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POPULATIONS OF *HALOBATES* (HEMIPTERA: GERRIDAE) ACROSS TWO OCEANS

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ABSTRACT - Specimens of the sea-skater *Halobates* (Gerridae) were collected in 63% of net tows taken during a 14-month expedition (October 1981 to December 1982) across the Atlantic and the Pacific Oceans between Plymouth, England and Sydney, Australia. Seven species were found including all five open-ocean species (*H. micans*, *H. sobrinus*, *H. splendens*, *H. sericeus* and *H. germanus*) and two coastal species (*H. robustus* and *H. proavus*). The occurrence and abundance of *H. micans* in the Atlantic Ocean were positively correlated with seawater temperatures. There was a remarkable similarity between the distribution and age structure of the Atlantic *H. micans* population in the present study and that of a 1978 expedition along the same cruise track, indicating a high degree of zoogeographical constancy. Although different *Halobates* species do co-occur, limits of distribution of the five Pacific species appeared to be well defined. However, we still do not know what determines the distribution patterns of these surface-dwelling insects.

INTRODUCTION

Halobates is the only insect genus to have overcome obstacles of a pelagic existence on the open ocean. Much of the early literature on the biology, ecology and distribution of the genus can be found in Cheng (1985). Although over 40 species have been described, most are coastal in habitat and only five are exclusively pelagic (Cheng, 1989a). The majority of the nearshore *Halobates* species occur in the Indo-Pacific, in bays and lagoons associated with mangroves or other coastal vegetation. Although a few are widely distributed along island coasts about half of the known species are endemic to islands or island groups (Cheng, 1989a). This high degree of endemism is also found in other marine water-striders (Andersen, 1991a). Phylogenetic relationships among *Halobates* species and ecological evolution of the genus were presented recently by Andersen (1991b). New species continue to be discovered especially from island shores of Southeast Asia, e.g. *H. murphyi* from Papua New Guinea (Polhemus & Polhemus, 1991), *H. elephanta* from Bombay (Andersen & Foster, 1992), and *H. lannae* from the Northern Territories, Australia (Andersen & Weir, 1994).

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Pelagic *Halobates* are found in tropical or sub-tropical waters, between latitudes 40°N and 40°S where the sea-surface temperatures remain above 20°C in the winter. Five species are found in the Pacific, three occur in the Indian Ocean, but only one, *H. micans*, occurs in the Atlantic (Herring, 1961). Although the ranges of the various species have been established (Cheng, 1989b), how such patterns are determined, or how stable they are in space and time, is not known. Our present knowledge about these sea-skaters is based on collections from the field. None of the pelagic species has yet been successfully reared in the laboratory, consequently experimental studies have been considerably hampered. Data presented here provide an opportunity to compare sea-skater populations with those from Operation Drake, a previous expedition undertaken by the same ship in 1978-80 (Mitchell, 1981). Eventually these data may help to answer questions relating to their distributions.

MATERIALS AND METHODS

During the 14-month expedition on the brigantine "Eye of the Wind" from October 1981 to December 1982, 247 net-tow samples were collected, of which 201 were taken by the neuston net which catches organisms at the sea surface and from the uppermost 5-10 cm of the water column (Holdway & Maddock, 1983). In the first 34 neuston tows we employed a net with a mouth opening measuring 10 x 30 cm. However, after the ship left the Canary Islands, a larger net was constructed with an opening measuring 20 x 60 cm, to increase gape area and thus reduce the necessary towing time. This larger net was used for the remainder of the voyage. All nets were towed for 30 minutes at a speed of about 4.5 knots (≈8kmh^{-1}). Neuston tows were made at intervals during the day or night when sea conditions allowed the net opening to remain semi-submerged during the entire operation, thereby achieving a sampling efficiency of almost 100%. The data are therefore quantitative. Additional samples were collected by using a non-closing plankton net towed obliquely through the water column (29 tows) or at the surface (6 tows), or by mid-water trawls (5 tows). Six dip-net samples were taken in shallow bays around Vanuatu (tows 220-225).

Both neuston and plankton samples were collected from the windward side of the ship, since the leeward side tends to be barren due to the shadowing effect of the hull (Zaitsev, 1970). Data on wind speed and direction, cloud cover, air and water temperatures, local time, latitude and longitude were recorded for each sample. Some physical data together with station locations are presented in Tables 1 and 2.

The organisms collected by the nets were sorted into major taxa on board ship. *Halobates* specimens were preserved in 70% ethanol. Identification to species and developmental stages, using keys given in Herring (1961), Cheng (1975) and Cheng & Maxfield (1980), and analyses of data were carried out at the Scripps Institution of Oceanography.

RESULTS

Area of sampling - The cruise track of the "Eye of the Wind" and areas where each *Halobates* species was collected are shown in Figure 1. After sailing from Plymouth, England, the ship headed south towards the Canary Islands, then south-westerly towards the Panama Canal. After passing through the canal she sailed westwards to the Galàpagos, Pitcairn I., the Tuamotu Archipelago, Tahiti, Fiji, and Vanuatu before docking at Sydney harbour, Australia.

Species composition - Seven *Halobates* species were collected including all five pelagic species (*H. micans* Eschscholtz 1822, *H. sobrinus* White 1833, *H. splendens* Witlaczil 1886, *H. sericeus* Eschscholtz 1822 and *H. germanus* White 1883), and two coastal species (*H. robustus* Barber 1925, endemic to the Galàpagos Islands, and *H. proavus* White 1883, a widely distributed Indo-Pacific species). Specimens of two other coastal insect genera, *Hermatobates* (Hermatobatidae) and *Halovelia* (Veliidae), were also collected.

