Title

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ORIGINAL ARTICLE

Distribution of the oceanic insects *Halobates* (Hemiptera: Gerridae) off the south coast of Japan

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Abstract

Specimens of ocean skaters *Halobates* were collected off the south coast of Japan in the East China Sea in 1995, and from the Kumano-nada Sea to the East China Sea in 1998 and 1999. Three species were identified: *H. micans*, *H. germanus* and *H. sericeus*. We found two species co-occurring in comparable densities in different years, a phenomenon not hitherto reported in other regions of the ocean. We discuss distributions of the three *Halobates* species with special reference to the influence of the Kuroshio Current, temporal variations of sea-surface temperature, and monsoonal winds.

Key words: East China Sea, Kuroshio Current, marine insect, sea skater.

INTRODUCTION

Of more than one million known insect species, five species of ocean skaters *Halobates* (*H. micans* Eschscholtz, *H. sericeus* Eschscholtz, *H. sobrinus* White, *H. germanus* White and *H. splendens* Witlaczil) are the only insects found in the high seas (Cheng 1985). They are totally wingless throughout their life cycle, and live exclusively at the air–sea interface.

Sea skaters are distributed in warm tropical or subtropical waters. Their worldwide distribution ranges have been determined by plotting collection records from different cruises over many years (Cheng 1985, 1989). Only *H. micans* lives in the Atlantic Ocean, while both *H. micans* and *H. germanus* live in the Indian Ocean. All five species live in the Pacific Ocean: *H. sobrinus* and *H. splendens* are found off the coast of Central and South America, *H. micans* in the equatorial zone from approximately 20°S to 20°N but extending north along the Kuroshio Current, *H. sericeus* with an amphitropical distribution living in areas to the north and south of *H. micans*, and *H. germanus* in the western Pacific Ocean from approximately 30°S to 30°N.

There are large overlaps in the distribution ranges of *H. micans*, *H. germanus* and *H. sericeus* from approximately 7°N to 33°N in the western North Pacific, hereafter referred to as 'overlap region' (see fig. 2 in Cheng 1985). This overlap region covers the westernmost area of the North Equatorial Current (NEC) and a large part of the Kuroshio Current. One interpretation for this overlap is that all three species actually do co-occur there. It is also possible that actual distributions of the species are normally separate, but temporal changes of their distributions resulted in the apparent overlap.

To date, no region with different species co-occurring in comparable densities has been reported. Ikawa *et al.* (2002) showed that in the NEC region west of the Mariana Islands (the southern part of the overlap region) *Halobates* spp. rarely co-occur, but ranges of the dominant species change temporally.

Off the south coast of Japan (the northern part of the overlap region where the major surface current is the Kuroshio), *H. micans*, *H. germanus* and *H. sericeus* are known to occur (summarized by Cheng 1989). Savilov

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(1967) collected *H. micans* and *H. sericeus* in the western area of the Pacific Ocean, but gave no detailed data on how often they were caught together or on their densities.

In 1995, 1998 and 1999, we conducted three cruises off the south coast of Japan from the Kumano-nada Sea to the East China Sea, to determine whether two or more *Halobates* spp. actually co-occur in substantial densities in that region.

MATERIALS AND METHODS

In 1995, *Halobates* samples were collected in the East China Sea during a cruise on the *R/V Chofo Maru* operated by the Nagasaki Marine Observatory. Samples were collected at 32.2°N, 129.2°E on 29 June and 1 July by surface horizontal tow with a ring net (50 cm in mouth diameter and 330 μm mesh size). Because the sampling was not quantitative, we used the data only to compare the species composition with those caught in 1998 and 1999.

