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HALOBATES IN THE BANDA SEA (INDONESIA): MONSOONAL DIFFERENCES IN ABUNDANCE AND SPECIES COMPOSITION

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ABSTRACT

The sea-skater *Halobates* was collected in eastern Indonesian waters during the SNELLIUS II Expedition in August 1984 (SE monsoon) and February/March 1985 (NW monsoon). About 200 specimens were caught in 18 tows at offshore sites in August, in the upwelling season, but more than 1,000 in 18 tows in February, when the mixed layer was nutrient-depleted and chlorophyll-poor. The Indo-Pacific species *H. germanus* predominated in the catches during both cruises, its density being inversely related to surface chlorophyll concentration. Reproductive activity of *H. germanus* was highest in oligotrophic conditions, the relative abundances of nymphs and of cast skins being much higher in February than in August. Shifts in the population structure in February suggested a development time of about 7 days or less per stadium at a surface seawater temperature of 29°C. The cosmopolitan *H. micans* and the coastal *H. flaviventris* and *H. princeps* were absent or rare in August but present in most catches in February; some specimens of the latter two species were found at stations more than 150 km from the nearest shore.

The only oceanic insect genus, *Halobates,* is confined to tropical and subtropical regions, at sea-surface temperatures of 18°C or higher (Cheng, 1985). About 45 species have been described, of which at least 10 are found in the Indo-Pacific Convergence zone, the presumptive center of origin of *Halobates* (Cheng, 1985, 1989). Most of these are coastal species, occurring along shores, in mangrove swamps and near coral reefs, but two, *H. micans* and *H. germanus,* belong to the small group of open-ocean species. Occurrence and abundance of the various species in the Indo-Pacific Convergence zone are only partially known, and for both *H. micans* and *H. germanus* earlier records were virtually limited to the Andaman Sea, South China Sea, Celebes Sea and Coral Sea (Cheng, 1973a; Cheng and Shulenberger, 1980; Cheng and Holdway, 1983). Indonesian waters, namely the Java Sea, Flores Sea, Banda Sea and Arafura Sea, appeared blank on the distribution maps of these two species, although *H. germanus* was caught in large numbers during the passage of the EYE OF THE WIND through the Java Sea in April 1980 (Cheng and Holdway, 1983). With the Indonesian-Dutch Snellius II Expedition, originally initiated by UNESCO, the opportunity arose to collect *Halobates* in the eastern part of the area, in the transition zone between the deep Banda Sea and the shallow Arafura Sea. In relation to the topography and the biannual changes in the direction of the surface currents, Wyrtki (1958, 1961) suggested that there was seasonal upwelling in this zone. During the SNELLIUS II Expedition, the region was therefore surveyed twice, once in the SE monsoon (August 1984) and once in the NW monsoon (February/March 1985). In accordance with Wyrtki's hypothesis, the cruise in the SE monsoon showed upwellings in the Aru Basin and in the adjacent shelf part of the Arafura Sea (Zijlstra et al., 1990), with the amounts of nutrients, chlorophyll, plankton and nekton 2–3 times as high as for the cruise in the NW monsoon (Zijlstra and Baars, 1987; Baars and Zijlstra, in press). These findings offered an interesting base on which to study the *Halobates* specimens caught in the neuston sampler employed during these cruises. No clear seasonality in open-ocean *Halobates* species has been established

