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# Disjunct Distributions of *Halobates* (Hemiptera: Gerridae) in the Pacific Ocean[1]

LANNA CHENG[2]

ABSTRACT: Five species of *Halobates* are specially adapted to a pelagic life. They all occur in the Pacific Ocean, each with a well-defined zoogeographical range. Only two species were caught in a series of samples collected between Hawai'i and Tahiti: *H. sericeus* Eschscholtz, with an amphitropical distribution, and *H. micans* Eschscholtz, occupying the equatorial zone separating the northern and southern populations of the former. This disjunct distribution pattern may be maintained by zonal equatorial current systems. Although mixing of the two species may occur during seasonal weakenings of the currents, the two populations of *H. sericeus* appear to be quite separate, with little or no possibilities of genetic exchange.

FIVE SPECIES OF the marine insect genus *Halobates* (*H. micans* Eschscholtz, *H. sericeus* Eschscholtz, *H. germanus* White, *H. sobrinus* White, and *H. splendens* Witlaczil) are specially adapted to live exclusively in the open ocean (Cheng 1985). They all occur in the Pacific, with a general distribution extending from latitudes 40° N to 40° S (Herring 1961). Within this area the ranges of the various species may overlap, but areas of high population densities are quite separate (Cheng and Shulenberger 1980). *Halobates micans* is the only cosmopolitan species. In the Pacific it is found between 10° N and 10° S, with a northward extension in the Kuroshio Current along the Japanese coast (Cheng 1989). *Halobates sericeus* has an amphitropical distribution and occupies areas to the north and south of *H. micans*. The remaining three species are more coastal in habitat, with *H. germanus* occurring in the western Pacific and the other two species off the Pacific coasts of Central and South America (Cheng 1989).

As part of the North Pacific Shuttle Experiment (NORPAX), a series of scientific cruises was carried out from January 1979 to June 1980. The main objectives were to measure transports of the four major zonal tropical currents—the North Equatorial Current (NEC), North Equatorial Countercurrent (NECC), South Equatorial Current (SEC), and South Equatorial Countercurrent (SECC)—and to develop an effective ocean circulation monitoring system (Wyrtki et al. 1981). There were 15 monthly cruises between Honolulu, Hawai'i (21° 25′ N, 157° 55′ W) and Papeete, Tahiti (17° 45′ S, 149° 30′ W). On a time- and space-available basis, a few biological projects, including this study, were accepted as part of the program. Hydrographic measurements and biological samples were taken along three meridians in a regular pattern. The planned NORPAX sampling grid traversed an area where the northern (20° N to 10° N) and southern (10° S to 20° S) populations of *H. sericeus* are known to be separated by an equatorial population of *H. micans,* thus providing an excellent opportunity to investigate the following questions: (1) Is there a clear range separation between the two populations of *H. sericeus?* (2) If so, is the separation maintained throughout the year? (3) Do opportunities occur for the two populations to intermingle during seasonal weakenings of eastward or westward zonal currents, offering possibilities for gene exchange?

## MATERIALS AND METHODS

*Halobates* specimens were collected by an 80 by 30 cm neuston net towed at 4.5 kts (~7 km/hr) for about 30 min (Clarke 1987). Sam-

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[2] Scripps Institution of Oceanography, University of California, La Jolla, California 92093-0202.

pling was carried out at 1° intervals along three longitudinal meridians, 150° W, 153° W, and 158° W, except for one sample (79-11-8) that was taken at 156° W. Neuston tows were made on six legs (nos. 1, 4, 5, 7, 9, and 11). *Halobates* were sorted from other organisms and preserved in 70% ethanol.

Adult insects were identified to species and sexes based on external morphological characters (Cheng 1975). Immature specimens were assigned to nymphal instars by measuring lengths of the midfemur (Cheng and Maxfield 1980). When nymphs of more than one species were found in the same sample, additional morphometric measurements were made for positive identification.