Frequency and occurrence - Among 241 net tows, 151 contained *Halobates*. 147 were caught by the neuston net, only four by the plankton net (tows 23, 101, 105 and 142) and none by the mid-water trawl. No *Halobates* were found in the first 22 net tows between latitudes 43°N and 33° N where the sea water was generally below 20°C, the lower limit of their temperature tolerance. Beyond Madeira Island (32°50'N 17°00'W) *Halobates* were caught in the majority of the neuston tows. Of the 83 Atlantic tows, 49 were positive, and of 158 Pacific tows (excluding inshore dip-net samples), 102 were positive (100 with various pelagic species, 2 with *H. robustus*).

All but six of the samples containing *Halobates* were collected by the larger neuston net. Numbers of insects in those samples (tows 23, 27, 29, 31, 33 and 34) were small (1-3 specimens), and were excluded from quantitative considerations in this study.

Although 46% of the tows contained less than 10 specimens each, there were more samples with more than 50 insects in the Pacific (13%) than in the Atlantic (6%). Frequency distributions of the three dominant species are presented in Figure 2. The frequencies and co-occurrences of the five pelagic *Halobates* species in the Pacific Ocean are given below (for details see Table 2):-

1) *H. micans* was caught in two tows (90 and 93) with 10 and 98 individuals respectively, and in both cases co-occurred with *H. sobrinus*.

2) *H. sobrinus* was collected in 10 tows, occurring by itself in eight. Five tows contained less than 10 insects each, two had 10-20, and the remaining three (tows 85, 86 and 87), with 86, 30 and 57 individuals respectively, were taken at an area around 6°N and 81-83°W.

3) *H. splendens* was caught in nine tows, but only two (118 and 121) had 10 or more insects. It co-occurred with *H. sericeus* in tow 125.

4) *H. sericeus*, the commonest of the Pacific species in this study, was caught in 53 tows. It co-occurred in one tow with *H. splendens* (see above) and in 15 tows with *H. germanus*. In 10 out of the 15 tows where it co-occurred with another species there were less than 10 insects per tow. In the seven tows with more than 50 insects (127, 128, 129, 137, 153, 154 & 156) it was the only species found.

5) *H. germanus* was collected in 44 tows, co-occurring with *H. sericeus* in 15 (see above). 69 specimens were caught in tow 194, together with two *H. sericeus*; in all the other tows there were fewer than 40 per tow.

Day/night differences - During the expedition attempts were made to collect day and night tows in equal numbers to determine whether there was any evidence of net-avoidance. The data showed no significant differences between day and night catches for *H. micans* and *H. sericeus*. Although the mean night catch was higher than the mean day catch for *H*

germanus (t = 0.40) and *H. sobrinus* (t = 0.77), the differences were not significant (P > 0.05) (Table 3.)

Temperature effects - During the Atlantic crossing, surface water temperatures ranged from 16.9° to 28.6°C. *Halobates micans* was absent in waters below 20°C (no tows were taken at temperatures below 16° or above 28°C; see Table 4), and its occurrence (Pearson correlation coefficient: r = 0.64) and abundance (r = 0.92) were correlated with increasing temperature.

In the Pacific Ocean a wider temperature range of 16.0° to 30.2°C was recorded. *Halobates* was again absent in waters below 20°C, and its numbers were low until seawater temperatures exceeded 25°C (Table 5).

Abundance and age distribution - In the Atlantic Ocean a total of 764 *Halobates micans* were collected in 49 tows. In the Pacific, 2,059 pelagic *Halobates* were caught in 98 tows. The total number of each species caught, mean number of insects per tow, range, % of adults, numbers of males and females, and sex ratios are given in Table 6. Since there were only two samples of *H. micans* from the Pacific, these were excluded. *H. splendens* was the rarest while *H. sericeus* was the most abundant. Adults constituted almost 50% of the total *H. micans*, *H. sobrinus* and *H. sericeus* collected, but were much less common in samples of the other two species. Although there were slightly more males than females of *H. sobrinus* and *H. germanus*, and slightly less males than females of *H. micans* and *H. sericeus*, the sex ratios were not significantly different from 1 (P < 0.90). The number and age distributions of nymphs of each species are given in Table 7. The first instar was generally the least abundant except for *H. germanus*, where there were almost equal numbers of each stage. Sexes of nymphs are distinguishable only in the final instar, in which we found more males than females (P ≤ 0.75) for all species.

Reproductive seasonality - Data for *Halobates micans* from the Atlantic Ocean were pooled into 16 groups according to sampling duration (not more than 48 hours, except for group 1) and area covered (not more than 3°, or ~270 km, in both latitude and longitude). The percentages of adults and nymphs in each group are shown in Figure 3. Although the proportions of the different stages varied from group to group, we could not detect any clear seasonal progression in nymphal development.

DISCUSSIONS AND CONCLUSIONS

Halobates species were found in 63% of all surface tows taken along the cruise track of the "Eye of the Wind" between Plymouth, England and Sydney, Australia. All five pelagic species as well as two coastal species were collected.

