HETEROPTERA OF ALDABRA ATOLL AND NEARBY ISLANDS, WESTERN INDIAN OCEAN, PART 1. MARINE HETEROPTERA (INSECTA); GERRIDAE, VELIIDAE, HERMATOBATIDAE, SALDIDAE AND OMANIIDAE, WITH NOTES ON ECOLOGY AND INSULAR ZOOGEOGRAPHY

BY
D. A. POLHEMUS

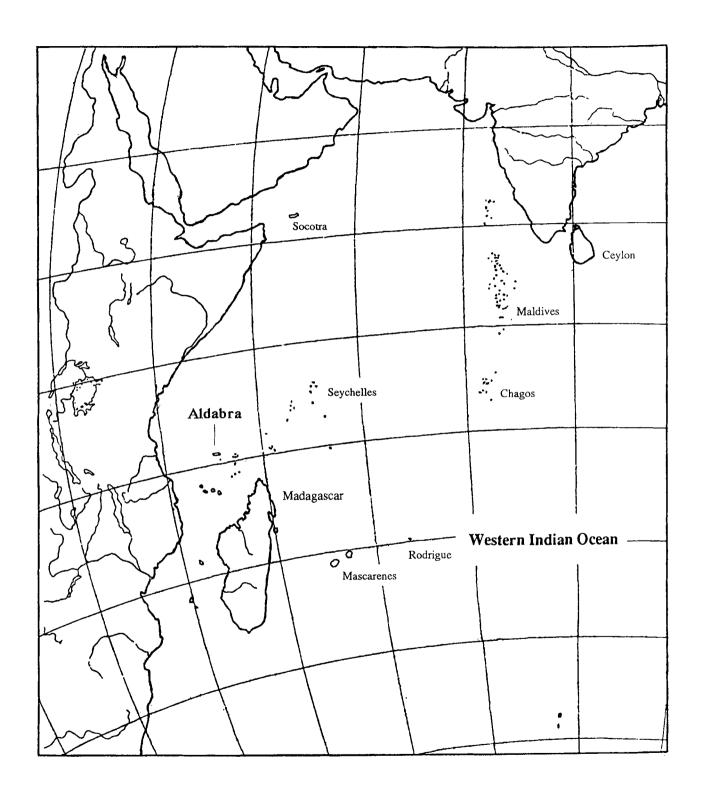
ISSUED BY

NATIONAL MUSEUM OF NATURAL HISTORY

SMITHSONIAN INSTITUTION

WASHINGTON, D.C., U.S.A.

SEPTEMBER 1990



HETEROPTERA OF ALDABRA ATOLL AND NEARBY ISLANDS, WESTERN INDIAN OCEAN, PART 1. MARINE HETEROPTERA (INSECTA): GERRIDAE, VELIIDAE, HERMATOBATIDAE, SALDIDAE AND OMANIIDAE, WITH NOTES ON ECOLOGY AND INSULAR ZOOGEOGRAPHY

BY

DAN A. POLHEMUS

ABSTRACT

Ten species of Heteroptera are now known from marine habitats at Aldabra and Cosmoledo atolls. Nine of these species, *Halobates micans*, *Halobates germanus*, *Halobates flaviventris*, *Halobates alluaudi*, *Halobates poseidon*, *Hermatobates djiboutensis*, *Halovelia seychellensis*, *Salduncula seychellensis*, and *Corallocoris aldabrae* are marine obligates, while one, *Microvelia diluta diluta* is a primarily freshwater species that appears to have opportunistically colonized tidally flooded sinkholes. The distributions of the marine species are not homogenous around Aldabra, but are instead divided among three distinct zones: the exposed seaward shores on the eastern and southern coasts, the sheltered seaward shores on the western and northern coasts, and the lagoon. These areas harbor distinctive species assemblages whose composition is based on the ecological preferences of the individual species involved. It is hypothesized that the effects of the strong southeast monsoon have led to a richer assemblage of species on the leeward side of the island. A key to all marine species is provided, accompanied by maps detailing their distributions on Aldabra.

INTRODUCTION

This report presents the systematic results of an intensive sampling program concentrating on Heteroptera in marine habitats at Aldabra atoll (9° 24′ S, 46° 20′ E), from March 5 to March 25, 1989. Additional smaller collections were also made at Cosmoledo atoll (9° 41′ S, 47° 35′ E) during the return trip from Aldabra, and since the faunas of the two islands are nearly identical the results of the Cosmoledo collections are included in this report as well.

This work is divided into two sections. The first deals with the ecological preferences and local zoogeographical patterns exhibited by marine Heteroptera on Aldabra atoll. The second part contains a systematic treatment and distributional records for the individual species involved. Additional information on the systematics of *Halobates* species occurring on Aldabra and nearby atolls may be found in Polhemus and Polhemus (in press). Chapters dealing with all the marine groups treated herein, with information on their biology and ecology, may be found in *Marine Insects*, edited by Cheng (1976).

Department of Entomology, NHB 127, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560

All the collections discussed below were made by the author, primarily through the use of hand held dip nets with 45 cm. diameter hoops. Similar nets were skimmed along the water surface from boats during circuits around the outer rim of the island and in transits across the lagoon; collections made in this latter fashion are referred to as net tows in the subsequent discussions. All specimens are held in the collections of the Department of Entomology, Smithsonian Institution, Washington, D. C. (USNM) and the J. T. Polhemus collection, Englewood, Colorado (JTPC). CL numbers following localities refer to a code used by the author to reference ecological data. A detailed map of Aldabra atoll showing the localities discussed herein may be found in Stoddart and Westoff (1979). The individual islets making up the outer rings of Aldabra and Cosmoledo atolls are noted in bold face in the material examined sections. Latitudes and longitudes were determined using a Satnav global positioning system.

ECOLOGY

Habitat

Stoddart (1967) classified Aldabra as an elevated atoll, raised several meters above present sea level and occupying an ancient volcanic platform with steeply plunging outer slopes. The island is ring-like, formed in the shape of an elongate oval with the long axis oriented east-west. Its length is approximately 34 kilometers, and its maximum width 15 kilometers. The outer rim consists of 18,800 hectares of dry land and 2000 hectares of mangroves enclosing a lagoon of 14,200 hectares, and is broken by four passes on the western and northern sides; these are, clockwise from the west, the Passe Femme, Grande Passe, Passe Gionnet and Passe Houareau. All of these passes are relatively deep, with the Grande Passe having a maximum depth of 24 meters (79 feet) at its entrance, while the lagoon is shallow, averaging only 2 to 3 meters (6.5 to 10 feet) in depth at low tide. The tidal range at Aldabra is high, reaching 2.6 meters (8.5 feet) on the outer coasts. Due to the relatively small size of the passes in relation to the area of the lagoon the tidal lag between the sea and the more remote portions of the lagoon may be 4 to 5 hours, and current velocities in the passes can reach 6 meters per second.

