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Species Composition and Distribution of Ocean Skaters *Halobates* (Hemiptera: Gerridae) in the Western Pacific Ocean

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Abstract. Five species of ocean skaters *Halobates* are the only insects that have successfully colonized the ocean. In the western Pacific Ocean, three species of *Halobates*, *H. micans*, *H. sericeus* and *H. germanus*, are known to occur over a wide area. We investigated the spatio-temporal features of *Halobates* during the three cruises of R/V Hakuho Maru in the western Pacific in 1994, 1995 and 1998. During these cruises, the area between latitudes 7°N–22°N and longitudes 125°E–150°E was surveyed in all cruises, and in this area *H. germanus* was absent while *H. micans* and *H. sericeus* were caught every year. In 1994 and 1995, *H. micans* was found almost to the exclusion of *H. sericeus* and in 1998 *H. sericeus* was found almost to the exclusion of *H. micans*, suggesting that these two species rarely co-occur, while their distribution ranges change temporally. We examined water surface temperature, prevailing winds and the El Niño event as possible factors responsible for the replacement of *H. micans* by *H. sericeus* in 1998. On the ocean surface, oceanic diffusion is constantly acting to disperse *Halobates* in all directions. However, local distribution patterns of *H. micans* and *H. sericeus* were highly clumped, suggesting that these species have the ability to aggregate against oceanic diffusion.

Key words: Ocean skaters, species composition, distribution, the western Pacific Ocean, *Halobates* spp.

Introduction

Five species of ocean skaters, *Halobates micans* Eschscholtz, *H. sericeus* Eschscholtz, *H. germanus* White, *H. splendence* Witlaczil and *H. sobrinus* White, are the only insects that have successfully colonized the open ocean. They are wingless and are confined to the ocean surface throughout their life stages. Two phylogenetic studies (Andersen, 1991; Damgaard *et al.*, 2000) concluded that the pelagic habit has evolved at least twice in the genus *Halobates*. These insects are widely distributed in the tropical and subtropical regions of the three major oceans. All five species occur in the Pacific Ocean. *Halobates micans* and *H. germanus* are found in the Indian Ocean but only *H. micans* occurs in the Atlantic Ocean (e.g., Herring, 1961; Cheng, 1989).

We collected ocean skaters in the western Pacific Ocean in 1994, 1995 and 1998 to investigate the spatio-temporal features of *Halobates* species. To date, only a few *Halobates* studies include repeated surveys of local populations (in the Banda Sea by Cheng *et al.*, 1990 and in the Atlantic Ocean by Cheng, 1973b). The paucity of repetitive, quantitative surveys that are indispensable for understanding the population ecology of *Halobates*, is largely due to difficulties in organizing regular cruises in the same region of the open ocean.

Three pelagic *Halobates* species, *H. micans, H. sericeus* and *H. germanus*, known to occur in the western Pacific, are distributed as follows: *H. micans* between ca. 20°N–20°S, except along the Kuroshio Current where it extends northward off the coast of Japan; *H. sericeus* with an amphi-tropical distribution between 12°N–40°N and 10°S–35°S; and *H. germanus* between 30°N–30°S (see the distribution maps by Savilov, 1967; Cheng, 1989). The distribution ranges of the pelagic *Halobates* species thus appear to overlap over a wide area in the western Pacific, including our sampling area. However, since the distribution maps of *Halobates* represent a compilation of collection records from a number of different cruises, spatio-temporal information cannot be elucidated. Thus, the apparent overlap of the three species could be generated by overlaying data from different years and seasons.

The first purpose of our study was to examine whether the three *Halobates* species actually do co-occur in our sampling area and whether their relative abundance fluctuates temporally. Our second purpose was to investigate the densities and distribution patterns of *Halobates* (random, uniform or clumped). It is not known how ocean skaters find conspecifics on the open ocean where storms, winds, and oceanic turbulence constantly act to disperse them in all directions (e.g., Okubo, 1971; Ikawa *et al.*, 1998). If their distribution patterns are contagious, they must have specific strategies to aggregate against the diffusive force on the ocean surface.

Materials and Methods

Halobates specimens were collected during the three expeditions of R/V Hakuho Maru of the University of Tokyo, KH-94-2 Leg.3, June 19–July 6 1994; KH-95-2, July 16–September 23 1995; and KH-98-2, May 24–June 20 1998. These expeditions were organized primarily to explore the spawning areas of the Japanese eel (*Anguilla japonica*), with most intensive surveys between latitudes 7°N–22°N and longitudes 125°E–150°E (hereafter, "common area"). The sampling area was extended beyond the common area as far as the South Pacific only in 1995. The track charts of the three cruises and the common area are shown in Fig. 1A.