## RESULTS

The duration of each leg of the expedition, latitudinal coverage, number of stations, total number of neuston tows taken, and number of tows containing *Halobates* are given in Table 1. The number of samples as well as sampling areas differed from leg to leg. *Halobates* were caught in all 62 neuston tows available for this study. They belonged to two species: *H. micans* and *H. sericeus*. Fifty-two were single-species samples: 46 with *H. micans* (Table 2) and six with *H. sericeus* (Table 3). The remaining 10 had both species in various proportions (Table 4). Most tows were taken at night (1800–0600 hours); only 12 were made during the day. The number of insects caught per tow ranged from one to 716. More than half (34) of the samples also contained shed skins (exuviae; see Tables 2–4).

The locations of the sampling stations and the numbers and species of *Halobates* captured during each leg are summarized in Figure 1. In legs 1 and 7 there was evidence for a distinct range separation between *H. sericeus* and *H. micans*. The former was found only north of 15° N and the latter between 11° N and 02° S. Although *H. sericeus* was collected at only one station during each of those legs, those tows contained 82 (sample 02-10) and 51 (sample 05-01) specimens, respectively, each comprising adults and nymphs of various developmental stages (Table 3). Eight of the 12 samples of *H. micans* collected during leg 7 had >50 specimens each, comprising both adults and nymphs (Table 2).

Although mixed-species samples were found in legs 4, 5, and 9, samples in legs 4 and 5 consisted mostly of one species, with the minor species represented by only one or two individuals (Figure 1). For example, in samples 05-03 and 05-04 there were, respectively, 134 and 123 specimens of *H. sericeus,* but only one male and one female each of *H. micans;* in sample 05-05 there were 22 specimens of *H. micans,* but only one female *H. sericeus* (Table 4). In leg 9, however, both species co-occurred in five out of 10 stations (Figure 1). In the three northern stations (11-01, 11-11, and 11-12) *H. micans* was the dominant species, co-occurring with only one or two specimens of *H. sericeus;* in the two southern stations (11-07 and 11-08) both species occurred in almost equal numbers (Table 4).

## DISCUSSION

Early distribution records of oceanic *Halobates* (Herring 1961) indicated that in the Pacific

TABLE 1

LEG NUMBER, DURATION, LATITUDES COVERED, NUMBER OF STATIONS, TOTAL NUMBER OF NEUSTON TOWS, AND NUMBER OF POSITIVE TOWS

| LEG NO. | DURATION (1979) | LATITUDES (°N/S) | NO. OF STATIONS | NO. OF TOWS | NO. WITH *Halobates* |
|---|---|---|---|---|---|
| 1 | 8 Feb.–23 Feb. | 15 N–00 N | 10 | 4 | 4 |
| 4 | 11 May–6 June | 20 N–09 S | 23 | 22 | 22 |
| 5 | 18 June–13 July | 16 N–15 S | 14 | 14[a] | 13 |
| 7 | 25 Aug.–10 Sept. | 18 N–02 S | 13 | 13 | 13 |
| 9 | 7 Nov.–20 Nov. | 08 N–04 S | 11 | 11 | 10 |

[a] One tow aborted.