Aldabra lies in the driest sector of the western Indian Ocean, receiving an annual rainfall of about 940 mm. per year (Stoddard and Mole, 1977). The majority of this rainfall occurs between late November and April, when the island is under the influence of the northwest monsoon, which reaches its height in January and February. During the remainder of the year, from May to early November, the island is swept by the relatively dry southeast monsoon. The two wind regimes are not equivalent; the northwest monsoon winds tend to be lighter and more intermittent, with occasional heavy storms, while the southeast monsoon winds are strong and steady, frequently attaining velocities between 10 and 20 knots. As a result, sea conditions are considerably rougher during the southeast monsoon, and the exposed southern and eastern coasts of the atoll are heavily battered by waves at this time of year.

Due to its isolation and lack of human disturbance, Aldabra harbors one of the most diverse assemblages of marine Heteroptera known on Earth. The structure of the atoll and its consequent variety of habitats, in particular the configuration of the shore and the reefs immediately offshore, has had a marked effect on the distribution of these insects. Based on my collections at Aldabra, the following environmental divisions are perceived to be particularly important to the marine Heteroptera, and are referred to in the subsequent discussions:

A. Fore reef: this is interpreted as the section of the fringing reef sloping seaward from the tidally exposed reef crest or from the shore platform in areas where the reef crest

is lacking. It is essentially unprotected from the effects of wind and surf coming in off the

surrounding open ocean.

B. Reef crest: this term refers herein to the offshore portion of the fringing reef exposed at low tide. Reef crests are well developed on the western and northern sides of Aldabra along Picard, Polymnie and Malabar islands, but essentially absent on the eastern and southern sides of Grande Terre island from Point Hodoul to Pointe aux Vaqua, except for a small section of platform reef in the bight east of Dune Jean Louis.

- C. Back reef: this is the section of the reef lying between the reef crest and the shore. It is generally present in the form of a shallow lagoon with a floor of coral rubble or sand, and in many places, such as in the vicinity of the research station, is exposed at low tide. In areas where a reef crest is lacking the back reef environment is also absent.
- D. Seaward shore: this is the actual outer shore of the island proper, and may take several forms. At the reseach station and in a few other isolated coves or "anses" it is composed of a beach of fine white coralline sand. More typically it is a vertical or undercut jagged limestone cliff dropping directly to the water, as seen along nearly the entire seaward coast of Malabar and Polymnie. At other points, particularly on the eastern and southern coasts of Grande Terre, this cliff may be low and fronted by a sloping shelf of relatively smooth limestone the runs out under the sea but is exposed at low tide. These three types of seaward shores are referred to as sandy, vertical, and sloping respectively.
- E. Passes: these are the channels by which the waters of the lagoon communicate with the open ocean. They have strong tidal fluxes that give them the characteristics analogous to flowing rivers in freshwater systems. Their shores are primarily vertical cliffs.
- F. Mangroves: refers to the fringing mangrove estuaries that surround much of the inner lagoon. These are composed primarily of Avicennia marina and Rhizophora mucronata in the eastern end of the lagoon, while a small patch of Sonneratia alba occurs just inside the Passe Femme at the western end. Mangroves on Aldabra are entirely confined to the shores of the lagoon except for a small stand in the extremely protected cove at Au Park on the seaward shore of Malabar.
- G. Lagoon: this term refers to the inner lagoon beyond the mangrove estuaries. The waters of the lagoon are relatively calm in comparison to the open ocean, although a swell may form from wind action. The floor of the lagoon is primarily white sand in the central section and carbonate mud at the eastern and western ends.
- H. Lagoon islets: these are small detached limestone islets, frequently circular in shape, with sides strongly undercut by wave and tidal action. Typically they attain a mushroom-like form with the upper limit of undercutting lying at the high tide line.
- I. Bassins: this term applies to small to large limestone sinkholes in the interiors of the islands making up the outer rim, particularly Picard. These sinkholes are connected with the sea through subterranean passages and are flooded with seawater, usually permanently but in some cases only at high tide. Many such bassins are present behind the research station, including Bassin Lebine, Bassin Cabri, and the Upsidedown Jellyfish Pool.

Local Distribution of Genera and Species

Hermatobates: Foster (1989) studied the biology of Hermatobates weddi on Fiji, and found that the insects occurred primarily along the reef crest, emerging at low tide from their hiding places amid air pockets in coral rubble to forage on the calm pools formed on the reef crest itself or on protected areas of water immediately seaward. Essentially the same pattern was reported by Cheng (1977) for species on New Caledonia and the Great Barrier Reef of Australia, and by J. Polhemus (1982) for H. haddoni at Darwin, along the coast of the Arafura Sea. In addition, I have observed similar behavior

among Hermatobates species occurring on the island of Sumbawa in the Lesser Sunda chain of Indonesia, and on Malupore Island off the southeastern coast of New Guinea. At Aldabra, however, the Hermatobates species present, H. djiboutensis, displayed a markedly different behavior pattern. Adults and late instar immatures were nearly absent on the reef crest, but instead were typically encountered in the deep water over the fore reef between 500 and 1000 meters offshore, in areas subject to moderate swell. Here they would run across the surface of the sea in company with various Halobates species, and could be captured by trolling a net from the bow of a moving boat. Individuals appeared to be more abundant in areas where seaweed and other organic debris formed loose floating mats on the water surface. The presence of Hermatobates did not appear to be correlated with tide stage, since captures were made at both low and high tides, and all captures were made during daylight hours, even though Usinger and Herring (1957), Cheng and Leis (1980), and Cheng and Schmitt (1982) have suggested on the basis of circumstantial evidence that Hermatobates forage primarily at night.

In contrast to the adults, immatures in early developmental stages (instars I - III) were encountered only in reef crest habitats at low tide. In addition, the only mating pair of adults captured was taken on the reef crest offshore of the research station at dead low tide. It thus appears that mating, oviposition, and early maturation of this species at Aldabra occur on the reef crest, as is typical for *Hermatobates* in other regions, but that adults and late instar immatures then forage seaward of the reef crest on the deep waters over the fore reef and do not necessarily return to hiding places in the coral blocks at high tide, a behavior pattern not previously reported. *H. djiboutensis* was found at Aldabra only in areas with well developed reef crests, these being primarily on the western and northern sides of the island, plus the small sheltered area on the south coast of Grande Terre near Anse Vaqua. This distribution is shown in figure 1. The restriction of this species to areas with reef crests is further evidence supporting the hypothesis that such

habitats are necessary as oviposition sites and refugia for immatures.

These observations contradict previous conclusions and generalizations about adult Hermatobates behavior derived by Esaki (1947), Usinger and Herring (1957), Cheng (1977), and Foster (1989) from observations on populations in the western Pacific. Several factors may be responsible for this. Since the observations at Aldabra were made in March, during the calm period between the northwest and southeast monsoons, it is possible that the behavior patterns recorded may be seasonal, and that during times of the year when the sea surface is more constantly disrupted the insects forage nearer the reef crest. On the other hand, it may also be that H. djiboutensis possess different foraging patterns than other Indo-Pacific Hermatobates species. This latter hypothesis must be investigated more critically, since I have also observed H. djiboutensis on Mauritius where it exhibited the "typical" Hermatobates behavior pattern, emerging from coral rubble at low tide and skating on shallow back reef waters at Big Black River Bay. Further investigations on the ecology of this and other species will be necessary to resolve such questions, and to understand why presently accepted concepts of adult Hermatobates behavior are inapplicable to H. djiboutensis at Aldabra.