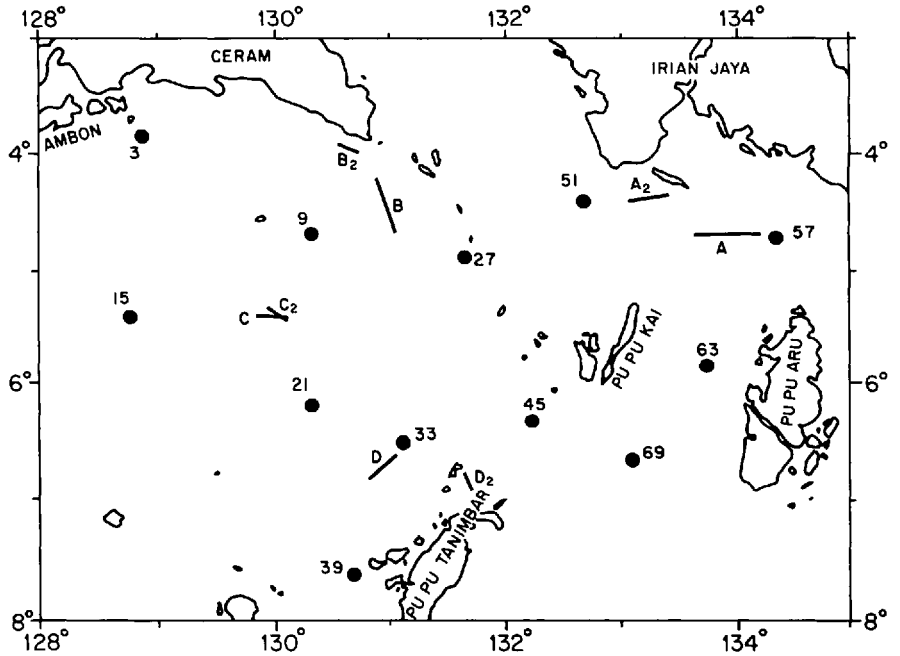

Figure 1. The eastern Banda Sea with the locations of survey stations (dots) and drogue stations (lines), with A–D referring to August 1984 and A_2–D_2 to Feb/March 1985.

so far (Cheng, 1973a; 1985); the present data are, to our knowledge, the first that can be examined to establish whether this holds for tropical areas with marked seasonal shifts in the trophic conditions of the mixed layer.

Materials and Methods

Neuston was sampled on two legs of R/V Tyro during the Snellius II Expedition. Under the theme "Pelagic Systems," both cruises comprised a survey of more than 70 stations (indicated by numerals) followed by four drogue stations (A–D) (Fig. 1). One neuston tow was made at each of the survey stations located in the evening (12 in total), whereas at the drogue stations we made one tow during darkness and one tow during daylight (Table 1). Most of the sites of the survey stations were the same for the two cruises, but those for A, B and D were different (Fig. 1). The first survey was between 1–12 August, and the drogue stations were sampled between 17–30 August 1984. We took no samples at station C. The second survey and drogue stations were from 9–20 February and 23 February–8 March 1985. Tows at survey stations 45 and 51 were cancelled due to rough seas. All stations were at sites with bottom depths of 1,500 m or more, except for D2, in among the northern islands of Pu Pu Tanimbar, with a depth of 400 m. Distances from nearest shore were 25 km or more, except for A2, B2 and D2, which were only 10–15 km offshore (Fig. 1). Sea surface temperatures in August 1984 varied between 25.7–26.6°C and surface salinities between 32.8–34.4‰. For February 1985 these variables ranged between 28.0–30.0°C and 33.4–34.3‰ (Zylstra et al., 1990).

The net used was of the David-Hempel type (manufacturer HydroBios, Kiel, W. Germany) but it was equipped with only the upper net, not the second one with the opening entirely below the surface (Hempel and Weikert, 1972). During the second cruise we arranged two nets side by side, thus doubling the catch area. Mesh size was 500 μm. The net opening was 30 cm wide and 15 cm high, with the lower half submerged in the water. Towing was from midships, at a distance of about 30 m away from the hull, by a nylon rope that normally did not touch the water in front of the net except during a heavy swell. Neuston was sampled at the same time as operation of a Rectangular Midwater Trawl (RMT) at the stern. RMT hauls, and consequently neuston tows, were done at a speed of 2 knots (3.5 km h^{-1}). During short drops in ship's speed between successive RMT hauls the neuston net was kept in the water. Total towing times varied but generally were between 180 and 240 minutes (Table 1).