TABLE 2

*Halobates micans:* TOTAL NUMBER OF INSECTS CAUGHT AND NUMBERS AT EACH DEVELOPMENTAL STAGE

| SAMPLE NO. | NO. OF INSECTS | I | II | III | IV | V MALE | V FEMALE | ADULT MALE | ADULT FEMALE |
|---|---|---|---|---|---|---|---|---|---|
| 02-04 | 17 + 9e | 1 | 2 + 1e | 3 + 1e | 2 + 2e | 4e | 1e | 4 | 5 |
| 02-05 | 2 + 2e | 0 | 0 | 1 | 2e | 0 | 0 | 1 | 0 |
| 02-06 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 05-06 | 716 + 9e | 0 | 4 | 2 | 45 + 2e | 65 + 3e | 66 + 4e | 273 | 261 |
| 05-07 | 56 | 0 | 0 | 1 | 6 | 7 | 1 | 12 | 29 |
| 05-08 | 14 | 0 | 0 | 1 | 3 | 1 | 0 | 6 | 3 |
| 05-09 | 8 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 5 |
| 05-10 | 28 | 0 | 0 | 0 | 5 | 2 | 1 | 12 | 8 |
| 05-11 | 34 + 2e | 2 | 8 + 1e | 9 + 1e | 4 | 2 | 2 | 3 | 4 |
| 05-12 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| 05-13 | 5 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 0 |
| 05-15 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 05-16 | 34 | 6 | 5 | 11 | 8 | 0 | 0 | 1 | 3 |
| 05-17 | 68 + 1e | 3 + 1e | 9 | 23 | 12 | 2 | 1 | 10 | 8 |
| 05-18 | 103 + 5e | 1 | 24 | 41 + 2e | 29 + 2e | 2 | 4 + 1e | 1 | 1 |
| 05-19 | 177 + 17e | 4 | 34 + 4e | 57 + 6e | 42 + 4e | 10 | 20 + 3e | 5 | 5 |
| 06-01 | 42 + 3e | 0 | 0 | 3 | 19 + 3e | 4 | 2 | 6 | 8 |
| 06-02 | 8 + 4e | 0 | 0 | 0 | 1e | 2e | 1 + 1e | 3 | 4 |
| 06-03 | 103 + 1e | 8 | 20 | 23 | 18 | 15 | 7 + 1e | 4 | 8 |
| 06-04 | 48 | 10 | 15 | 14 | 5 | 0 | 3 | 0 | 1 |
| 06-07 | 12 | 0 | 0 | 1 | 2 | 0 | 1 | 4 | 4 |
| 06-08 | 115 + 3e | 9 | 47 + 1e | 46 + 2e | 10 | 0 | 1 | 1 | 1 |
| 07-01 | 50 + 1e | 0 | 0 | 0 | 8 | 3 | 6 + 1e | 14 | 19 |
| 07-02 | 23 + 1e | 1 | 1 | 2 | 5 + 1e | 1 | 1 | 4 | 8 |
| 07-03 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 07-04 | 34 | 0 | 0 | 0 | 0 | 7 | 1 | 12 | 14 |
| 07-07 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 07-08 | 134 + 21e | 0 | 0 | 2 + 1e | 8 + 9e | 40 + 5e | 53 + 6e | 15 | 16 |
| 07-09 | 6 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 |
| 08-01 | 78 + 2e | 0 | 1 | 0 | 6 + 1e | 2 | 4 + 1e | 27 | 38 |
| 08-02 | 18 | 1 | 3 | 1 | 0 | 1 | 0 | 4 | 8 |
| 08-03 | 83 | 0 | 12 | 6 | 1 | 1 | 0 | 26 | 37 |
| 08-04 | 133 | 0 | 5 | 11 | 10 | 7 | 1 | 45 | 54 |
| 08-05 | 14 + 2e | 0 | 3 | 6 + 1e | 2 | 0 | 3 + 1e | 0 | 0 |
| 08-06 | 117 + 2e | 0 | 2 | 6 | 29 | 34 | 34 + 2e | 3 | 9 |
| 08-07 | 109 | 0 | 9 | 4 | 2 | 6 | 1 | 39 | 48 |
| 08-08 | 61 | 0 | 1 | 0 | 1 | 0 | 0 | 31 | 28 |
| 08-09 | 20 | 0 | 0 | 0 | 1 | 0 | 0 | 6 | 13 |
| 09-01 | 11 + 4e | 0 | 1 | 0 | 3 + 4e | 1 | 0 | 3 | 3 |
| 09-1A | 66 + 1e | 1 | 14 | 12 | 21 | 4 + 1e | 7 + 1e | 1 | 6 |
| 09-02 | 94 + 5e | 1 | 5 | 25 + 3e | 42 + 2e | 6 | 11 | 3 | 1 |
| 11-03 | 37 | 1 | 7 | 4 | 1 | 3 | 3 | 12 | 6 |
| 11-04 | 46 | 0 | 0 | 6 | 6 | 9 | 6 | 9 | 10 |
| 11-05 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 3 |
| 11-06 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 |
| 11-09 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

NOTE: I-V, nymphal instars 1-5; e, exuviae.