Halobates: Five species of Halobates were collected at Aldabra during the present survey. Two of these, H. micans and H. germanus, belong to a pelagic group of species which occur solely in open ocean habitats and do not generally approach closely to land. By contrast, the three remaining species, H. flaviventris, H. alluaudi, and H. poseidon, belong to the nearshore species group, members of which are restricted to coastal habitats and do not forage far onto open waters. This basic division of ecological preferences has important consequences for the distribution of these species at Aldabra.

The two oceanic species, *H. micans* and *H. germanus*, were encountered only 1000 meters or more offshore, either over the fore reef or on the deeper ocean beyond; they were never seen over the reef crest and back reef or in the lagoon (see figs. 2 and 3).

These were the only two species of *Halobates* present offshore of the eastern and southern coasts of the island, which have vertical or sloping seaward shores exposed to the full force of the southeast monsoon and lacking major reef crest and back reef development. The two species were often taken sympatrically and did not appear to partition the ocean environment in any fashion.

By contrast, the three nearshore species showed distinct segregation of habitats. *H. flaviventris* was most typically encountered over the fore reef 500 to 1000 meters offshore, often in company with *Hermatobates djiboutensis*. It was not seen inshore of the reef crest in the back reef, passes, or in the lagoon (see fig. 3). Individuals were widely separated, appearing to forage independently, and this species was never observed forming schools. Typically only one or two specimens would be taken in a net tow for every ten or twenty *H. alluadi* captured. In its behavior *H. flaviventris* appeared to be intermediate between the strictly open ocean species and those confined to nearshore habitats. Its tendancy to cruise over fore reef waters parallel to the reef crest was similar to the behavior pattern observed for *H. princeps* White in the Malay Archipelago.

H. alluaudi was sympatric with H. flaviventris in the vicinity of the reef crest and over the fore reef just beyond, but was more typically found inside the reef crest skating over the back reef lagoon adjacent to sandy or vertical seaward shores, and was almost never seen more than 1000 meters offshore. It was also common along the margins of the lagoon, primarily in the vicinity of the passes or the rocky lagoon islets, but here again it was absent from the central lagoon more than 1000 meters offshore (see fig. 4). H. alluaudi is a fast, powerful and agile swimmer, and at Passe Femme and Passe Gionnet individuals of this species were observed holding station along the channel margins against the incoming tide, thus foraging in place as the tidal flux washed past them in a manner analogous to that seen among freshwater Gerridae on flowing streams. This species occasionally formed small schools in sheltered spots at low tide, but for the most part appeared to be relatively well dispersed on the water and not exceptionally social.

H. poseidon was found only in conjunction with mangroves, and was thus almost entirely confined to the margins of the lagoon. Individuals were also present in several flooded limestone sinkholes on Picard Island. This species, which does not swim with nearly the same speed or power as H. alluaudi or H. flaviventris, was never seen more than 500 meters offshore, and usually stayed within the shelter of the mangrove estuaries (see fig. 5). This was the only Halobates species on Aldabra to typically occur in large schools during all tide stages, and many mating pairs were observed. In many aspects its behavior appeared similar to that reported for H. fijiensis by Foster and Treherne (1986), which was studied on Fiji and also found to be restricted to the mangrove and back reef zones.

Because of these habitat preferences, the central section of the lagoon was basically devoid of *Halobates*. The two nearshore species along the lagoon margins, *H. poseidon* and *H. alluaudi*, did not stray far enough from shore to reach the mid-lagoon waters. By contrast, the remaining species, which have habits that would allow them to exploit these areas far from shore, seemed to be unwilling to enter the narrow passes connecting the lagoon with the ocean beyond, and were therefore confined solely to the outside of the atoll. It thus appears that the combination of aversion to open waters on the part of some species and aversion to shoreline proximity on the part of others leaves the central lagoon essentially unexploited by *Halobates*. The only individuals ever seen here were a few stray individuals of *H. alluaudi* which had apparently been carried inward on the strong tidal flux from the Grande Passe during the high tide filling cycle.

Also notable was the absence of any nearshore *Halobates* species from the seaward shores on the southern and eastern sides of the atoll, a pattern analogous to that seen in the previously discussed *Hermatobates djiboutensis*. This seems to be due to the effects of the southeast monsoon, which batters these coasts with extremely heavy wind and seas for

nearly half of each year, from June through October. Foster and Treherne (1986) found that strong onshore winds had a marked effect on the distribution of *Halobates fijiensis* in Fiji, and at Aldabra it also appears that the combination of rough wind-driven seas and a shoreline lacking refuge space in the form of a reef crest or back reef effectively excludes the nearshore *Halobates* species from these exposed sections of the atoll.

In addition to providing oviposition sites and shelter from wave action, shoreline features were also used by *Halobates* to escape the effects of the equatorial sun. When low tides occurred during the middle of the day large sand flats were exposed along the inner margin of the lagoon inside of the Passe Femme. Rising from these flats were lagoon islets of various sizes, all undercut and sheltering pools of seawater at their bases. These shaded pools were the low tide retreats for vast schools of *Halobates poseidon* and *Halobates alluaudi*, which occurred in mixed species assemblages containing both adults and immatures. These schools were seen only on shaded pools beneath the overhanging lips of the lagoon islets, primarily on the sides of the islets receiving a cooling breeze, and were absent on nearby pools of similar size and depth that were unsheltered and open to the full force of the sun. In such unsheltered pools the water temperature exceeded 40° C., which was clearly intolerable to *Halobates*, while in the sheltered pools the seawater temperature was 28-30° C. The afternoon low tides thus forced these two species into temporary sympatric assemblages of abnormal density in shady refugia, from which they then dispersed upon the subsequent turn of the tide.

Finally, there is the question of how populations of H. poseidon and other marine Heteroptera became established in the bassins of Picard Island. Since many of these bassins are connected to the sea only via completely water filled subterranean passages it seems unlikely that the colonization was effected by adults or immatures merely swimming or floating in on the tides. Instead, it seems that the bassins represent isolated pockets of marine habitat that have been colonized by chance dispersals, a hypothesis supported by several observations. All the bassins sampled contained one of the three following species of marine Heteroptera: Halovelia seychellensis, Microvelia diluta, or Halobates poseidon. It is important to note, however, that no individual bassin contained more than one of these species. H. poseidon, for instance, was found in only two of the many bassins sampled, the Upsidedown Jellyfish Pool and Bassin Lebine, and in these bassins no other marine Heteroptera species occurred. In Bassin Cabri only Halovelia seychellensis was present, and in another small bassin behind the research station only Microvelia diluta. This suggests that whichever species of surface dwelling Heteroptera is first able to colonize a given bassin is subsequently able to dominate it and to exclude other invading species, and that colonization of the bassins has proceeded in a haphazard fashion. M. diluta produces a percentage of winged adults in each generation and would thus intuitively seem to have an edge in colonizing the bassins, but in fact it is present in only approximately one third of them. The other two species involved do not produce winged individuals and must have reached the bassins by other means. This colonization may have been accomplished by various agencies, including wind dispersal of adults or immatures during storms, similar storm mediated transport of eggs laid on floating debris, or transport of eggs on the feet or feathers of sea birds.