Table 1. Sampling data comprising stations, duration of tow, total number of *Halobates* specimens and species composition (g = *H. germanus*, m = *H. micans*, p = *H. princeps*, f = *H. flaviventris*). Numbers refer to nymphs plus adults, but include no cast skins. Survey stations are night tows; X's mean no tows performed. *: Incomplete sample due to malfunctioning of the net opening

	August 1984			Feb/March 1985			
	Tow (min)	Total no. (one net)	Species	Tow (min)	Total no. Net A	Total no. Net B	Species
Survey station							
3	85	8	g	90	0	0	
9	64	5	g	185	53	30	g, p, f
15	120	0		175	32	31	g, p, f
21	248	0		195	41	33	g, m, p, f
27	190	0		185	54	69	g, m, p, f
33	173	12	g	180	100	95	g, m, f
39	311	1	p	180	101	64	g, m, p
45	332	26	g	X			
51	187	0		X			
57	190	0		175	103	91	g, p, f
63	215	2	g	195	76	84	g, m, p, f
69	179	2	g	175	36	38	g, m
Drogue station							
A day	195	4	g	180	6	0*	g, m, p, f
night	275	6		160	4*	9	
B day	170	14	g, f	120	10	5	g, p, f
night	192	102		205	74	64	
C day	X			230	98	71	g, p, f
night	X			220	334	255	
D day	340	5	g	100	1	5	g, m, f
night	231	9		90	22	24	

At the survey stations, tows started around 2030 hr (local time), and at the drogue stations the night tows started between 2000 and midnight. Starting times of the daylight tows varied between 0900 and 1430.

On board, total neuston catches were preserved in 70% alcohol. After the return of R/V TYRO to Holland, *Halobates* specimens were separated from the other material, preserved in 4% formalin in seawater, and sent to the Scripps Institution of Oceanography for further identification. In the present study we have generally presented absolute numbers recorded, but we have also converted the data to numbers per 1,000 m^2, being the surface scanned by one net opening (August 1984) in about one hour, or by two net openings (February 1985) in half that time.

RESULTS

Abundance and Species Composition.—In August 1984, *Halobates* was caught at 7 of the 12 survey stations and at all three drogue stations (Table 1). Numbers were relatively low, except for the night tow at station B. A total of 196 specimens were caught. All but two of the specimens caught belonged to *H. germanus* (Table 2). The exceptions were one adult female each of *H. princeps* and *H. flaviventris*.

The abundance and composition of the *Halobates* caught during February 1985 were very different from those of August 1984. No insects were caught at station 3, but at all 13 of the remaining stations not only were insects caught but more than one *Halobates* species was recorded. At some stations as many as four species co-occurred: *H. germanus, H. micans, H. flaviventris* and *H. princeps* (Table 1). A total of 2,113 insects were collected during this season, but as two nets were employed instead of one this number has to be halved for comparison with August 1984. After correcting for a small difference in total towing time, 3,700 against

Table 2. Species and age composition of *Halobates* (Numbers refer to absolute numbers caught, pooled for all tows)

Species	Nymphal stage						Adult		Total	% Adult
	I	II	III	IV	V♂	V♀	♂	♀		
August 1984										
H. germanus		2	3	4	13	22	69	81	194	77
H. flaviventris								1	1	
H. princeps								1	1	
Feb/March 1985										
H. germanus	37	293	402	285	81	91	266	256	1,711	31
H. micans	3	5	18	13	18	21	45	61	184	58
H. flaviventris			1	14	21	21	62	57	176	68
H. princeps	2	2	1	6	5	4	14	8	42	52

3,040 minutes respectively (Table 1), the ratio between the total catches is about 1:6.5. As in 1984, the commonest of the species caught in 1985 was *H. germanus* (Table 2). Regarding the distribution patterns of the four species in 1985, highest numbers of *H. flaviventris* and *H. princeps* occurred at northern stations (nos. 9, 15, 27, 57, B), and those of *H. micans* at southern stations (nos. 33, 39, 69). *H. germanus* occurred in 1985 at all but one station without a clear predominance in any of the subregions in the study area. Highest numbers of *H. germanus* (584 insects) were found in the night tow at station C. This station, near the small volcanic island of Manuk, is in the most "open" part of the eastern Banda Sea, which had seemed less populated more than 3 weeks earlier when night tows at stations 9, 15 and 21 (surrounding station C, cf. Fig. 1) yielded only 71, 27 and 59 specimens of *H. germanus* respectively.