Halobates micans was the only species found in the Atlantic Ocean. Only three Atlantic samples contained more than 50 specimens each, all from the area around 14°30'N and 51°30'W where they apparently aggregate.

The present cruise track was similar to that of Operation Drake across the Atlantic but much further south in the Pacific (Cheng & Holdway, 1983). There was a remarkable similarity in both the occurrence and overall age distributions of *Halobates micans* between these two expeditions in the Atlantic (Fig. 4), indicating a high degree of zoogeographical stability. A

similar comparison for the Pacific species was not possible since the season and the areas sampled by the two expeditions were different.

The distribution ranges of *Halobates* spp. in the Pacific Ocean were well delimited. *H. micans* was caught in two of the first 10 neuston tows and was absent throughout the remainder of the Pacific crossing. *H. sobrinus*, the first species caught in the Pacific, occurred in 9 subsequent tows until the ship arrived at the Galàpagos Islands. Thereafter *H. splendens* was the sole species collected between latitudes 1° and 8°S until 8°48'S (tow 125) where it co-occurred with *H. sericeus*. The latter was then the only species caught until 23°32'S (tow 158), where it co-occurred with *H. germanus*. These two species co-occured between latitudes 18° and 20°S and longitudes 140° and 150°W (tows 176 - 194). In waters further west (tows 195 - 216) *H. germanus* became the dominant species, but as the ship sailed further south beyond 20°S (tows 228 - 247) it was replaced by *H. sericeus*. The eastern limit of *H. germanus*, previously recorded at 140°W (Cheng & Shulenberger, 1980), was extended to 125°W.

Eight specimens of the endemic *Halobates robustus* were caught around the Galàpagos islands (tows 101 & 105). This species rarely ventures far from shore but in inshore waters it can occur in very dense patches with more than 100 insects per m^2 (Birch et al., 1979). 180 specimens of another coastal species, *H. proavus*, were caught by dip-netting at Meskelyne Is. off Vanuatu, together with six specimens of *Halovelia*, a much smaller marine veliid often found together with coastal *Halobates* (Andersen, 1989). One specimen of *Hermatobates*, an uncommon coastal marine hermatobatid usually associated with coral rubble or stone jetty (Cheng, 1977; Foster, 1989), was caught in tow 206 with *H. germanus*.

Halobates have good eyesight and are able to avoid capture by towed nets during the day and on bright moonlit nights (Cheng, 1973; Cheng & Enright, 1973). Although higher night catches have been reported for multi-species samples of *Halobates* from the Banda Sea (Cheng et al., 1990) and for *H. micans* from the Gulf of Mexico (Cheng & Wormuth, 1992), we found no significant difference between densities of day and night samples in the present study. Possibly our sample sizes were too small and variances were too large.

We did not catch any *Halobates* in waters where the temperature was below 20°C. *H. splendens* was caught only in waters between 25° and 26°C. Although *H. sericeus* was found at temperatures ranging from 20° to 28°C, it was most abundant at 25°-26°C. The highest numbers of *H. germanus* were found betweem 27° and 28°C, while *H. sobrinus* seemed to prefer even warmer waters (27°-30°C), and was the only Pacific species collected above 29°C. Whether water temperatures where the insects occur reflect specific preferences or tolerances of each species is not known. Our sample sizes are too small to permit meaningful statistical analyses except for *H. micans* in the Atlantic, where a positive correlation was found between insect abundance and seawater temperature, as was shown in an earlier study by Cheng & Schulz-Baldes (1981).

Halobates are rather common organisms of the open ocean. In tropical seas where the water temperatures are above 20°C they are collected in almost every neuston tow. They appear to form stable populations and may be locally abundant, but how such local aggregations are formed and maintained is not known. Physical factors operating at the ocean surface, such as currents, winds, gyres, or warm-core rings may play important roles. We also do not know how their population densities vary with climatic changes, availability of potential prey, predation, interspecific competition, or other biological factors.