Halovelia: A single species of Halovelia, H. seychellensis, was present on Aldabra, but it occupied a wide variety of habitats. Individuals were most typically encountered along vertical seaward shores sheltered by a reef crest and back reef; in these locations they would skate at low tide on small pools which formed amid coral rubble which had fallen from the cliffs or eroded from the reef crest. This behavior pattern is very similar to that reported by Andersen (1989) for H. malaya on Phuket Island, Thailand, and also close to that described by Kellen (1959) for H. bergrothi (as H. marianarum), which occurred among volcanic rocks bordering an artifical lagoon in Samoa. On Aldabra moderate numbers of H. seychellensis were also found just north of

the research station where several long ridges of wave-smoothed limestone ran obliquely into the back reef lagoon, creating elongate rock rimmed pools at low tide. As discussed above, this species was also present in several limestone sinkholes on Picard island, notably Bassin Cabri and several other nearby pools that are connected by a common cavern system. The insects generally stayed near the margins of these sinkholes, and retreated beneath rock overhangs at the onset of rain squalls. Despite their small size and general preference for nearshore habitats, stray individuals of *H. seychellensis* were occasionally taken up to 500 meters offshore, along both the outer margin of the atoll and in the lagoon.

Salduncula: The intertidal saldid Salduncula seychellensis was found only on sloping seaward shores along the southern and eastern coasts of the atoll in areas heavily battered by the southeast monsoon. In these areas a broad pediment of relatively smooth limestone exposed at low tide slopes gently upward to a narrow beach. This beach in turn fronts a low but jagged cliff that marks the limit of the intertidal zone. S. seychellensis was found only on this cliff, being absent on the narrow beach, sloping pediment, and other isolated limestone prominences separated from the cliff but connected with the shore at low tide. Immatures of all instars and adults emerged with the falling tide from hiding places amid the porous limestone rock of the cliff face and foraged over its surface. The insects moved slowly if left alone, but if pursued the adults were quick to fly, while the immatures would head for the shelter of small crevices or cavities in the rock. Individuals of S. seychellensis would continue to forage even after the tide had turned, waiting until the cliffs began to receive spray from breaking waves before returning to their hiding places in the rocks.

At Cosmoledo atoll this species was found in a somewhat different situation near the Johannes Point settlement on Menai island. Here the insects occurred on large blocks of coral rubble bordering the back reef lagoon. This indicates that the apparent preference for wave swept shores on Aldabra may be misleading, and that this unobtrusive species may in fact be distributed around the entire seaward shore of the latter atoll.

Corallocoris: Dwarf coral bugs belonging to the species Corallocoris aldabrae are known from a single locality on Aldabra: the western margin of the Passe Houareau near Middle Camp. The insects were found here at low tide running on and within a collection of rounded 3-6 centimeter long coral cobbles lying on top of a bed of firm sand adjacent to a sloping exposure of limestone at the high tide line. They appeared to be very localized in their occurrence, since a search of other similar looking sites nearby in the same cove and several other adjacent coves produced no trace of them, nor were they found in other similar habitats on other parts of the atoll even after diligent searching.

Individuals of *C. aldabrae* were not easy to collect, due to their small size and considerable jumping ability; the most successful method involved slowly removing the coral cobbles and watching for the small black insects as they hopped away across the white sand, then sucking them into an aspirator. When pursued the insects would spring away, or seek the shelter of pockets, holes and overhangs in the cobbles and limestone shelf rock. The present observations would indicate that this species forages interstitially within the cobble beds, which may account for its difficulty of detection and capture.

This habitat is quite different than that reported for *Omania naruensis* by Herring and Chapman (1967), who found the insects in the interstices of coral pinnacles in the back reef lagoon on Nauru, or for *Omania marksae* which has been taken from coral boulders in the back reef lagoon on Kwajalein atoll (A. R. Gillogly, pers. comm.). It is however, similar to the habitat in which J. T. Polhemus and I have taken *Omania marksae* in Singapore, where the insects occurred amid beach drift and coral cobbles adjacent to an exposed ridge of limestone beach rock. Kellen (1960) also reported *Corallocoris samoensis* from a beach of volcanic rocks bordering a lagoon in Samoa, although these rocks were much larger than the small coral cobbles that formed *Corallocoris* habitat on

Aldabra. As with *Hermatobates*, it appears that the behavior patterns and habitat preferences of Omaniidae are not uniform throughout the Indo-Pacific, even within individual species.

Microvelia: Although basically a freshwater species, Microvelia diluta was taken from several tidally flooded limestone sinkholes on Picard island which can be rightfully considered marine habitats, since they fill with salt water on a diurnal basis and harbor chitons on their walls. The insects ran about and aggregated on the open water surface at high tide when the sinkholes were innundated, then foraged on the damp mud and rock floors of the sinkholes during low tide when the water drained out. This same species was also an opportunistic colonist of freshwater habitats throughout the atoll, including temporary rainwater pools in limestone, rain barrels, and covered water cisterns.

Summary

Although at first glance Aldabra might seem a relatively homogenous environment for marine Heteroptera, the collections made during the present survey clearly indicate that the species present are not uniformly distributed around the atoll. Instead they occupy three major zones: a.) the exposed outer coast (the eastern and southern seaward shores which are swept by the full force of the southeast monsoon and lack an offshore reef crest); b.) the sheltered outer coast (the western and northern seaward shores which are protected from the southeast monsoon and have a well developed reef crest, plus the sheltered indentation on the south coast near Anse Vaqua); and c.) the lagoon. The exposed outer coast is the poorest in terms of species, harboring only the two pelagic Halobates, H. micans and H. germanus, plus the intertidal saldid Salduncula seychellensis which appears to be restricted to it (figs. 2, 3, 8). In contrast, the sheltered outer coast supports the most species, and is essentially the only area in which Hermatobates djiboutensis, Halobates flaviventris, and Corallocoris aldabrae are found (figs. 1, 4, 9). The lagoon is relatively species poor, but is the primary habitat of the mangrove associated Halobates poseidon (fig. 6). Both of the latter two zones share Halobates alluaudi and Halovelia seychellensis (figs. 5, 7), which appear to make little distinction between them. It thus appears that the strong southeast monsoon, either through its immediate actions of wind and surf or via its effects on the topography of the shoreline, has produced a marked habitat partitioning among the marine Heteroptera of Aldabra.

In addition to these patterns, we see the unusual occurrence of three species, *Halovelia seychellensis*, *Microvelia diluta*, and *Halobates poseidon*, in the limestone bassins of Picard Island. Such colonization of flooded cave systems by marine Heteroptera has not been previously reported from other atolls, although the author and J. T. Polhemus took *Halovelia depressa* from a similar seaside limestone sinkhole in southwestern Madagascar (see discussion in Andersen, 1989).