TABLE 3

*Halobates sericeus:* TOTAL NUMBER OF INSECTS CAUGHT AND NUMBERS AT EACH DEVELOPMENTAL STAGE

| SAMPLE NO. | NO. OF INSECTS | I | II | III | IV | V MALE | V FEMALE | ADULT MALE | ADULT FEMALE |
|---|---|---|---|---|---|---|---|---|---|
| 02-10 | 82 + 4e | 4 + 1e | 2 | 9 | 1 + 1e | 5 + 2e | 5 | 17 | 39 |
| 05-01 | 34 + 2e | 6 | 7 + 1e | 14 + 1e | 3 | 0 | 0 | 1 | 3 |
| 05-02 | 222 + 10e | 27 | 15 + 3e | 35 + 5e | 36 + 2e | 19 | 31 | 25 | 34 |
| 06-05 | 19 | 1 | 0 | 1 | 2 | 1 | 4 | 6 | 4 |
| 07-10 | 45 + 4e | 12 | 10 + 1e | 12 + 1e | 4 + 2e | 0 | 4 | 1 | 2 |
| 09-03 | 51 + 2e | 1 | 2 + 1e | 9 | 22 + 1e | 4 | 5 | 2 | 6 |

NOTE: I–V, nymphal instars 1–5; e, exuviae.

TABLE 4

MIXED-SPECIES SAMPLES: TOTAL NUMBER OF EACH *Halobates* SPECIES CAUGHT AND NUMBERS AT EACH DEVELOPMENTAL STAGE

| SAMPLE NO./SP. | NO. OF INSECTS | I | II | III | IV | V MALE | V FEMALE | ADULT MALE | ADULT FEMALE |
|---|---|---|---|---|---|---|---|---|---|
| 05-03/m | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 05-03/s | 134 + 10e | 16 + 2e | 20 + 4e | 7 + 2e | 9 + 2e | 8 | 11 | 21 | 42 |
| 05-04/m | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 05-04/s | 123 + 1e | 14 + 1e | 36 | 26 | 22 | 0 | 0 | 1 | 24 |
| 05-05/m | 22 + 1e | 0 | 0 | 3 + 1e | 1 | 3 | 3 | 4 | 8 |
| 05-05/s | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 06-09/m | 304 + 26e | 10 + 1e | 5 + 3e | 42 + 8e | 148 + 10e | 34 + 2e | 48 + 2e | 9 | 8 |
| 06-09/s | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 07-05/m | 27 + 2e | 0 | 0 | 0 | 1 | 5 | 4 + 2e | 8 | 9 |
| 07-05/s | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11-01/m | 23 | 0 | 0 | 3 | 1 | 0 | 0 | 10 | 9 |
| 11-01/s | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11-07/m | 9 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 2 |
| 11-07/s | 14 + 1e | 0 | 0 | 3 | 5 | 2 | 2 + 1e | 1 | 1 |
| 11-08/m | 42 + 2e | 2 | 7 | 11 + 1e | 7 + 1e | 1 | 0 | 4 | 10 |
| 11-08/s | 71 + 4e | 0 | 0 | 4 | 33 + 3e | 17 + 1e | 13 | 2 | 2 |
| 11-11/m | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 3 |
| 11-11/s | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 11-12/m | 13 + 2e | 0 | 2 | 6 | 4 + 1e | 0 | 1e | 0 | 1 |
| 11-12/s | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |

NOTE: m, *micans*; s, *sericeus*; I–V, nymphal instars 1–5; e, exuviae.

Ocean *H. micans* ranged between 10° N and 10° S; *H. sericeus* occurred between 10° and 35° N and between 10° and 35° S and was generally absent from the intervening area occupied by *H. micans*. However, in Herring's distribution map of *H. sericeus* there were three records near the equator (map 2, p. 227). Because no detailed collection data were given, it is not known whether those records represented one or two stray specimens or a more substantial presence of the species.