Six kinds of nets were used for sampling during the cruises, i.e., ORI-surface (160 cm in mouth diameter) and MTD-horizontal (80 cm in mouth diameter), which swept the ocean surface continuously; and ORI-oblique, IKPT-oblique, IKPT-horizontal, and IKPT-step, which were towed underwater. Ship speed was about 2.0–2.5 kt during sampling. The organisms

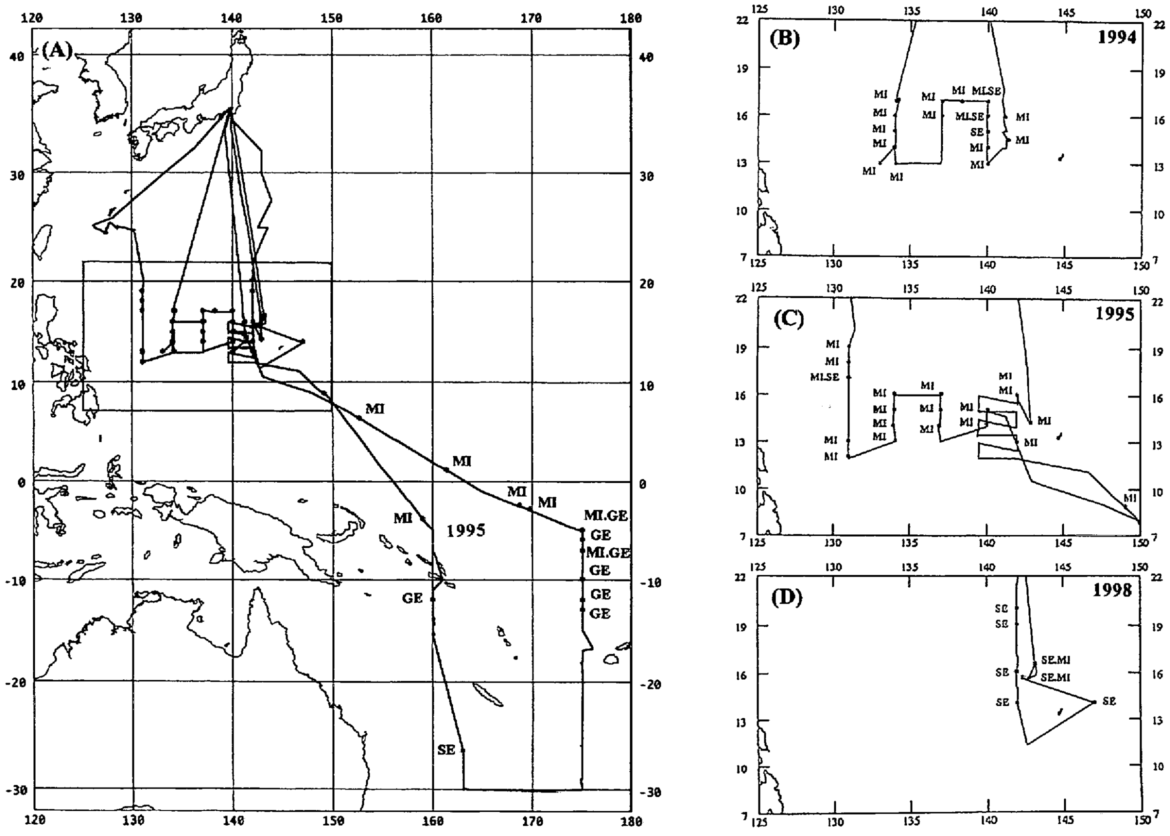

Fig. 1. (A) Track charts of the three Hakuho Maru cruises in the western Pacific with locations where *Halobates* species were captured. Boxed area (common area) between latitudes 7°N–22°N and longitudes 125°E–150°E was intensively surveyed by all three cruises. The extended sampling area south of the common area was only covered in 1995. (B), (C), and (D) are cruise tracks in the common area for 1994, 1995 and 1998, respectively. MI=*H. micans*, SE=*H. sericeus*, GE=*H. germanus*.

collected with each net were sorted on board. *Halobates* samples were preserved in 99% ethanol and stored at −80℃.