In 1998 (21–31 July) and 1999 (19–29 July) ocean skaters were collected from the Kumano-nada Sea to the East China Sea during cruises on the *R/V Seisui Maru* operated by Mie University. As shown in Figure 1, the two cruises followed similar tracks. In 1998, samples were collected at 13 stations (Fig. 1A) with a neuston net (20 × 60 cm in mouth diameter and 330 μm mesh size) towed at the sea surface at approximately 2 knots (~3.5 km/h) for 30–120 min. In 1999, samples were collected by using a slightly bigger neuston net (30 × 80 cm in mouth diameter) but with the same mesh size and towed at the same speed for 30–100 min (Fig. 1B). *Halobates* spp. were sorted on board and preserved in 99% ethanol. The area towed was calculated by multiplying the width of the net opening by the distance towed. Densities of *Halobates* spp. were estimated by using the number of insects caught in the towed area.

We chose an area close to the Kuroshio branch which leads to the Tsushima Warm Current for more intensive sampling at approximately 31.3°N, 127.5°E (stations A4–A7 in Fig. 1A) in 1998, and at approximately 31.0°N, 127.5°E (stations B5–B9 in Fig. 1B) in 1999. We used data from this area for comparison with those from 1995 where sampling was carried out from a more restricted area near by. Satellite image data of sea-surface temperatures of this area were obtained from the Modular Ocean Data Assimilation System (MODAS) (Fox *et al.* 2002a,b).