SYSTEMATICS

KEY TO THE ADULTS OF SPECIES OF OBLIGATELY MARINE HETEROPTERA OCCURRING ON ALDABRA AND COSMOLEDO ATOLLS

- 1. a. Wings always present, although often coleopteriform; semiaquatic bugs occurring along the margins of the sea...............(Leptopodomorpha)..2
 - b. Wings absent; bugs living on the water surface.....(Gerromorpha)..3

2. a. Minute bugs, body length 1-2 mm.; dorsal coloration uniformly dark; wings thickened and lacking visible venation; posterior portion of head with a collar; living interstitially amid coral cobbles
3. a. Hind femur short, not exceeding tip of abdomen; small blackish bugs living near shore, often on pools amid coral rubble
4. a. Middle tibia and tarsi bearing long plumes of swimming hairs on inner margins; male fore femur not greatly swollen, lacking teeth
5. a. Width of head between the eyes greater than its length; interocular width about 4 times the width of an eye; body usually unicolorous silvery grey, lacking extensive yellow or brownish markings on the thoracic and abdominal venter or on the dorsum of the head; open ocean species
6. a. Smaller species, length of male less than or equal to 4.00 mm., length of female less than or equal to 3.80 mm.; male left styliform process not bent upwards, lying horizontally in lateral view; male tergite IX with patches of black bristles on lateral wings
7. a. Foreleg with the length of tarsal segment I longer than or equal to the length of tarsal segment II
8. a. Foreleg with length of tarsal segment I less than or equal to 2/3 the length of tarsal segment II; male left styliform process not bent outward or visible from above

HERMATOBATIDAE

Hermatobates djiboutensis Coutiere and Martin Fig. 1

Hermatobates djiboutensis Coutiere and Martin 1901. Bull. Mus. Nat. Hist. Paris, 4, ser. 1: 172. Type-locality: Red Sea, Djibouti.

Discussion: This species is widely distributed in the western Indian Ocean, from the Red Sea southward along the east coast of Africa and eastward to Madagascar, the Mascarenes, the Aldabra group, and the Maldives.

Material examined: ALDABRA ATOLL, Grande Terre: calm sea 1000 m. offshore of south coast, east of Dune Jean Louis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989, CL 8018. Malabar: calm sea 1000 m. offshore of north coast between Passe Gionnet and Anse Malabar, 09:00 hrs., high tide, 12 March 1989, CL 8032. Picard: reef crest and calm sea offshore of Aldabra Research Station, 13:00 hrs., 9 March 1989, CL 8024. Polymnie: calm sea 1000 m. offshore of north coast between Grande Passe and Passe Gionnet, 10:00 hrs., 19 March 1989. COSMOLEDO ATOLL, Menai: calm sea offshore off northeast tip, 9° 42' 04" S, 47° 32' 00" E, 16:00 hrs., 27 March 1989, CL 8041.

GERRIDAE

Halobates micans Eschsholtz Fig. 2

Halobates micans Eschscholtz 1822. Entomographien 1: 107, pl. 2, fig. 3.

Type-locality: given as "Im sudlichen stillen Meere und im sudlichen atlantischen Meere" [types presumably in University of Dorpat].

Halobates streatfieldanus Templeton 1836. Trans. Entomol. Soc. London, 1: 230, pl. 22, fig. A.

Halobates wullerstorffi Frauenfeld 1867. K. K. Zool-Bot. Gesell. Wien, Verh., 17: 458, pl. 12, fig. 5.

Halobates inermis Dahl 1893. Plankton-Exped., Ergeb., 2: 6, figs. 4, 5, 7, 8.

Discussion: This pelagic species is widely distributed throughout all the tropical oceans of the world (see Andersen, 1982, pg. 370, fig. 629).

Material examined: ALDABRA ATOLL, Grande Terre: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989. COSMOLEDO ATOLL, Menai: on calm sea 1000 meters offshore of northeast tip, 18:00 hrs., 27 March 1989. West North: calm sea offshore of west side, 18:00 hrs., 27 March 1989, CL 8042. Wizard: net tow on calm offshore sea, 7 March 1989, 21:00 hrs., CL 8017. INDIAN OCEAN, Somali Basin: 8° 59' 62" S, 48° 33' 28" E, 28 March 1989, on calm sea; 8° 21' 87" S, 49° 32' 23" E, 29 March 1989; 7° 44' 20" S, 50° 26' 39" E, 30 March 1989; 7° 6' 78" S, 51° 20' 75" E, 30 March 1989.

Halobates germanus White Fig. 3

Halobates germanus White 1883. Voyage Challenger, Rept. Zool., 7 (19): 50, pl. 1, fig. 6. Type-locality: given as "North Pacific Ocean".

Discussion: This pelagic species is widely distributed in the Indian and western Pacific oceans (see Andersen, 1982, pg. 370, fig. 629).

Material examined: ALDABRA ATOLL, Grande Terre: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989; sea 1000 m. offshore of Pointe aux Vacoas, 26 March 1989. Malabar: net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032. Picard: calm sea off Anse Var, 19 March 1989. COSMOLEDO ATOLL, Menai: calm sea 500 meters offshore of Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 13:00 hrs., 27 March 1989, CL 8041. West North: calm sea offshore of west side, 18:00 hrs., 27 March 1989, CL 8042.

Halobates flaviventris Eschsholtz Fig. 4

Halobates flaviventris Eschscholtz 1822. Entomographien 1: 109, pl. 2, fig. 5. Type-locality: given as "Im sudlichen atlantischen Meere", doubted by Herring (1961) [types presumably in University of Dorpat].

Discussion: This elongate silvery species is typically found cruising parallel to the reef crest 500 to 1000 meters offshore. It is widely distributed on islands throughout the Indo-Pacific region, but is unknown from the coast of East Africa. Distant (1913) recorded this species from Port Sudan in the Red Sea, but this distribution has not been subsequently reconfirmed. Polhemus and Polhemus (in press) note that Distant's (1913) records of *H. alluaudi* from Coetivy and the Amirantes likely represent misidentified specimens *H. flaviventris*.

Material examined: ALDABRA ATOLL, Grande Terre: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989. Picard: net tow 100 meters offshore of rocky coast from Research Station to Grande Passe, 16 March 1989 (USNM). Polymnie: in net tow 30 m. offshore of north coast from Grande Passe to Passe Gionnet, 16 March 1989, CL 8034. Malabar: net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032 (USNM). COSMOLEDO ATOLL, Menai: calm sea 500 meters offshore of Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 13:00 hrs., 27 March 1989, CL 8041.

Halobates alluaudi Bergroth Fig. 5

Halobates alluaudi Bergroth 1893. Rev. Ent. Caen 12: 204. Type-locality: Seychelles Islands, Mahe, Port Victoria [types in Paris Museum according to Herring (1961)].

Discussion: This large silvery species is a strong skater and typically occurs along rocky seaward shores. The presently known distribution includes the granitic Seychelles and the atolls of the Aldabra group.

Material examined: ALDABRA ATOLL, Grande Terre: Anse Mais, 18 March 1989. Ile Esprit: rocky shore and mangroves on south side, 24 March 1989. Ile Michel: offshore of mangroves on west side, 22 March 1989, CL 8037. Malabar: Passe Houareau at Middle Camp, 19 March 1989, CL 8036; net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032; Passe Gionnet, 20 March 1989. Picard: rocky islets and mangrove clumps of Sonneratia alba at La Gigi, near Passe Femme, 11 March 1989, CL 8027; offshore reef crest at Research Station, 9 March 1989, CL 8024; net tow 100 meters offshore of rocky coast from Research Station to Grande Passe, 16 March 1989; net tow in lagoon from Passe Gionnet to Passe Femme, 20 March 1989. COSMOLEDO ATOLL, Menai: calm sea offshore of settlement site at Johannes Point, 27 March 1989, CL 8041. MAHE: L'Islette Bay, Port Glaud, 1 April 1989, CL 8043.