For estimating population densities or evaluating spatial patterns of distribution, we used data from ORI-surface and MTD-horizontal nets which sampled the ocean surface only. However, for determining species compositions, age structures and sex ratios, we combined all data from the six kinds of nets.

Results and Discussion

Number of Halobates *caught and net types*

The net types, the numbers of total tows and the numbers of positive tows (i.e., tows in which *Halobates* were caught) and the numbers of *Halobates* captured are presented in Table 1. The majority of the specimens were collected with ORI-surface or MTD-horizontal in 1994 (69 out of 86 individuals), and with ORI-surface in 1995 (140 out of 196 individuals) and 1998 (456 out of 459 individuals). Obviously, this is because ocean skaters are confined to the ocean surface and only these two nets sampled the sea surface consistently. The other nets sampled underwater, so *Halobates* would be captured only when the nets were lifted out of the water.

Species composition and relative abundance

Halobates micans, H. sericeus and *H. germanus* were expected to be found in the common area according to the distribution maps by Savilov (1967) and Cheng (1989). However, as is shown in Table 2 and Figs. 1B, 1C and 1D, *H. germanus* was not collected, and only *H. micans* and *H. sericeus* were found in the common area during all three cruises. In 1994 and 1995, *H. micans* was predominant (collected in 80 out of 86 samples and 155 out of 156 samples, respectively), while in 1998, 457 samples contained *H. sericeus* and only two contained *H. micans*. Thus, only one species, either *H. micans* or *H. sericeus*, was dominant in the common area during each of three cruises. Our results suggest that these two species probably rarely co-occur and that their population densities and/or distribution ranges may change temporally. Possible physical factors responsible for the different relative abundance of the two species in the common area are discussed below.

1) Surface temperature

Oceanic *Halobates* species are found in tropical or subtropical waters where the sea-surface temperature

Table 1. Net type, numbers of total and positive tows and numbers of *Halobates* collected in 1994, 1995 and 1998.

Year	Net type	No. total tows	No. positive tows	No. *Halobates* collected
1994	ORI-surface	16	9	23
	ORI-oblique	31	2	2
	IKPT-oblique	54	9	13
	IKPT-horizontal	22	2	2
	MTD-horizontal	6	6	46
1995	ORI-surface	17	5	140
	IKPT-oblique	138	13	15
	IKPT-step	90	20	41
1998	ORI-surface	51	21	456
	IKPT-horizontal	23	1	3

Table 2. Species and age composition of *Halobates*, and sea surface and air temperatures in the common area in 1994, 1995 and 1998. V, IV, III, II, and I indicate nymphal stages. Number of exuviae in brackets.

Year	Species	Adult		Nymphal stage						Egg	Total	% Adult	% Females	Sea surface/air temperature (℃)*
		♀	♂	V♀	V♂	IV	III	II	I					
1994	*H. micans*	26	20	11	4	9(1)	9	1	0	0	80(1)	58	61	
	H. sericeus	1	3	1	1	0	0	0	0	0	6			
	Total	27	23	12	5	9(1)	9	1	0	0	86(1)			30.4/28.3
1995	*H. micans*	60	42	10	14	17	11(6)	1	0	0	155(6)	66	56	
	H. sericeus	0	1	0	0	0	0	0	0	0	1			
	Total	60	43	10	14	17	11(6)	1	0	0	156(6)			29.6/27.6
1998	*H. micans*	2	0	0	0	0	0	0	0	0	2			
	H. sericeus	139	93	66	59	68	24	7	1	0	457	51	57	
	Total	141	93	66	59	68	24	7	1	0	459			29.2/27.9

* average sea-surface and air temperatures at locations with positive tows in the common area.

remains above 20℃. *Halobates micans*, occupying the equatorial band, lives in warmer waters than does *H. sericeus* (Cheng, 1989). If there is a considerable yearly and/or seasonal fluctuation in the sea-surface temperature in the common area, it may affect the distribution and abundance of each species. The common area, however, belongs to the western Pacific warm pool where sea-surface temperatures are constantly high with almost no seasonal cycle (Delcroix, 1998). In fact, as is shown in Table 2, there was little variation in sea-surface (29.2–30.4℃) and air temperatures (27.6–28.3℃) among the three cruises. Therefore, sea-surface temperature is not a factor in the distributions and/or densities of the two species in the common area.