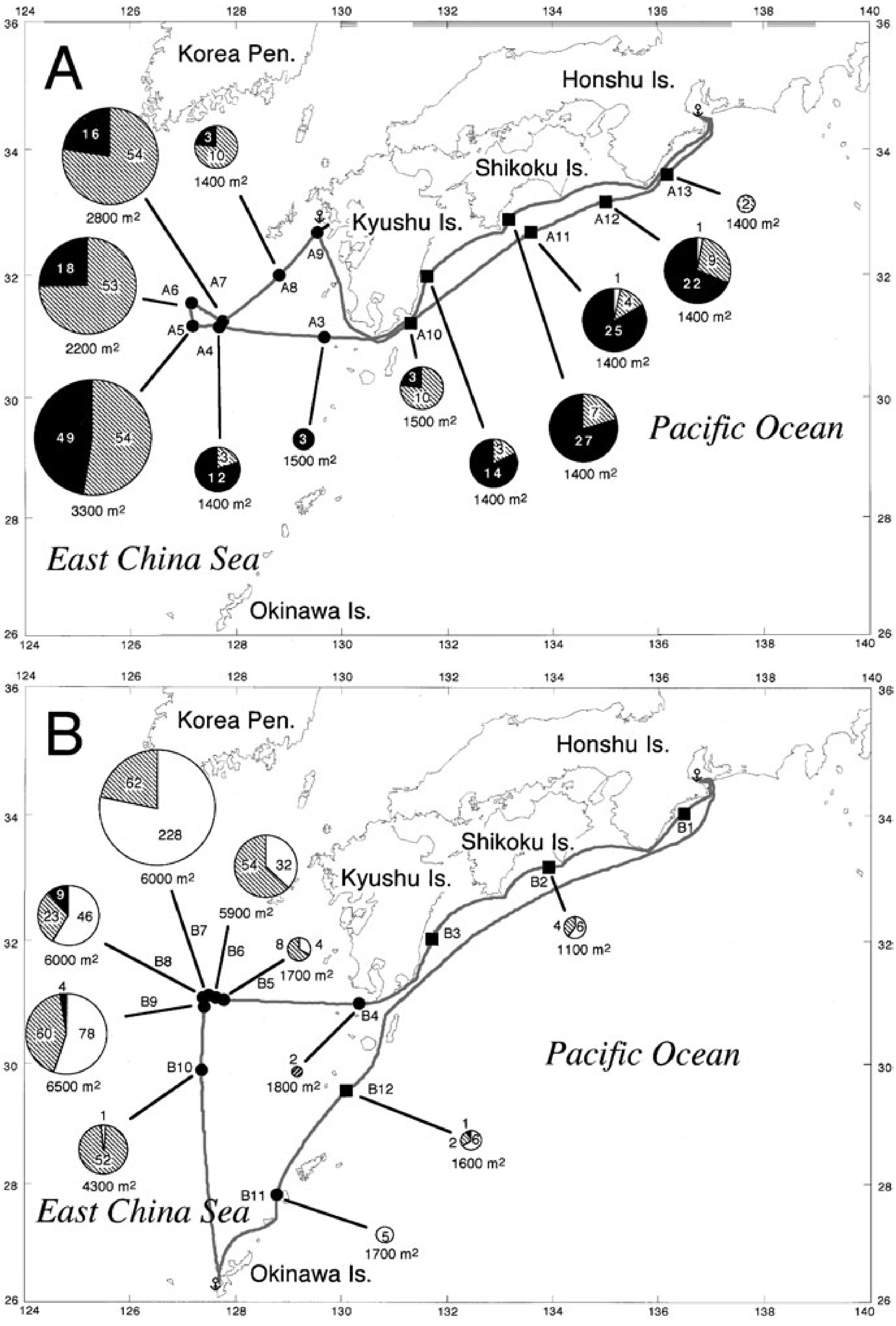
RESULTS

The cruise track showing sampling stations, and numbers and species of *Halobates* captured in 1998 and 1999, are presented in Figure 1A,B. In 1998, we caught 209 individuals of *H. germanus* and 192 *H. micans*, but only two *H. sericeus* (Table 1). The average densities per km^2 calculated were 9300 for *H. germanus*, 8600 for *H. micans* and 90 for *H. sericeus*. In 1999, *H. sericeus* and *H. germanus* were predominant, and we collected 406 and 267 specimens, respectively, but only 15 individuals of *H. micans*. The average densities were 6900 for *H. germanus*, 10 500 for *H. sericeus* and 390 for *H. micans*. It is interesting to note that among the three oceanic *Halobates* found in the Kumano-nada Sea to the East China Sea, two different species co-occurred in comparable densities but that dominant species changed temporally.

In 1998, *H. germanus* and *H. micans* were codominant (Table 1; Fig. 1A), with estimated densities of 12 000/km^2 and 7200/km^2 in the East China Sea (stations A3–A9), and 4100/km^2 and 11 000/km^2 off the Pacific Coast (stations A1, A2 and A10–A13), respectively. However, *H. germanus* was more abundant in the East China Sea, while *H. micans* predominated off the Pacific Coast. The hypothesis that in 1998 ratios of *H. germanus* and *H. micans* in the East China Sea and off the Pacific Coast are equal is discarded at the level much lower than 1% by Fisher's exact probability test.

Species compositions of *Halobates* in the area intensively sampled in the East China Sea in 1995, 1998 and 1999 are presented in Table 2. The dominant species varied from year to year. In 1995, out of 292 specimens captured in total, 273 were *H. sericeus*, 18 were *H. germanus*, and only one was *H. micans*. In 1998,

Figure 1 Study areas and collection of *Halobates* between the Kumano-nada Sea and the East China Sea in (A) 1998 and (B) 1999. ■, Sampling stations off the Pacific coast; ●, stations in the East China Sea. Lines connecting sampling stations indicate cruise tracks. For sampling stations where *Halobates* were caught, species compositions were indicated by pie diagrams. Pie diagrams: ■, *H. micans*; □, *H. sericeus*; ▧, *H. germanus*. The area of a pie diagram is proportional to the number of *Halobates* caught. Figures in pie diagrams indicate the numbers of *Halobates* captured, and figures under pie diagrams indicate areas towed.


A
Korea Pen.
Honshu Is.
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Pacific Ocean
East China Sea
Okinawa Is.
B
Korea Pen.
Honshu Is.
Shikoku Is.
Kyushu Is.
Pacific Ocean
East China Sea
Okinawa Is.