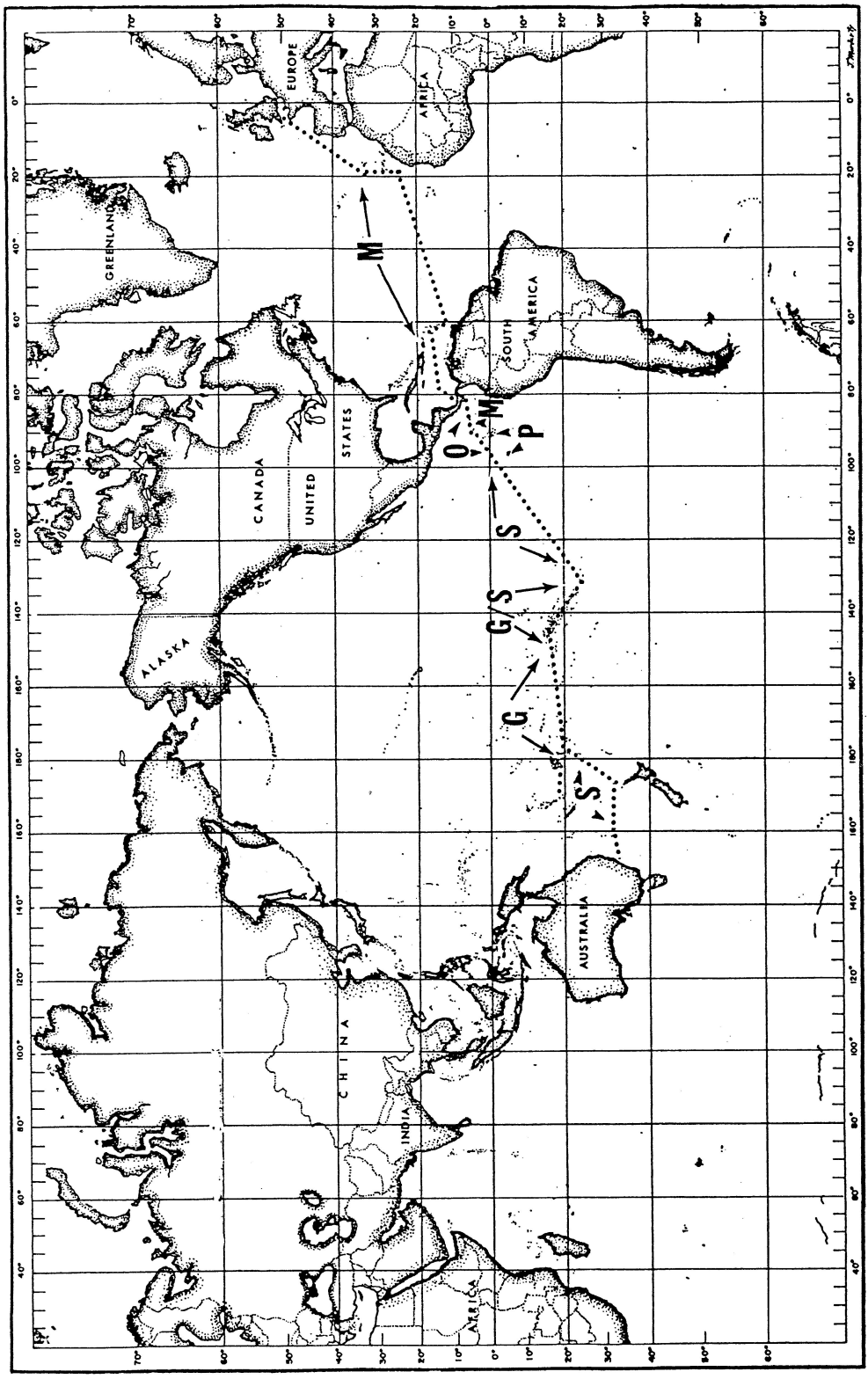

Fig.1. Cruise track of the "Eye of the Wind" in the Atlantic and Pacific Oceans, showing areas where specimens of pelagic *Halobates* species were caught. M = *micans*, O = *sobrinus*, P = *splendens*, S = *sericeus*, G = *germanus*.

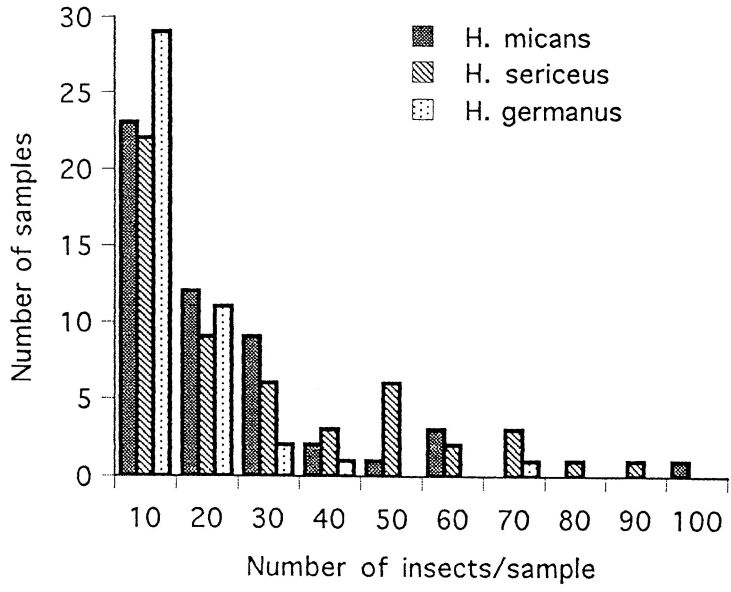

Fig. 2. Frequency distributions of *Halobates micans*, and of *H. sericeus* and *H. germanus* in the Atlantic and Pacific Oceans respectively.