2) Seasonal change of prevailing winds

Since ocean skaters live at the ocean surface, the wind would play an important role in determining their distribution ranges. Actually, the large-scale distributions of oceanic *Halobates* species appear to be delimited by major surface currents, which are created by wind drag (Cheng, 1989). Therefore, seasonal changes of prevailing winds might also influence temporal fluctuations in the distribution ranges of *Halobates* species, possibly blowing them over long distances.

The 24-year mean of monthly wind stress in the North Pacific (Kutsuwada, 1987) shows that the direction of prevailing winds over the common area is southwestward from November to April, then the winds reverse and blow northward from June to September. Hence, the prevailing winds blow so as to carry *Halobates* species northward during the summer and southward during the winter.

In general, *H. micans* occupies the equatorial band. In the North Pacific, *H. sericeus* had been found to be distributed north of *H. micans*' habitat zone, the boundary of which is between ca. 12°N–20°N (Cheng, 1985, 1989). In the common area, the prevailing winds might have caused a northward shift of the boundary of the two species during the summer and a southward shift during the winter.

In the present study, the sampling period of 1998 (May 24–June 20) was a little earlier than that of 1994 (June 19–July 6) or 1995 (July 16–September 23). The predominance of *H. sericeus* in 1998 could therefore be due to the fact that the population had not yet been blown north of the common area. Thus, the seasonal change of prevailing winds might be one of the factors which determine relative abundances of *H. sericeus* and *H. micans*.

3) Effect of El Niño

In the western Pacific, El Niño events are chiefly associated with fresher than average surface salinity, westerly wind anomalies, above average precipitation, and sea level decrease (Delcroix, 1998). Some anomalous physical conditions related to the 1997–1998 El Niño event might have been responsible for the predominance of *H. sericeus* in the common area. In the North Pacific, *H. sericeus* generally lives north of *H. micans*' habitat, whereas *H. micans* generally lives in the equatorial band where the water is less saline due to higher precipitation. The salinity front, separating the northern high salinity water from the southern low salinity water in the North Pacific, may serve as a boundary of the distribution ranges of *H. sericeus* and *H. micans*. Kimura *et al.* (1999, 2001) analyzed the salinity data along 137°E and compared the mean salinity from 1972 to 1998 with that of the years when typical El Niño events were observed. During the normal years, the salinity front was located about 16°N. During the El Niño event in 1997–98, however, the salinity front was shifted southward from 16°N to 10°N. Populations of *H. sericeus* might have shifted southward to the common area with the southward shift of the high salinity water in 1997–1998.

However, fluctuations in the distribution and abundance of *Halobates* populations may not be caused by any external factors. We will not have any decisive answer until we obtain more data on the population dynamics of the *Halobates* species concerned.

The numbers of each *Halobates* species captured outside the common area in 1995 are presented in Table 3. The locations of positive tows and the species caught are indicated in Fig. 1A. A total of 28 *H. micans* specimens were collected between lat. 7°N–7°S and only one adult female *H. sericeus* was found at ca. 26°S. Eleven *H. germanus* were caught around

Table 3. Species, sex and age composition of *Halobates* captured outside the common area in 1995 (symbols as for Table 2).

Species	Adult		Nymphal stage						Egg	Total
	♀	♂	V♀	V♂	IV	III	II	I		
H. micans	6	4	3	2	11	2(1)	0	0	0	28(1)
H. germanus	9	2	0	0	0	0	0	0	0	11
H. sericeus	1	0	0	0	0	0	0	0	0	1

Melanesia, although we found none in the common area during these three cruises (Table 2). In general, the locations where the three species were found agreed with known distributions of these species (Cheng, 1989).

Population structure, density and local distribution pattern

In the common area, the adult ratio of *H. micans* caught in 1994 was 58%. In 1995, it was 66%. For the species *H. sericeus*, the adult ratio was 51% in 1998 (Table 2). The figures for the eastern tropical Pacific were 44% for *H. sericeus* and 65% for *H. micans* (Cheng & Shulenberger, 1980). In the Atlantic Ocean, percentages of adult *H. micans* varied from ca. 25% to 70% (Cheng, 1973b; Cheng & Shulz-Baldes, 1981). Such variations in adult ratios could be due to seasonality of their reproductive cycle. However, no seasonality of *Halobates* life cycle has been demonstrated so far (Cheng, 1985). The sex ratios of *H. micans* and *H. sericeus* were nearly 50% for all three cruises (Table 2). This has been found also in other studies (e.g., Cheng, 1973a; Cheng & Shulenberger, 1980; Cheng & Shulz-Baldes, 1981; Cheng *et al.*, 1990; Cheng & Holdway, 1995).