Table 1 Numbers of tows, total areas swept, species, numbers and average densities of *Halobates*

Year	Total no. tows (no. positive tows)	Total area swept (m^2)	Species caught	Total no. insects	Average density (no. per km^2)	Density in the East China Sea (no. per km^2)†	Density off the Pacific Coast (no. per km^2)‡
1998	13 (12)	22 400	*H. germanus*	209	9 300	12 000	4 100
			H. sericeus	2	90	0	240
			H. micans	192	8 600	7 200	11 000
1999	12 (10)	38 700	*H. germanus*	267	6 900	9 900	1 200
			H. sericeus	406	10 500	15 000	2 400
			H. micans	15	390	530	200

†Average densities of insects caught at stations A3–A9 in 1998 and stations B4–B11 in 1999; ‡average densities of insects caught at stations A1, A2 and A10–A13 in 1998 and stations B1–B3 and B12 in 1999.

Table 2 Date, location, sea-surface temperatures and species compositions of *Halobates* caught in the East China Sea in 1995, 1998 and 1999

Date	Location	No. *Halobates* caught (%)				Sea-surface temperature (°C)
		H. germanus	*H. sericeus*	*H. micans*	Total	
1995						
June 29, July 1	32.2°N, 129.2°E	18 (6.2)	273 (93.5)	1 (0.3)	292	23.2
1998						
July 23–26	31.3°N, 127.5°E	164 (63.3)	0 (0)	95 (36.7)	259	28.9
1999						
July 21–23	31.0°N, 127.5°E	207 (34.0)	388 (63.7)	14 (2.3)	609	27.6

only *H. germanus* and *H. micans* were found, with 164 and 95 specimens, respectively. In 1999, *H. sericeus* and *H. germanus* were dominant, with 388 and 207 specimens, respectively, and only 14 specimens were *H. micans*. The mean sea-surface temperature in this study area was highest in 1998 (28.9°C), lowest in 1995 (23.2°C) and intermediate in 1999 (27.6°C) (Table 2; Fig. 2).

DISCUSSION

Our study has shown that two different *Halobates* species can co-occur in comparable densities and that the species compositions may change temporally. We present here some of the physical factors that may be responsible for these observations.

Co-occurrence of *Halobates* spp. from the Kumano-nada Sea to the East China Sea

In the area between the Kumano-nada Sea and the East China Sea, we found that in 1998, *H. germanus* and *H. micans* co-occurred in comparable densities, but that in 1999, *H. germanus* and *H. sericeus* co-occurred (Table 1). In most tows, we collected more than one species (Fig. 1A,B). *Halobates* species are known to form aggregates (Savilov 1967; Birch *et al.* 1979). If such aggregations are only formed by one species, the present results would indicate that groups of more than one species can occur in a small area (between 1000 and 6000 m^2) covered by a single net tow.

The Kuroshio Current, a western boundary current in the North Pacific, could be responsible for this co-occurrence. It originates east of the Philippine coast and flows poleward across the habitat zones of *H. micans*, *H. germanus* and *H. sericeus*. In the East China Sea, the Kuroshio flows north-eastward along the Ryukyu Islands and exits to the Pacific Ocean through the Tokara Strait, flowing north-eastward along the south-eastern shore of Japan. In the North Pacific Ocean, *H. micans* and *H. germanus* are mostly found south of the habitat zone of *H. sericeus*. The strong poleward flow of the Kuroshio could transport large numbers of *H. micans* and *H. germanus* from the south to the north, bringing the three species together. Eddies of various sizes are known to be generated by frontal disturbances in the Kuroshio. In cyclonic eddies, primary production is accelerated due to nutrients supplied by upwelling (Kimura *et al.* 1997). These eddies may also