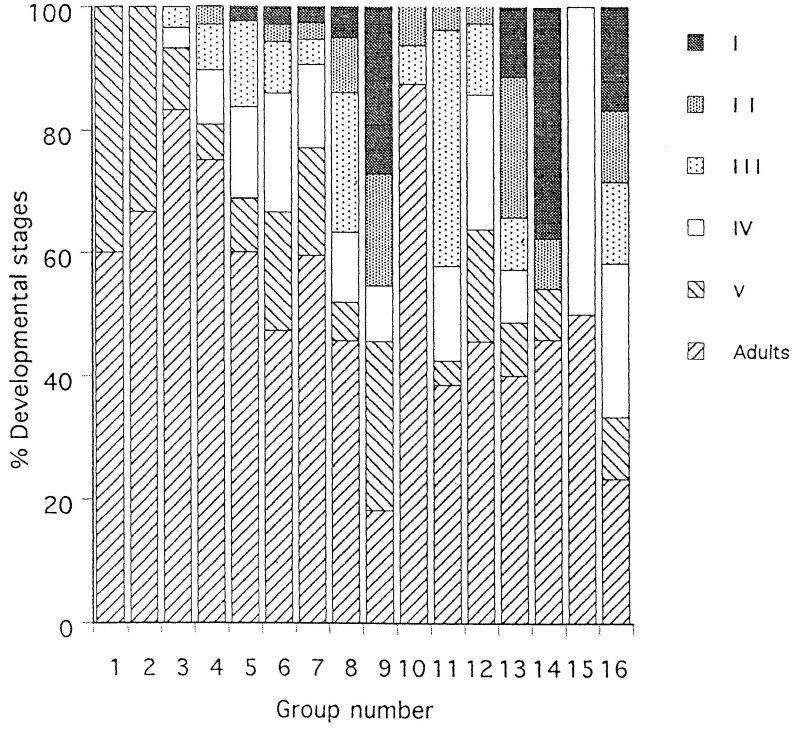

Fig. 3. Age distributions of Atlantic *Halobates micans* samples pooled into 16 groups as follows: 1 (tows 23-29), 2 (tows 31-35), 3 (tows 41-42), 4 (tows 43-47), 5 (tows 48-52), 6 (tows 53-54), 7 (tows 56-59), 8 (tows 60-64), 9 (tows 65-66), 10 (tows 67-68), 11 (tow 69), 12 (tows 71-75), 13 (tow 77), 14 (tows 78-79), 15 (tow 80), 16 (tows 81-83). For locations of tows see Table 1. I-V = nymphal stages 1-5. (Specimens from tows 70 and 76 were not available for study.)

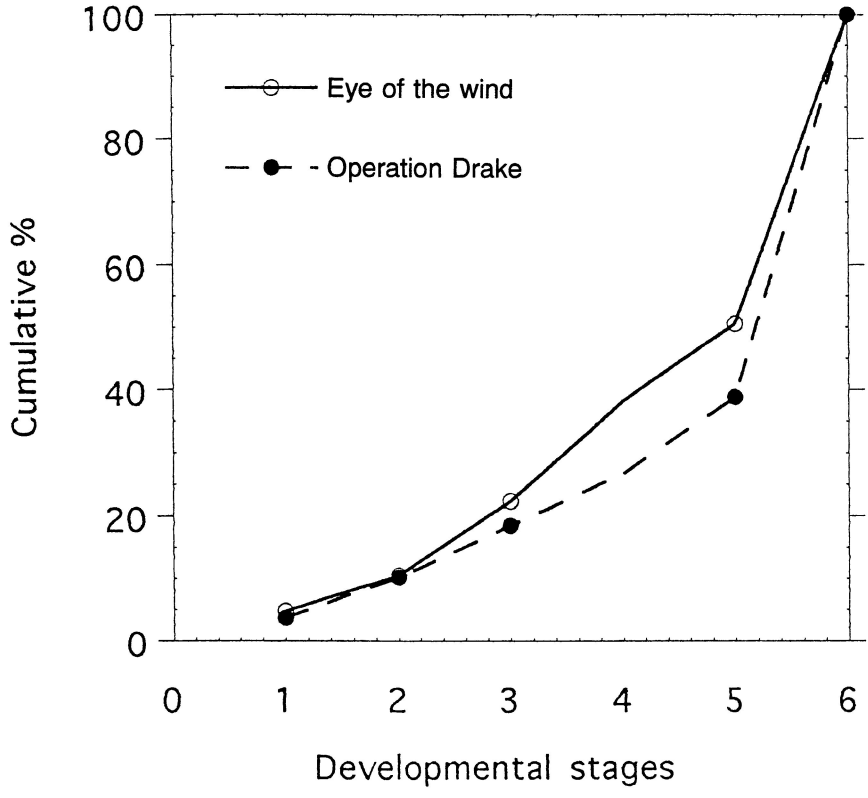

Fig.4. Comparison of cumulative percentage curves of age structure of Atlantic Ocean *Halobates micans* populations collected during the "Eye of the Wind" expedition (23 Nov 1981 - 13 Jan 1982) and from Operation Drake (6-20 Dec 1978). 1-5 = nymphal stages 1-5, 6 = adults. $P \leq 0.02$ (Komogorov-Smirnov 2-sample test; Tate and Clelland, 1959)

Although the ocean surface is seemingly a habitat without obvious physical barriers, the distributional ranges of the five Pacific *Halobates* species are remarkably well-defined. What delimits their geographical distributions is not clear. The substrate of their habitat is fluid and constantly subject to displacement by currents and winds. Within 1-2 months of a *Halobates*' lifetime, currents may have moved the water mass underlying their habitat many hundreds of kilometers, and winds may have displaced the surface layers hundreds of kilometers in wholly different directions. If we add to these passive shifts of the environment the active movements of insects unconstrained by lateral physical boundaries, striding towards the sun or moon as the predominant source of light shifts across the sky from east to west, one must recognize that problems of *Halobates* distributions are more than usually complex. Further difficulties arise from the sporadic nature of sampling dictated by pre-determined cruise tracks. Nevertheless, our data indicate a considerable degree of constancy in their geographical ranges.

Since the sea-skaters are strictly ocean-surface dwellers, their movements must be controlled largely by physical forces acting on the surface film. Thus, if we could find out how the limits of distribution of each species are determined, such information might help us understand effects of various physical processes at the sea surface, such as lateral diffusion, El Niño events, and local upwellings.