We estimated population densities and local distribution patterns for *H. micans* in 1994 and *H. sericeus* in 1998 in the common area, since these were the only data with sufficient numbers of surface tows. Average *Halobates* density (numbers/km^2) was calculated by dividing the total number of insects caught by the total area swept. Average densities for *H. micans* and for *H. sericeus* were 3×10^3 and 7×10^3, respectively (Table 4). Maximum density per tow was 3×10^4 for *H. micans* and 7×10^4 for *H. sericeus*.

To evaluate the local distribution pattern, i.e., uniform, random or clumped, we calculated Morisita's index, which gives a measure of dispersion (Morisita, 1962),

$$I_\delta = q \sum (X_i - 1)X_i / T(T-1) ,$$

where q is the number of sampling sites (i.e., number of tows in the present study), X_i is the number of individuals captured in the i-th sampling site and $T = \sum X_i$ is the total number of individuals captured. However, Morisita's method assumes that samples are taken from units with the same area, whereas our samples were collected by sweeping various areas of the sea surface. To normalize the sampling area, we calculated the density of ocean skaters at each tow and multiplied the density by the smallest area among the towed areas where one or more ocean skaters were captured. Evidently, this operation results in underestimation of contagiousness. Another problem is that numbers of insects captured are usually no longer integers as a result of this operation. Morisita's index semantically assumes that X_i's are integers, and if not, a negative value of $(X_i-1)X_i$ could occur. Here, we calculated Morisita's index in two different ways: 1) using normalized numbers of *Halobates* captured (X_i) irrespective of their non-integrality ($I_{\delta1}$); and 2) by rounding up the decimal part of normalized numbers X_i'($I_{\delta2}$). We adopted the ceiling operation because it usually gives a smaller value of Morisita's index, hence a more conservative estimate of contagiousness is obtained. Rounding down the part under the decimal point usually results in overestimation of the index.

Since the observed distribution patterns of *H. micans* in 1994 and of *H. sericeus* in 1998 appeared strongly clumped, we tested whether this was significant. As is shown in Table 4, irrespective of the method of estimation, we found Morisita's indices ($I_{\delta1}$ and $I_{\delta2}$) for both species to be far greater than 1.0. Tests utilizing F-distribution also showed these results to be statistically significant (99% one-sided). Thus, we conclude that the distributions of these two *Halobates* species were highly clumped.

Pelagic as well as coastal *Halobates* species are known to form aggregations. Savilov (1967) observed large swarms of *Halobates* species on the ocean surface. *H. robustus*, an endemic species in the Galapagos Islands, forms dense aggregations in mangrove-fringed shores (Birch *et al.*, 1979). We do not know how pelagic *Halobates* aggregate. Coastal *Halobates*, which live in rather restricted environments with to-

Table 4. Estimates of average and maximum densities and Morisita's index for *H. micans* and *H. sericeus*.

Species	Total no. tows	No. positive tows	Total area swept (m^2)	Total no. insects	Average density (#/km^2)	Maximum density (#/km^2)	Morisita's index	
							$I_{\delta1}$	$I_{\delta2}$
1994								
H. micans	20	13	24,076	64	3×10^3	3×10^4	5.347*	4.808*
1998								
H. sericeus	50	20	67,521	452	7×10^3	7×10^4	5.901*	5.702*

* significantly contagious at 99% level: one-sided test of $f = \{I_\delta(N-1)+n-N\}/(n-1)$ with F-distribution $F(n-1, \infty)$.

pographical variations, could more easily find their conspecifics by using landmarks such as mangrove roots (Birch *et al.*, 1979). However, on the ocean surface there are no boundaries or conspicuous objects to serve as possible landmarks. Moreover, oceanic diffusion is constantly acting to disperse *Halobates* in all directions (e.g., Okubo, 1971; Ikawa *et al.*, 1998). Pelagic *Halobates* species, therefore, must have some specific means to form aggregations, possibly by using convergence of the sea water such as Langmuir circulation (Okubo, 1980).

In conclusion, data collected on *Halobates* in the western Pacific during a three-year period of cruises showed that the distribution ranges and population densities of these pelagic insects were not static but varied temporally and spatially. Seasonal samplings over a period of years are indispensable for further understanding of the spatio-temporal features of *Halobates* populations.

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