During the R/V *Vityaz* cruises in the Pacific between 1957 and 1961, *Halobates* were collected at about 250 stations. Data from these cruises were analyzed by Savilov (1967:255–256), who reported that *H. sericeus* had very clearly established northern and southern limits. It was "... completely absent from the streams

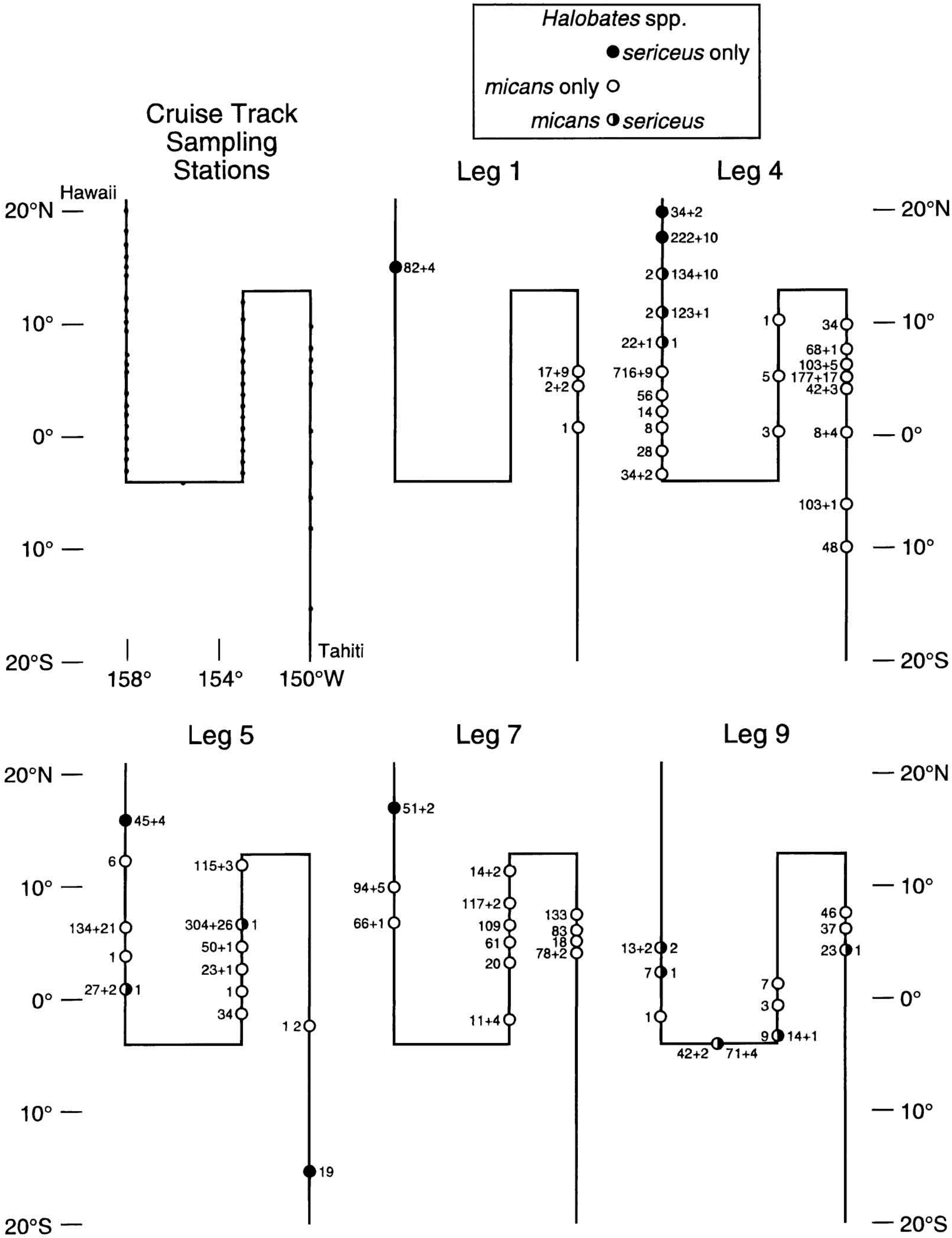


FIGURE 1. Cruise track of NORPAX, locations of sampling stations, and numbers of *Halobates* species caught at each station during legs 1, 4, 5, 7, and 9.

of the South Equatorial Current adjacent to the Countercurrent," and the central equatorial region was occupied by *H. micans*. The two species were found together in only a limited area in the Kuroshio Current (Savilov 1967).