Table 1. Tow number, date, time, station location, seawater temperatures and number of *Halobates micans* caught during Atlantic Ocean crossing of the "Eye of the Wind" (e = exuviae).

Tow no.	Date	Local time	Latitude	Longitude	Temp. °C	Number insects
23	04.11.81	1845	32°37"N	16°55"W	22.0	3
27	06.11.81	0100	30°05"N	15°58"W	21.5	1
29	07.11.81	0650	30°05"N	15°58"W	22.0	1
31	18.11.81	0615	26°39"N	17°58"W	22.4	1
33	19.11.81	0340	25°11"N	19°24"W	22.8	2
34	"	0945	"	"	23.7	1
35	"	1750	"	"	22.8	5
41	21.11.81	2300	24°14"N	21°14"W	23.3	20+1e
42	22.11.81	0410	22°40"N	23°31"W	23.6	10
43	23.11.81	0905	21°54"N	25°28"W	23.6	16
44	"	1345	"	"	24.5	3
45	24.11.81	0100	21°23"N	27°33"W	24.2	15
46	"	0430	"	"	24.1	9
47	"	1900	"	"	24.6	25
48	25.11.81	0030	20°50"N	29°31"W	24.5	25
49	"	0430	"	"	24.7	22+1e
50	26.11.81	0230	20°36"N	31°03"W	24.9	9
51	"	0540	"	"	25.0	15
52	"	1120	"	"	25.2	9
53	27.11.81	0250	19°40"N	32°16"W	21.0	23+2e
54	"	0615	"	"	22.2	13+1e
56	28.11.81	1800	19°20"N	34°06W	26.5	11
57	29.11.81	0250	18°56"N	35°27"W	25.5	20
58	"	0600	"	"	"	24+1e
59	"	1500	"	"	26.0	19+1e
60	30.11.81	1305	18°05N	38°33"W	26.5	4
61	"	1620	"	"	25.7	8
62	"	2345	"	"	25.8	9
63	01.12.81	1030	17°36"N	39°53"W	26.0	47+2e
64	"	2355	"	"	"	11
65	02.12.81	0345	17°14"N	41°39"W	"	4
66	"	2015	16°57"N	42°50"W	26.3	7
67	03.12.81	0530	16°34"N	44°05"W	26.0	12
68	"	1230	16°22"N	44°45"W	26.5	4
69	04.12.81	0330	15°45"N	46°26"W	26.8	26+2e
70	"	0830	15°32"N	47°04"W	27.0	27
71	05.12.81	1100	14°53"N	49°30"W	27.5	13+2e
72	06.12.81	0159	14°34"N	51°18"W	27.0	30
73	"	0330	"	"	"	54
74	"	1250	14°22"N	51°57"W	28.1	56+2e
75	"	2255	"	"	27.0	56+2e
76	14.12.81	1055	13°16"N	60°55"W	28.6	4
77	22.12.81	1800	14°55"N	60°37"W	27.8	35
78	23.12.81	0320	16°30"N	66°02"W	27.4	16
79	"	1020	"	"	27.8	8
80	11.1.82	1935	17°06"N	64°59"W	27.5	2
81	12.1.82	1555	16°30"N	66°02"W	27.2	2
82	13.1.82	1105	15°05"N	68°03"W	"	21+1e
83	"	1615	"	"	"	37

Table 2. Tow number, date, time, station location, seawater temperatures, *Halobates* species and number of insects caught during Pacific crossing of the "Eye of the Wind" (e = exuviae).