Halobates poseidon Herring Fig. 6

Halobates poseidon Herring 1961. Pacific Insects, 3: 287, figs. 52-54. Type-locality: Kenya, Mombassa Island, Port Tudor [holotype in British Museum (Natural History)].

Discussion: This small dull colored species is common among mangroves from the east coast of Africa eastward to Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, Grande Terre: mangrove estuary lined with Avicennia marina at upper end of L'Eglise Channel, off Takamaka Arm, 14 March 1989, CL 8031; Abbott's Creek, 23 March 1989; Anse Mais, 18 March 1989. Ile Michel: mangroves on west side, 22 March 1989, CL 8037. Malabar: Passe Houareau, 19 March 1989, CL 8036; Passe Gionnet, 16 March 1989, CL 8035; Camp Frigate, 20 March 1989. Picard: rocky islets and mangrove clumps of Sonneratia alba at La Gigi, near Passe Femme, 11 March 1989, CL 8027; Entre Deux, 20 March 1989; Upsidedown Jellyfish Pool, nr. Aldabra Research Station, 9 March 1989, CL 8022; Bassin Lebine, 9 March 1989, CL 8023. COSMOLEDO ATOLL, Menai: along sheltered sandy shore lined with Avicennia marina, on lagoon side across from Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 27 March 1989, 10:00 hrs., CL 8041.

VELIIDAE

Halovelia seychellensis Andersen Fig. 7

Halovelia seychellensis Andersen 1989. Entomol. Scand., 20: 191. Type-locality: Seychelles, Mahe, Belle Ombre.

Discussion: This small blackish species is common amid coral rubble at the base of limestone cliffs. The presently known distribution includes the granitic Seychelles, northern Madagascar, Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, Grande Terre: mangrove channel at Abbot's Creek, off of Takamaka Arm, 23 March 1989; east side of Passe Houareau, 23 March 1989. Ile Esprit: rocky beach with mangroves on south side, 24 March 1989. Ile Michel: rocky shore and mangroves on NW coast, 22 March 1989, CL 8037 Malabar: Passe Gionnet, 16 March 1989, CL 8035; Passe Houareau, near Middle Camp, 19 March 1989, CL 8036. Picard: Bassin Cabri, behind Aldabra Research Station, 9 March 1989, CL 8021; offshore intertidal reef crest at Aldabra Research Station, 9 March 1989, CL 8024; nearshore reef and rocks at Aldabra Research Station, 9 March 1989, CL 8025. COSMOLEDO ATOLL, Menai: rocky shore near Johannes Point settlement site, 9°41'68"S, 47°32'26"E, 27 March 1989, CL 8041.

Microvelia diluta diluta Distant 1909

Microvelia diluta Distant 1909. Ann. Mag. Nat. Hist., ser. 8, vol 3: 500. Type locality: Bengal, Calcutta.

Discussion: A more thorough discussion of this primarily freshwater species will be presented elsewhere in a report dealing with the freshwater Heteroptera of Aldabra. The localities listed below are only those representing salt water habitats.

Material examined: ALDABRA ATOLL, Picard: small tidally flooded limestone sinkhole behind Aldabra Research Station, water temp. 27° C., 10 March 1989, CL 8026. COSMOLEDO ATOLL, Menai: tidally flooded limestone sinkhole nr. Johannes Point settlement site, 27 March 1989, CL 8041.

SALDIDAE

Salduncula seychellensis Brown Fig. 8

Salduncula seychellensis Brown 1954. Ann. Mag. Nat. Hist., 7: 855. Type-locality: Seychelles, Mahe.

Discussion: This small black saldid is known from rocky intertidal habitats on the granitic Seychelles, Madagascar, Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, Grande Terre: intertidal rocks and cliffs at Cinq Cases, 13 March 1989, CL 8030; intertidal rocks and cliffs at Dune Jean Louis, 9° 27' 16" S, 46° 23' 70" E, 24 March 1989, CL 8040. COSMOLEDO ATOLL, Menai: intertidal rocks at Johannes Point, nr. settlement site, 9° 41' 68" S, 47° 32' 26" E, 27 March 1989, CL 8041.

OMANIIDAE

Corallocoris aldabrae Cobben Fig. 9

Corallocoris aldabrae Cobben 1987. Rev. Zool. Africaine, 101: 24. Type- locality: Aldabra Atoll, Northeast Channel, Middle Island [= Passe Houareau, Malabar Island].

Discussion: This tiny species is known only from the Passe Houareau on Aldabra atoll.

Material examined: ALDABRA ATOLL, Malabar: rocky beach north of Middle Camp, Passe Houareau, 22 March 1989, CL 8036.

ACKNOWLEDGMENTS

The author wishes to acknowledge the support of Dr. Brian Kensley of the Smithsonian Institution in arranging for his participation on the expedition to Aldabra atoll. Special thanks are also due to the staff of the Aldabra Research Station, and to the crew of the sailing yacht "El Gringo", which served as a floating base of operations during this study. Early drafts of this manuscript were read by Dr. J. T. Polhemus, who provided many useful comments and suggestions. This research was supported by the Aldabra Program of the Smithsonian Institution, Washington, D. C., and was conducted in cooperation with the Seychelles Islands Foundation.

LITERATURE CITED

- Andersen, N. M. 1982. The Semiaquatic Bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography and classification. Entomonograph, Vol. 3. Scandinavian Science Press Ltd., Klampenborg. 455 pp.
- Andersen, N. M. 1989. The coral bugs, genus *Halovelia* Bergroth (Hemiptera: Veliidae). II. Taxonomy of the *H. malaya*-group, cladistics, ecology, biology, and biogeography. Entomologica Scandinavica, 20: 179-227.
- Brown, E. S. 1954. A new genus and species of Saldidae (Hemiptera-Heteroptera) from the Seychelles. Annals and Magazine of Natural History, ser. 12, vol. 7: 854-856.
- Cheng, L. (ed.). 1976. Marine Insects. North Holland, Amsterdam.