A general range separation of the two species was clearly shown in the eastern Pacific (Cheng and Shulenberger 1980) and along a transect at 155° W between latitudes 40° N and 14° S in the western Pacific (Cheng 1973). However, they occasionally co-occurred at stations around 20–25° N and 125–135° E, where *H. micans* had probably been carried beyond its normal northward range limit by the Kuroshio Current (Cheng 1973), as was also shown by Savilov (1967).

Data from the study reported here confirmed that the ranges of *H. micans* and *H. sericeus* are quite separate and that the latter species has a distinctly disjunct, amphitropical distribution. However, seasonal mixing of the two species does occur, and a few specimens of *H. sericeus* have been collected at stations beyond its normal northern or southern limits. Such occurrences are probably attributable to movements of the surface water, because these ocean skaters are totally wingless and are confined to the sea surface all their lives (Cheng 1985).

Little is known about mechanisms of water exchange between the subtropical gyres and the equatorial current system where *Halobates* live. Such exchanges are probably effected through the western boundary currents, where waters entering from the subtropical gyres flow eastward in the equatorial countercurrents. Therefore, mixing across latitudes may be related to the relative strengths of the countercurrents. The extent and frequency of such occurrences are not known, but they could determine the seasonal boundaries of the range of each *Halobates* species and also provide opportunities for mixing between populations.

According to Wyrtki and Kilonsky (1984) the equatorial current system is asymmetrical with respect to the equator, with a northern boundary around 18° N and a southern boundary around 8° S. The northern boundary of *H. micans* could therefore be expected to extend farther to the north than to the south. The NEC flows westward between 9° and 18° N and splits into two main branches around 15° N, with the southern branch being the stronger. The NECC flows eastward between 4° and 9° N and can reach a maximum speed of over 60 cm/sec. The SEC flows westward and has three branches, with the main branch flowing between the equator and 8° S. The eastward-flowing SECC, the weakest of the equatorial zonal currents, fluctuates between 7° and 14° S and may also have several branches. How these currents interact to delimit ranges of *H. sericeus* and *H. micans* has not been studied. The NECC may be the most important: it exhibits large seasonal variations, and in the central Pacific it is strongest during July and weakest or absent around April (Puls 1895, Knauss 1958).

During NORPAX the NECC was always present. The direction and mean velocities of surface currents for each leg were estimated by averaging zonal geostrophic velocity measurements taken at the three meridians (Figure 2). The eastward-flowing NECC was strongest during leg 1, when we observed a total separation of the two species among our samples. The weakening of the NECC during legs 3 and 4, from early April to early June, may have allowed a few specimens of *H. micans* to move northward or *H. sericeus* to move southward (Figure 1). Thus in the two mixed samples in leg 5, the odd specimens of *H. sericeus* within the predominantly *H. micans* range could have been strays. As the NECC strengthened toward August and September, we again found a clear separation of the two species in leg 7. However, although the NECC remained strong during legs 8 and 9 (Figure 2), half of the samples in leg 9 contained both species (Figure 1). What physical oceanographic factors could be responsible for such mixing of the two species during that period are unclear. Unfortunately, no direct measurements of surface winds or currents were made during the NORPAX cruises. Although estimates from zonal geostrophic velocity measurements can give the general direction and average velocity of surface currents, they may not represent what is actually happening at the time the samples were collected. Measurements of physical properties at the ocean surface made by satellites or Surface Velocity Program (SVP) drifters could provide data to answer such questions in the future.

