Figure 6 Top view of dead *Halobates sericeus* female.

from that of terrestrial insects ($-0.839 \Delta ^\circ\text{C}$) (75). When specimens were placed in water containing $\frac{1}{3}$ or 2 times the osmolarity of seawater ($0.33\times$ or $2\times$ SW) for 24 hr, hemolymph osmotic pressure decreased (to 435.8 m osmol l^{-1}) or increased (to 736.6 m osmol l^{-1}) and the animals became sluggish. Those placed on fresh water or $2\times$ SW died within 48 hr. Specimens placed on $0.5\times$ or $1.5\times$ SW, however, behaved normally and survived for up to 4 days. The coastal *H. flaviventris* was able to live on $0.5\times$ SW and even on fresh water for up to 7 and 5 days, respectively (L. Cheng, unpublished data). It may be more adaptable than the pelagic species, since it occasionally has to cope with heavy freshwater runoff after storms.

Halobates are agile insects and can skate at speeds of about 50–100 cm sec^{-1} (20). They can also jump to heights of 10–12 cm (24). The hydrofuge hairs covering their legs presumably help to reduce frictional drag (1). Their ability to jump is a very effective means of escaping from predators coming up from below or flying above them. Since there are no shelters of any kind on the open ocean, such agility is of considerable survival value.

It is reasonable to assume that food for these oceanic insects is usually less abundant than it would be at the surfaces of lakes, streams, or ponds and that they would need considerable energy reserves to tide them over periods of starvation. Lee & Cheng (58) found that two species of ocean skaters, *H. germanus* and *H. sericeus*, store triglycerides in amounts of up to 92% of their total lipids, but in their brackish-water (*Rheumatobates*) and freshwater (*Gerris*) relatives the corresponding values were much lower, in the range of 46–72%. Since triglycerides are easily metabolized, they are presumably useful energy reserves for these insects. Although these two ocean skaters store many of the same structural fatty acids as are common in insect lipids, they also contain the polyunsaturated fatty acids 20:4, 20:5, and 22:6, normally found only in marine zooplankton. Thus these *Halobates* store not only phospholipids and structural lipids common in other insects but also lipids peculiar to marine zooplankton. This has been shown also for the near-shore sea skater *H. fijiensis* by Holland et al (55). Some polyunsaturated fatty acids, such as 20:5 and 22:6, may be essential for membrane formation in marine animals, and, since insects are typically unable to synthesize long-chain fatty acids (above 18 carbon chains) or elongate the molecular chains of unsaturated fatty acids (50), they would have to obtain them from their diet, as suggested by Holland et al (55).

In freshwater as well as near-shore marine environments, gerrids are often found under shade during sunny periods, a behavior that presumably helps to protect the insects from possible damage from solar UV light. In the open ocean, however, there is no shade, and ocean skaters have had to evolve some kind of adaptation for UV protection. In certain insects some of the energy of the incident UV may be reflected or re-emitted by fluorescence, but these phenomena have not been observed in *Halobates*. The fate of UV energy in the

biologically damaging range (260–320 nm) absorbed by gerrid cuticles was studied by Cheng et al (31). We found that, although the UV-absorbance spectrum of the ocean skater *H. sericeus* was qualitatively similar to that of gerrids from brackish water (*Rheumatobates aestuarius*) and fresh water (*Gerris remigis*), at a wavelength of 280 nm only 0.0002% of the radiation is transmitted through the cuticle of *H. sericeus*, compared to 0.4% in *Rheumatobates* and 50% in *G. remigis*. It is probable that the relative opacity of *Halobates* cuticle is attributable to a high content of aromatic amino acids (notably tyrosine, tryptophan, and phenylalanine) (63), but this subject needs further investigation.

CONCLUDING REMARKS

The uniqueness of *Halobates* presents us with a variety of intellectual challenges. There is, first, its very existence in—more correctly, on—the sea. In spite of the common misconception that marine insects do not exist (to judge by textbooks in entomology and marine biology), there are in fact several hundred insect genera associated with marine littoral environments. However, *Halobates* is the only genus with species that are wholly oceanic. Why are there not more? How does *Halobates* succeed where others have failed? How can it withstand daily tropical insolation without a leaf or a sod to hide under in the heat of noon? How can it stalk about on a 3% solution of salts and nevertheless maintain a hypotonic blood? It may see rain too rarely; dew and streamlets are quite outside its ken. How does it walk on water? Without any possible shelter, how does it survive in storms? How does it find mates? These are some of the questions that we have started to answer, but there are others.

The world of *Halobates* is the most strictly two-dimensional habitat of any known animal. This habitat is a wavy interface that stretches for thousands of kilometers north and south, east and west. However, any deviation more than a couple of millimeters above or below the water surface must be outside this insect's immediate world. Yet virtually all of its prey must float up from below as plankton or fall from above as a sparse rain of aerial insects, for the habitat of *Halobates* is quite without its own primary sources of productivity. And all of its predators, likewise, except for its cannibalistic cousins, dive down upon it (as do birds like noddies) or swim up to snatch it from below (as do certain fishes, if they are quick enough).

A further question concerns subjects such as gene flow, speciation, and evolution. The ecology of *Halobates* has zoogeography without topology, for the ocean surface is featureless, undivided by mountain ridges, river valleys, or desert plains. How, in such circumstances, have different species evolved, and how do they maintain their differences? Temperature gradients? Perhaps, but could they suffice? It seems unlikely. Could currents and gyres be sufficiently

distinct and constant enough to delimit species? We do not know (at least, I don't). What observations should be made, and what experiments devised, that might help to answer such questions? If this review succeeds in presenting such problems to entomologists and marine biologists and if it promotes research that may answer some of these questions, I think it will have served its purpose.

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