- Cheng, L. 1977. The elusive sea bug *Hermatobates* (Heteroptera). Pan-Pacific Entomologist, 53: 87-97.
- Cheng, L. and E. W. Leis. 1980. Notes on the seabug *Hermatobates hawaiiensis* China (Heteroptera: Hermatobatidae). Proc. Hawaiian Entomol. Soc., 23 (2): 193-197.
- Cheng, L. and P. D. Schmitt. 1982. Marine insects of the genera *Halobates* and *Hermatobates* (Heteroptera) from neuston tows around Lizard Island, Great Barrier Reef. Aust. J. Marine Freshwater Res., 33: 1109-1112.
- Cobben, R. H. 1970. Morphology and taxonomy of Intertidal Dwarfbugs (Heteroptera: Omaniidae fam. nov.). Tijdschrift voor Entomologie, 113: 61-90.
- Cobben, R. H. 1987. New African Leptopodomorpha (Heteroptera: Saldidae, Omaniidae, Leptopodidae), with an annotated checklist of Saldidae from Africa. II. New taxa of Saldidae (except genus *Saldula*), Omaniidae, Leptopodidae, and a checklist of African shorebugs. Revue de Zoologie Africaine, 101: 3-30.
- Coutiere, H. and J. Martin. 1901. Sur un nouvel Hemiptere halophile. Bull. Mus. Hist. Nat. Paris, 4: 172-177.
- Dahl, F. 1893. Die *Halobates*-Ausbeute der Plankton Expedition. Ergeb. Plankt.-Exped. 2, G. a: 1-9.
- Distant, W. L. 1909. No. IV. 'Sealark' Rhynchota in The Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner, vol. 2. Transactions of the Linnaean Society of London, 2nd ser., 13: 28-48.
- Distant, W. L. 1913. No. IX. Rhynchota. Part I: Suborder Heteroptera in The Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner, vol. 5. Transactions of the Linnaean Society of London, 2nd ser., 16: 139-191.
- Esaki, T. 1947. Notes on Hermatobates haddoni Carpenter. Mushi, 18 (7): 49-51.
- Eschscholtz, J. F. 1822. Entomographien. Berlin, Lief. I, 128 pp., 2 pls.
- Foster, W. A. 1989. Zonation, behavior and morphology of the intertidal coral-treader *Hermatobates* (Hemiptera: Hermatobatidae) in the south-west Pacific. Zool. J. Linnean Soc., 96: 87-105.
- Foster, W. A. and J. E. Treherne. 1986. The ecology and behavior of a marine insect, *Halobates fijiensis* (Hemiptera: Gerridae). Zool. J. Linnean Soc., 86: 391-412.
- Frauenfeld, G. von. 1867. Zoologische miscellen. XI. Das Insektenleben zur see. K. Zool.-Bot. Gesell. Wien, Verh. 17: 425-464, Taf. 12, figs. 1-10.
- Herring, J. L. 1961. The genus *Halobates* (Hemiptera: Gerridae). Pacific Insects, 3: 223-305.

- Herring, J. L. and H. C. Chapman. 1967. A new species of *Omania* from Micronesia (Hemiptera: Saldidae). Proc. Entomol. Soc. Wash., 69: 354-359.
- Kellen, W. R. 1959. Notes on the biology of *Halovelia marianarum* Usinger in Samoa (Veliidae: Heteroptera). Ann. Entomol. Soc. Amer., 52: 53-62.
- Kellen, W. R. 1960. A new species of *Omania* from Samoa, with notes on its biology (Heteroptera: Saldidae). Ann. Entomol. Soc. Amer., 53: 494-499.
- Polhemus, D. A. and J. T. Polhemus. (in press). Distributional data and new synonymy for species of *Halobates* Eschscholtz (Heteroptera: Gerridae) in the atolls of the Aldabra group, western Indian Ocean. J. New York Entomol. Soc.
- Polhemus, J. T. 1982. Marine Hemiptera of the Northern Territory, including the first fresh-water species of *Halobates* Eschscholtz (Gerridae, Veliidae, Hermatobatidae, and Corixidae). J. Australian Entomol. Soc., 21: 5-11.
- Stoddart, D. R. (ed.). 1967. Ecology of the Aldabra atoll. Atoll Res. Bull., 118: 1-141.
- Stoddart, D. R. and L. U. Mole. 1977. Climate of Aldabra Atoll. Atoll Res. Bull., 202: 1-21.
- Stoddart, D. R. and T. S. Westoff (eds.). 1979. The terrestrial ecology of Aldabra. Phil. Trans. Royal Soc. London, B, 286. 263 pp.
- Templeton, R. 1836. Description of a new hemipterous insect from the Atlantic Ocean. Trans. Entomol. Soc. London, 1: 230-231.
- Usinger, R. L. and J. L. Herring. 1957. Notes on marine water striders of the Hawaiian Islands (Hemiptera: Gerridae). Proc. Hawaiian Entomol. Soc., 16 (2): 281-283.
- White, F. B. 1883. Report on the pelagic Hemiptera procured during the voyage of H. M. S. Challenger, in the years 1873-1876. Zool. Rep. Challenger Exp., 19: 1-82, 3 pl.

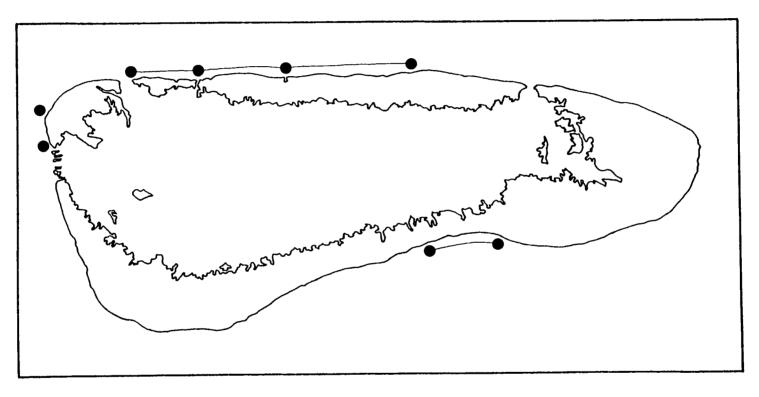


Figure 1. Distribution of *Hermatobates djiboutensis* at Aldabra atoll. Dots connected by lines indicate net tows.

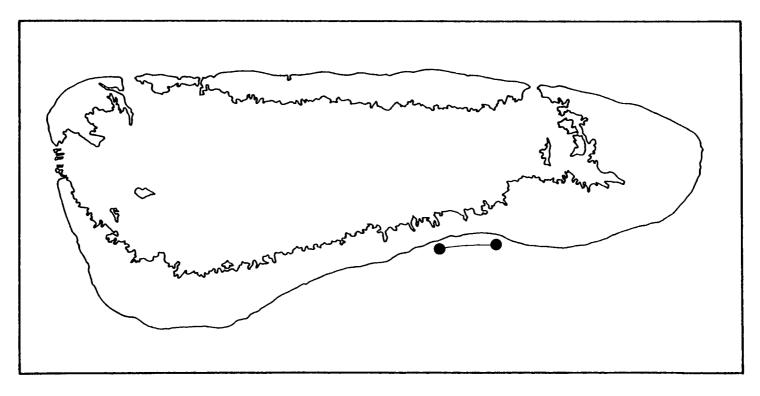


Figure 2. Distribution of *Halobates micans* at Aldabra atoll. Dots connected by lines indicate net tows.

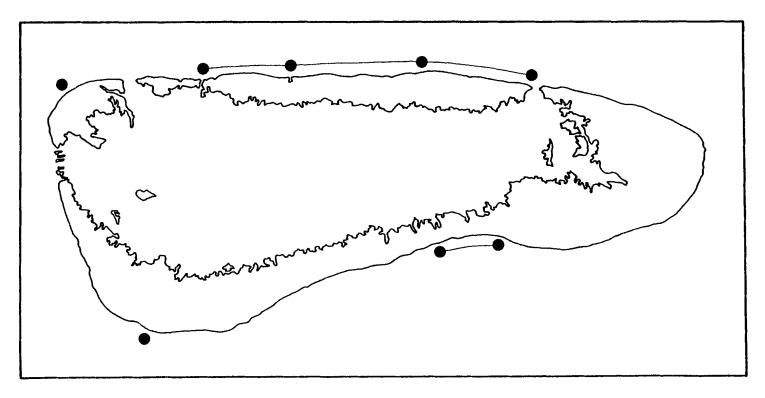


Figure 3. Distribution of *Halobates germanus* at Aldabra atoll. Dots connected by lines indicate net tows.