## CONCLUSIONS

This time series shows that, even on a limited temporal and spatial scale, the ranges of *H.*

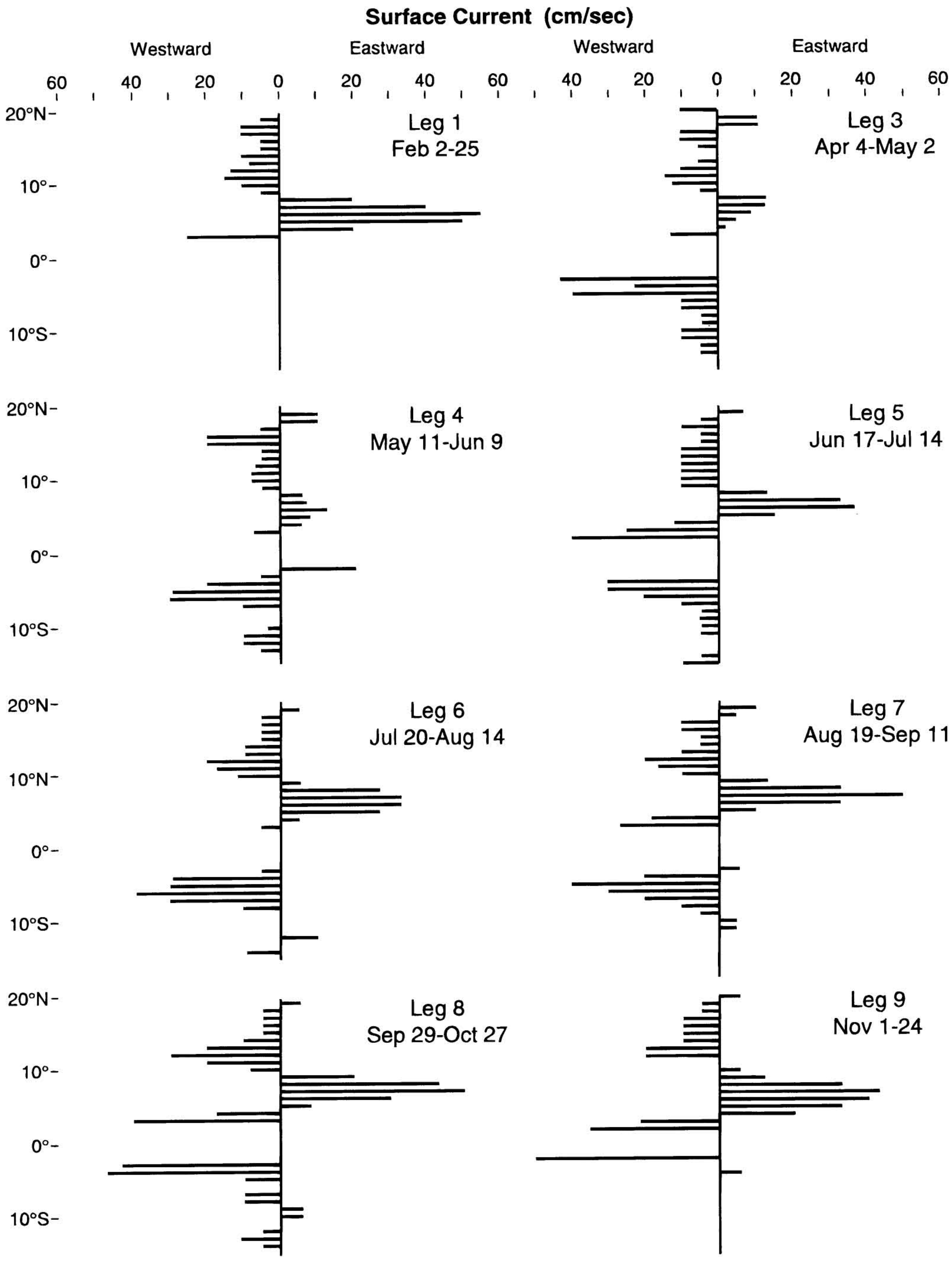


FIGURE 2. Direction and mean surface current velocities (cm $sec^{-1}$) during legs 1 and 3–9 of NORPAX. (Data from Taft and Kovala [1981] and Taft et al. [1982].)