Tow no.	Date	Local time	Latitude	Longitude	Temp. °C	Number insects	Species
85	28.1.82	0555	06°12"N	81°19"W	27.8	86+2e	*sobrinus*
86	"	0825	"	"	27.6	30+3e	"
87	30.1.82	0330	06°06"N	83°34"W	28.5	57	"
88	"	1815	06°16"N	84°48"W	30.2	14+5e	"
89	"	2035	"	"	"	7	"
90	31.1.82	0135	06°00"N	85°42"W	27.9	6	"
"	"	"	"	"	"	10	*micans*
91	"	1700	05°47"N	86°19"W	29.8	6+2e	*sobrinus*
92	04.2.82	2120	05°30"N	87°05"W	28.5	15	"
93	05.4.82	1400	04°11"N	88°01"W	27.8	17	"
"	"	"	"	"	"	98+5e	*micans*
94	06.2.82	0715	02°44"N	89°04"W	27.8	10	*sobrinus*
101	17.2.82	1700	00°40"S	91°05"W	-	5	*robustus*
105	19.2.82	0600			-	3	"
112	24.2.82	1255	01°00"S	92°36"W	26.5	1e	*splendens*
114	"	2355	"	"	25.4	2	"
115	25.2.82	0510	01°56"S	94°08"W	25.5	1e	"
118	26.2.82	1455	03°11"S	96°01"W	26.7	20+2e	"
119	27.2.82	1330	03°46"S	97°55"W	26.8	10+1e	"
121	28.2.82	1245	04°45"S	99°18"W	"	12	"
122	"	1430	05°13"S	99°52"W	"	10	"
123	01.3.82	1230	06°13"S	101°01"W	27.0	8	*splendens*
125	03.3.82	1030	08°48"S	105°24"W	26.2	1	"
"	"	"	"	"	"	4	*sericeus*
126	"	1505	09°10"S	105°57"W	"	18+2e	"
127	05.3.82	1010	11°58"S	109°36"W	25.6	71	"
128	07.3.82	0830	14°27"S	113°36"W	25.3	57+2e	"
129	"	1120	14°57"S	114°03"W	25.6	61+3e	"
130	"	1623	15°15"S	114°31"W	25.8	32	"
131	08.3.82	0030	14°53"S	114°03"W	25.3	47+1e	*sericeus*
133	"	1215	15°52"S	115°32"W	25.8	9	"
136	09.3.82	0230	16°17"S	116°11"W	"	2	"
137	"	0805	16°35"S	116°35"W	26.4	70+1e	"
138	"	0955	"	"	"	44+2e	"
139	10.3.82	0300	17°10"S	117°45"W	26.0	43	"
140	"	1135	17°28"S	118°14"W	26.3	18	"
142	12.3.82	0730	18°34"S	119°29"W	27.3	12	"
143	"	1155	18°50"S	119°42"W	26.8	1	"
144	"	2105	"	"	26.7	20	"
145	13.3.82	0245	19°37"S	119°56"W	25.7	41+1e	"
146	"	0735	"	"	27.1	26+1e	"
148	"	2355	19°58"S	120°10"W	26.6	19	"
149	14.3.82	0926	20°45"S	120°50"W	26.7	25+3e	"
150	"	1330	21°03"S	121°11"W	26.6	29	"
151	"	1915	21°22"S	121°30"W	26.5	36+1e	"
152	"	2315	"	"	"	47+1e	"
153	15.3.82	0240	21°59"S	122°14"W	26.4	89+10e	"
154	"	0655	"	"	"	58+3e	"
155	"	1035	22°21"S	122°46"W	26.7	37+4e	"
156	"	2210	22°41"S	123°22"W	26.5	68+7e	"
157	16.3.82	1850	23°32"S	125°37"W	27.1	12	"
158	"	2020	"	"	"	17+1e	"
"	"	"	"	"	"	1	*germanus*
159	17.3.82	0715	23°59"S	126°29"W	26.7	23	*sericeus*
160	18.3.82	0835	24°12"S	127°50"W	"	7	"
162	30.3.82	0540	24°29"S	127°50"W	27.8	2	"
"	"	"	"	"	"	14+1e	*germanus*
163	"	1440	"	"	28.4	10	"
"	"	"	"	"	"	1	*sericeus*
164	31.3.82	0915	23°31"S	134°27"W	27.5	1	"
"	"	"	"	"	"	15+1e	*germanus*

Table 2. – *Cont'd.*

Tow no.	Date	Local time	Latitude	Longitude	Temp. °C	Number insects	Species
168	07.4.82	0159	20°49"S	137°23"W	28.0	3+1e	"
169	"	1520	"	"	28.4	2	*sericeus*
171	08.4.82	0450	20°41"S	137°24"W	28.0	2	"
"	"	"	"	"	"	3	*germanus*
176	11.4.82	2015	19°22"S	137°56"W	28.3	34	*germanus*
"	"	"	"	"	"	26+2e	*sericeus*
177	12.4.82	0915	18°40"S	139°55"W	28.1	27+2e	"
"	"	"	"	"	"	11	*germanus*
178	"	1405	"	"	28.6	2	"
"	"	"	"	"	"	10+2e	*sericeus*
179	"	1640	"	"	"	48+9e	"
"	"	"	"	"	"	11	*germanus*
180	13.4.82	0840	18°25"S	142°12"W	28.2	5	"
"	"	"	"	"	"	17	*sericeus*
181	"	1555	"	"	28.1	11	"
"	"	"	"	"	"	7	*germanus*
183	14.4.82	0045	18°43"S	143°45"W	28.2	1	"
184	"	1045	"	"	28.5	6	*sericeus*
185	"	1230	"	"	"	3	"
"	"	"	"	"	"	25+1e	*germanus*
186	"	1350	"	"	28.4	1	"
187	"	1545	"	"	"	1	"
"	"	"	"	"	"	5	*sericeus*
188	"	2140	"	"	27.7	20+2e	*germanus*
189	16.4.82	0015	18°31"S	145°18"W	28.2	15	"
191	18.4.82	0045	17°51"S	148°14"W	"	14+1e	"
"	"	"	"	"	"	3	*sericeus*
192	"	0705	"	"	28.6	4	*germanus*
193	19.4.82	0120	17°27"S	149°48"W	28.1	4+1e	"
194	27.4.82	0230	17°21"S	150°02"W	28.4	69+5e	"
"	"	"	"	"	"	2	*sericeus*
195	05.5.82	1125	17°00"S	153°20"W	28.8	4	*germanus*
196	"	1655	"	"	28.7	17+3e	"
197	06.5.82	0355	17°30"S	155°13"W	28.2	14	"
198	"	2103	"	"	28.0	6+1e	"
199	08.5.82	1235	17°48"S	159°40"W	28.2	2	"
200	"	2350	"	"	28.0	4	"
201	09.5.82	1010	17°58"S	161°22"W	27.0	1+1e	"
202	"	1625	"	"	28.3	4	"
203	12.5.82	1445	19°05"S	169°21"W	27.4	4	*sericeus*
205	28.5.82	1856	18°42"S	173°13"W	26.0	2	*germanus*
206	29.5.82	1750	18°44"S	174°40"W	26.6	11+1e	"
207	30.5.82	0430	18°19"S	176°37"W	26.5	4	"
208	"	1415	"	"	27.6	3	"
209	"	2255	"	"	27.2	25	"
210	31.5.82	0430	17°54"S	177°42"W	26.8	3	"
211	"	1930	"	"	27.5	4	"
213	28.6.82	1735	18°23"S	175°04"E	25.5	12	"
214	29.6.82	0650	18°16"S	172°12"E	25.4	5	"
215	30.6.82	1450	18°33"S	169°25"E	24.4	5+1e	"
216	"	2050	"	"	24.3	5	"
217	05.7.82	1915	18°00"S	168°00"E	25.2	2	"
218	06.7.82	0410	"	"	25.5	7	"
219	07.7.82	0240	"	"	25.9	1	"
220	10.7.82	n.a.	16°30"S	167°30"E	n.a.	180+1e	*proavus*
228	01.10.82	2115	19°42"S	177°38"E	25.4	7+2e	*sericeus*
230	04.10.82	1750	23°50"S	179°28"E	21.5	2	"
231	"	2350	"	"	21.3	4+1e	"
244	09.12.82	0300	33°00"S	164°10"E	21.0	1	"
247	11.12.82	0555	32°30"S	160°49"E	20.9	2	"