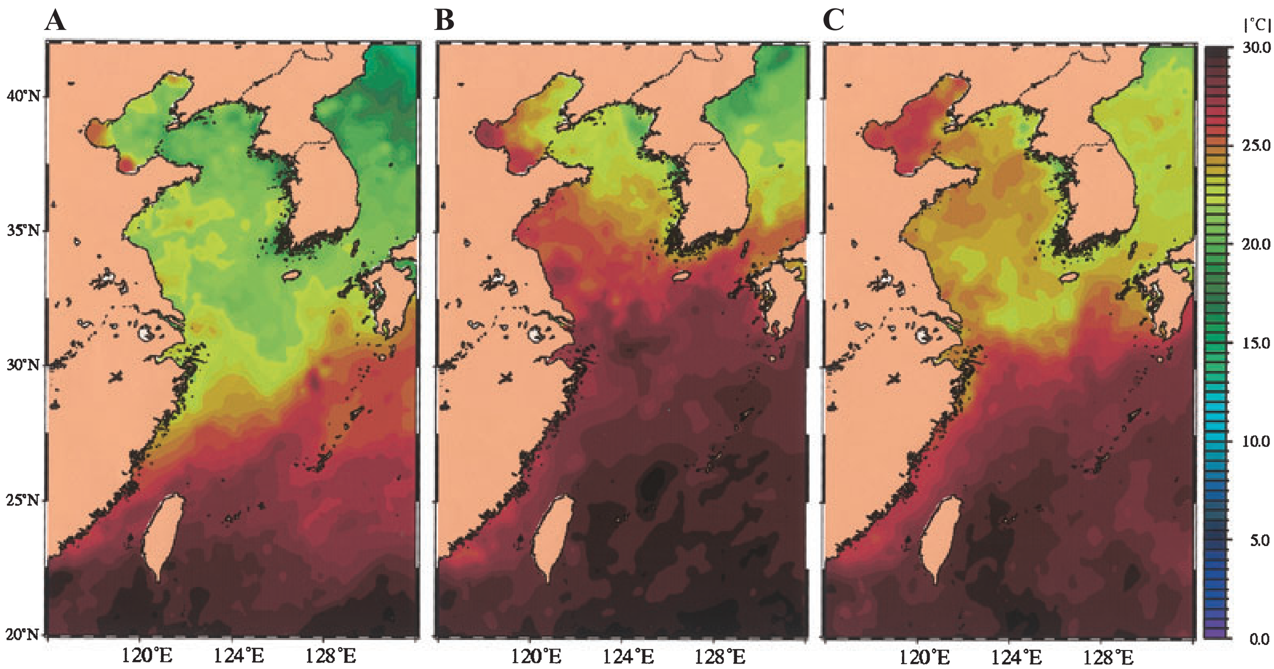

Figure 2 MODAS satellite images of sea-surface temperatures in the East China Sea and adjacent area on (A) 29 June 1995, (B) 24 July 1998 and (C) 21 July 1999. The images of 1998 and 1999 were retrieved from the website of the Naval Research Laboratory Stennis Space Center (http://www7320.nrlssc.navy.mil/altimetry/images/modas_images/Jul_24_1998/ecs_sst.gif and http://www7320.nrlssc.navy.mil/altimetry/images/modas_images/Jul_21_1999/ecs_sst.gif, respectively). The image of 1995 was provided by C. Barron of the Naval Research Laboratory Stennis Space Center.

provide a heterogeneous environment for *Halobates* spp., enabling the co-occurrence of different species.

Changes in species composition in the East China Sea

Species composition of *Halobates* in the East China Sea study area varied during the three years (Table 2). Physical factors such as temperature, winds and currents could strongly influence the distributions of *Halobates* spp. (e.g. Savilov 1967; Cheng 1985, 1989; Ikawa *et al.* 1998).

Sea-surface temperature

In the Pacific Ocean, *H. germanus* and *H. micans* are found in warmer waters than *H. sericeus*. In particular, *H. micans* appears to be confined to warm, tropical waters (Cheng 1989), with the sea-surface temperature for high densities being above 24°C (Cheng & Shulenberger 1980). If their habitat preferences reflect interspecific differences in low temperature tolerance, we may speculate that *H. micans* and *H. germanus* may be less tolerant of low temperatures than *H. sericeus*, with *H. micans* being the least tolerant. In the East China Sea, sea-surface temperatures are known to fluctuate seasonally. In our study area, sea-surface temperature fell to 17°C in the winter of 1999 (Japan Coast Guard 1999). Therefore, even though the Kuroshio may carry *H. micans* and *H. germanus* to the East China Sea in the winter, we would expect their densities to be low compared to that of *H. sericeus*, due to lower reproductive and/or survival rates. As the sea-surface temperature rises in the spring, we would expect the density of *H. germanus* to increase while that of *H. micans* might increase only during the summer when sea-surface temperatures become high enough for its reproduction.