*micans* and *H. sericeus* in the Pacific Ocean are generally separate. *Halobates micans* is restricted to a zone between 11° N and 10° S, with amphitropical populations of *H. sericeus* north and south of that region. The separate ranges of the two species are associated with the large-scale permanent surface circulation patterns. *Halobates sericeus* is well confined in the N and S anticyclonic subtropical surface gyres, whereas *H. micans* is found only in the zonal equatorial currents (Figure 3). However, there is evidence of mixing between the two species in our samples. Apart from one or two odd specimens in some mixed samples, which could be considered as strays, there are at least three instances where these two species co-occurred (Figure 3). Although the separation of northern and southern populations of *H. sericeus* appears to be permanent, data from this study do not allow us to speculate on whether intermingling of individuals from the two populations ever occurs. It is likely that the specimens of *H. sericeus* found in a mixed sample at latitude 12° N came from the northern population and those at 3° and 4° S came from the southern population.

There are no gross morphological distinctions between adults from the two *H. sericeus* populations. Because we are still unable to rear pelagic *Halobates* in the laboratory, we do not know whether they could interbreed. We are currently sequencing mitochondrial-DNA fragments of preserved insects in an attempt to find out whether the two disjunct populations of *H. sericeus* are genetically distinct.

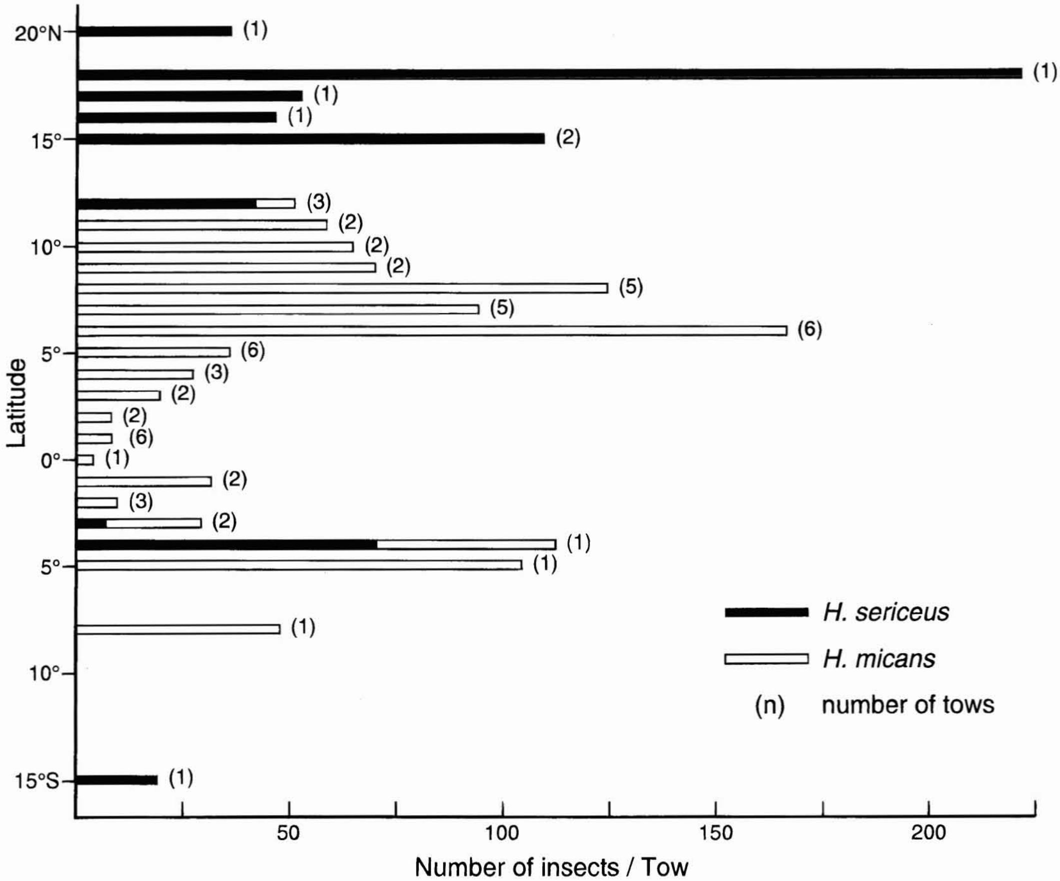


FIGURE 3. Species of *Halobates* and mean numbers of insects caught per tow by latitude. (Numbers in mixed samples not shown when <1; see Table 4 for details.)

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