Table 3. Numbers of day and night samples and mean number (± s.d.) of *Halobates* caught in the Atlantic (*H. micans*) and the Pacific (all other species) Oceans.

Halobates species	Day samples		Night samples	
	Number	Mean	Number	Mean
micans	23	15.0±15.5	26	17.3±14.0
sobrinus	4	15.8±10.5	6	30.8±33.0
sericeus	31	23.8±21.8	21	23.3±24.8
germanus	21	7.4±6.2	23	11.1±15.3
splendens	6	10.2±6.2	1	1.0±0

Table 4. Total number of neuston tows, number of positive tows and mean number (± s.d.) of *Halobates micans* caught at different seawater temperatures in the Atlantic Ocean.

Temp °C	Total tows	Positive tows	Mean
15	0	0	-
16	1	0	-
17	1	0	-
18	2	0	-
19	8	0	-
20	5	0	-
21	11	4	7.0 ± 2.7
22	11	4	5.3 ± 5.4
23	4	4	11.8 ± 8.3
24	8	8	15.4 ± 8.1
25	10	10	16.3 ± 12.5
26	9	9	4.3 ± 20.1
27	8	8	16.8 ± 13.6
28	2	2	30.0 ± 36.8
29	0	0	-

Table 5. Total number of neuston tows, number of positive tows and mean number (± s.d.) of insects collected per tow at different seawater temperatures of four *Halobates* species in the Pacific Ocean.

Temp °C	Total tows	*H. sericeus* +ve tows	*H. sericeus* mean	*H. sobrinus* +ve tows	*H. sobrinus* mean	*H. splendens* +ve tows	*H. splendens* mean	*H. germanus* +ve tows	*H. germanus* mean
20	6	2	1.5±0.5	0	-	0	-	0	-
21	5	2	3.0±1.0	0	-	0	-	0	-
22	0	0	-	0	-	0	-	0	-
23	1	0	-	0	-	0	-	0	-
24	3	0	-	0	-	0	-	2	5.0± 0
25	21	10	37.0±22.8	0	-	1	2.0± 0	6	4.8±3.8
26	34	18	34.1±23.2	0	-	7	9.0±5.9	4	4.8±3.8
27	25	8	9.5±8.3	5	29.8±29.3	0	-	11	8.9±7.8
28	26	13	12.4±13.3	2	36.0±1.0	0	-	21	12.1±15.2
29	2	0	-	1	6.0±0	0	-	0	-
30	2	0	-	2	10.5±3.5	0	-	0	-

Table 6. *Halobates* species, total number of insects collected, mean number (± s.d.) per tow, range, % adults, numbers of males and females, and sex ratios (male/female) (data for *H. micans* from the Atlantic alone, all other spp. from the Pacific).

Halobates species	Total	Mean #/tow	Range	Adults (%)	Males	Females	Sex ratio
micans	764	16.2 ±14.6	1-56	49.1	184	206	0.89
sobrinus	248	24.8 ±25.4	1-86	42.7	54	52	1.04
splendens	63	9.0 ±5.9	1-20	20.6	5	8	0.63
sericeus	1,229	23.2 ±22.8	1-89	50.2	292	325	0.90
germanus	411	9.3 ±11.9	1-69	31.4	66	63	1.05

Table 7. *Halobates* species, total number of nymphs, % of each nymphal stages (1-5) and sex ratios (male/female) of the 5th instar (number of exuviae in brackets).

Halobates species	Total number	I	II	III	IV	V	Sex ratio
micans	374	9.4 (0)	10.4 (0)	23.3 (4)	30.8 (120)	26.2 (2)	0.75
sobrinus	142	10.6 (0)	19.0 (2)	21.8 (2)	26.8 (7)	21.8 (1)	0.68
splendens	50	8.0 (1)	14.0 (0)	32.0 (1)	28.0 (2)	18.0 (1)	0.80
sericeus	612	17.0 (12)	19.3 (14)	17.8 (12)	22.1 (13)	23.9 (10)	0.76
germanus	282	19.3 (3)	23.6 (4)	19.6 (6)	20.7 (5)	16.8 (1)	0.88

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