This speculation appears to agree with the present findings (Table 2). In 1995, the sampling period was the earliest in the season of the three cruises, and the surface temperature of the East China Sea was the lowest (Fig. 2). Most *Halobates* captured were *H. sericeus* (93.5%). In 1999, when the sea-surface temperature was intermediate, *H. sericeus* was dominant (63.7%), followed by *H. germanus* (34.0%) and *H. micans* (2.3%). In 1998, when the surface temperature was the highest, 63.5% of the insects caught were *H. germanus*, 36.7% were *H. micans* and no

H. sericeus individuals were caught. However, the absence of *H. sericeus* in 1998 may not be attributable to the high sea-surface temperature, because large numbers of *H. sericeus* had been caught at sea-surface temperatures higher than 28°C in the eastern South Pacific Ocean (Cheng & Holdway 1995) and in the NEC region west of the Mariana Islands (Ikawa *et al.* 2002), suggesting that *H. sericeus* is tolerant of considerably high temperatures.

Seasonal changes in prevailing winds

Factor(s) other than the sea-surface temperature may also be responsible for species composition of *Halobates* in the East China Sea. In the NEC region west of the Mariana Islands, Ikawa *et al.* (2002) showed that species composition among *Halobates* could change greatly without extreme fluctuations in sea-surface temperature. Another factor which could possibly affect species composition of *Halobates* is the monsoonal wind that blows roughly southward in the winter and northward in the summer over the East China Sea and the path of the Kuroshio Current (Kutsuwada 1987; Ichikawa & Beardsley 2002). Because ocean skaters live at the sea surface where there is no shelter, monsoonal winds blowing constantly in the same direction could easily transport them and change their seasonal distribution ranges. In the summer, the prevailing southerly winds could enhance the northward transport of *H. germanus* and *H. micans* in the Kuroshio. In contrast, in the winter, the prevailing northerly winds could decrease the northward transport of these two species, resulting in lower densities of *H. germanus* and *H. micans* in the East China Sea. This could possibly account for the low densities of *H. germanus* and *H. micans* we observed in 1995, when samples were collected three weeks earlier than in 1998 and 1999 (Table 2).

Species composition in the East China Sea and off the Pacific Coast

In the East China Sea area we sampled in 1998, *H. germanus* outnumbered *H. micans*, whereas off the Pacific Coast, *H. micans* was much more abundant (Table 1; Fig. 1A). This difference can perhaps be explained by the difference in volume transport between the main stream of the Kuroshio Current and its branch. The main stream of the Kuroshio turns to the east just south of Kyushu Island in the East China Sea, and exits into the Pacific Ocean. Only part of the Kuroshio flows to the north, forming the Tsushima Warm Current. Our sampling stations along the Pacific Coast were either in or close to the Kuroshio main stream, while those of the East China Sea were within the branch of the Kuroshio. *Halobates micans* is usually found in the warmer waters of the equatorial zone, while the ranges of *H. germanus* extend further north and south into cooler regions (see the maps in Cheng 1989). Therefore, *H. micans* would be more closely associated with the warm waters of the Kuroshio than *H. germanus*, resulting in more specimens of *H. micans* being carried into the Pacific Coast rather than into the East China Sea.

In conclusion, our study suggests that densities and the species composition of oceanic *Halobates* spp. off the south coast of Japan may be determined by the flow of the Kuroshio Current, by temporal variations in sea-surface temperatures as well as by monsoonal winds. Seasonal samplings carried out over a period of years are needed to clarify the influence of physical factors on the population dynamics of these remarkable marine insects.

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