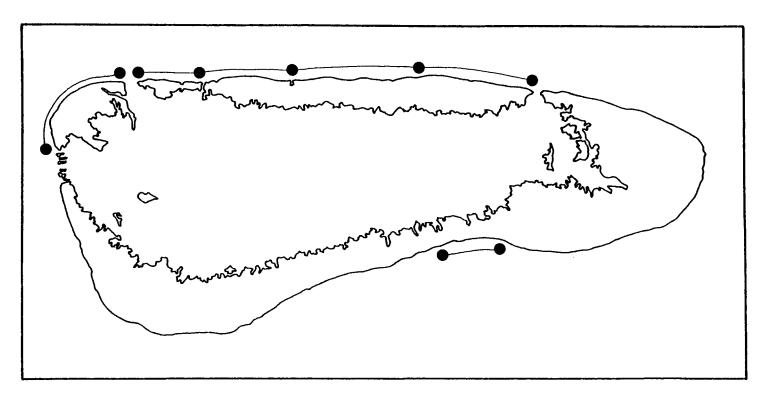


Figure 4. Distribution of *Halobates flaviventris* at Aldabra atoll. Dots connected by lines indicate net tows.

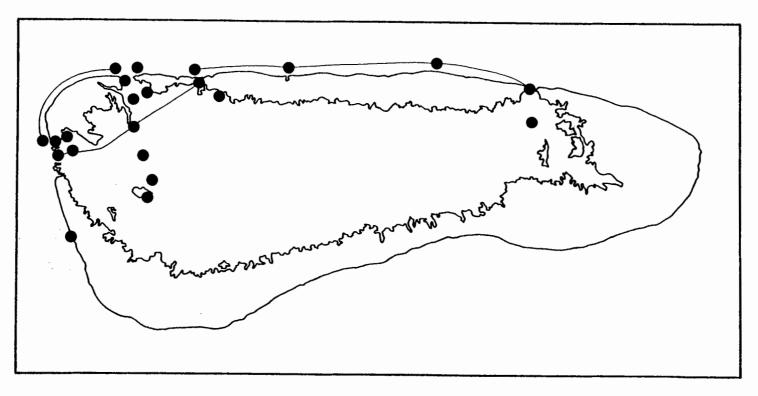


Figure 5. Distribution of *Halobates alluaudi* at Aldabra atoll. Dots connected by lines indicate net tows.

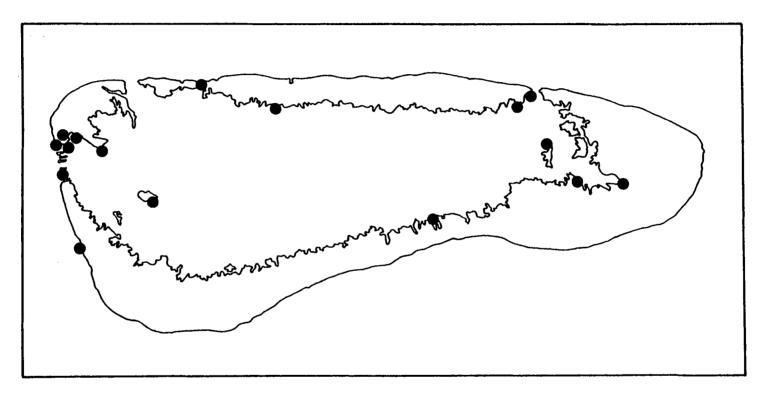


Figure 6. Distribution of *Halobates poseidon* at Aldabra atoll.

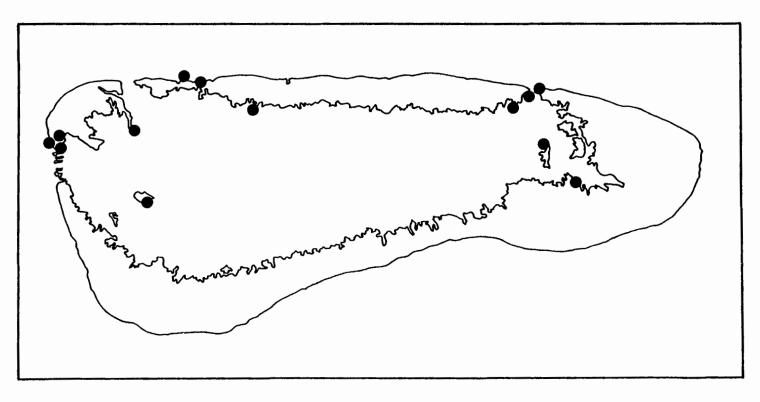


Figure 7. Distribution of *Halovelia seychellensis* at Aldabra atoll.

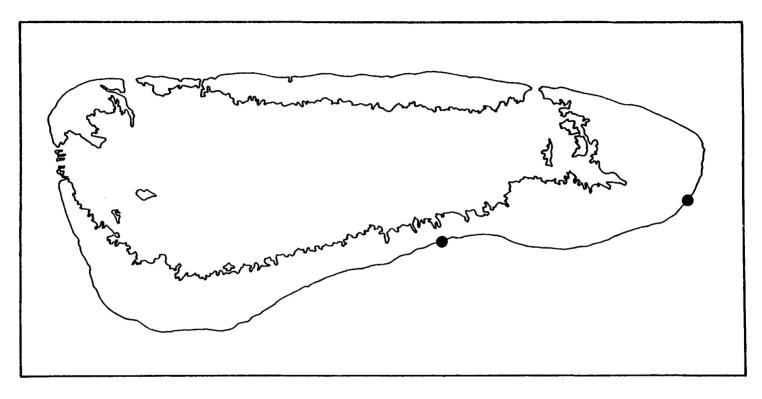


Figure 8. Distribution of Salduncula seychellensis at Aldabra atoll.

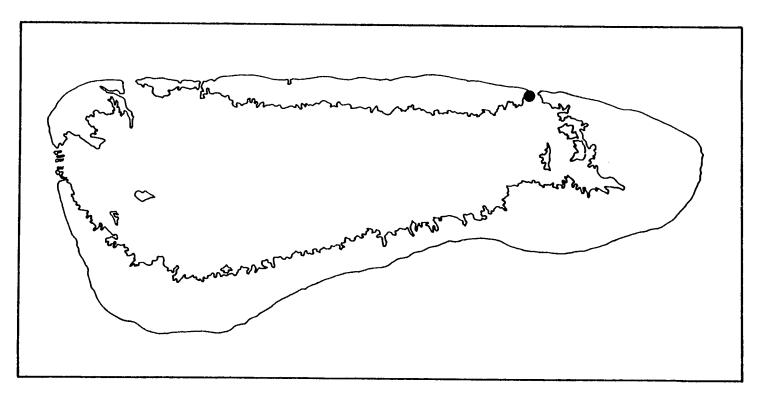


Figure 9. Distribution of Corallocoris aldabrae at Aldabra atoll.