Differences between night and daytime tows were not negligible: in all seven pairs of tows at the drogue stations, the night-time catches were higher (Table 1). After correction for differences in duration of tow, 903 specimens caught at night contrasted with only 223 caught by day. This four-fold decrease in number of insects caught by day is likely to result from net-avoidance (Cheng, 1973b). At our towing speeds of 2 knots, variations in the light of the moon will have caused variations in catch efficiency among night tows as well (Cheng and Enright, 1973), but as we kept no record of ambient light intensities, we were not able to determine this effect. In 1985, differences between the numbers caught in net A and in net B were sometimes considerable (Table 1), suggesting that factors such as the presence of the rope, deck lights, etc., may severely influence catches. Given that avoidance certainly occurred at night, the transformation of night catches into numbers per 1,000 m^2 should be regarded as giving minimum densities. The mean density of *H. germanus* in August was 3.1 per 1,000 m^2 (N = 15, night tows only), and in February 15.3 per 1,000 m^2 (N = 14). Mean numbers per 1,000 m^2 of the other species in February were 2.0 for *H. micans*, 1.9 for *H. flaviventris* and 0.4 for *H. princeps*. Differences between stations further from and stations closer to shorelines were insignificant. In February the pooled density of the coastal species *H. flaviventris* and *H. princeps* was 2.7 per 1,000 m^2 for the 7 stations 9, 15, 21, 33, 57, 69 and C and 1.8 per 1,000 m^2 for the other 7 stations closer to or in the lee of islands.

Population Structure and Development Rate.—Besides the larger number of specimens caught in February 1985 compared with August 1984, there was a marked

Table 3. Occurrences of cast skins of *Halobates*; pooled for all tows

Species	Nymphal stage						Total	% of total no. of nymphs
	I	II	III	IV	V♂	V♀		
August 1984								
H. germanus					1		1	2
Feb/March 1985								
H. germanus	2	11	39	10	11	18	91	8
H. micans			5		3	2	10	13
H. flaviventris				1	1	2	4	7
H. princeps					1		1	5

difference in the population structure between the two *Halobates* collections. In *H. germanus,* 77% of the specimens caught in August were adults (Table 2). Not a single first-instar nymph was caught, and very few of the three subsequent instars were represented. Most of the nymphs belonged to the final or fifth instar. In February/March, adults comprised only 31% of the total catch of *H. germanus* (Table 2). Among the nymphs of *H. germanus,* the first instar was least abundant, but the second, third and fourth instars were more abundant than the final instars. In the other three species caught in February/March, the population structure resembled to a large extent that of *H. germanus* in August. More than 50% of the specimens were adults, and the highest nymphal numbers were in the final instars (Table 2). First and second instars were recorded in *H. micans* and *H. princeps,* but not in *H. flaviventris.*

The absence or paucity of first-instar nymphs in the catches is most likely due to a low retaining efficiency of the net used. The youngest nymphs measure only about 1 mm in body length and 0.5 mm in body width, and thus can be expected to pass relatively easily in longitudinal position through 500 μm gauze. For similar reasons, the retaining efficiency for second and third instars was probably also less than 100%, so the population structure presented in Table 2 cannot be regarded as reflecting absolute abundances. Inter-monsoonal comparison between the relative abundances still remains valid, and points to a reproductive activity of *H. germanus* in the NW monsoon higher than in the SE monsoon. This is corroborated by the number of cast skins of *H. germanus* occurring in the catches (Table 3). In August, only one cast skin was found against 44 intact instars, whereas in February/March 91 cast skins were recorded against 1,189 instars. The relative abundances of cast skins thus differed by a factor of four between the two cruises. The relatively large numbers of cast skins of *H. germanus* in February reinforce the suggestion of a population growing much more actively than in August. It cannot be assumed that the rates of disintegration of cast skins differ between August and February. In *H. micans* and *H. flaviventris,* the proportions of cast skins were comparable to those of *H. germanus* in February (Table 3). (Numbers of *H. princeps* skins were too low to justify any such conclusions about this species.)

In February/March there were marked shifts in the population structure of *H. germanus* along the surface current from west to east (Fig. 2). Adults comprised only about one-third of the population in the "middle" of the eastern Banda Sea (station nos. 9, 15, 21) and near the Outer Banda Arc (nos. 27, 33, 39), whereas 5–8 days later in the Aru Basin (nos. 57, 63, 69) absolute numbers of nymphs were lower and of adults were much higher. This may indicate a progression of developmental stages with time. The doublings of the number of adults from

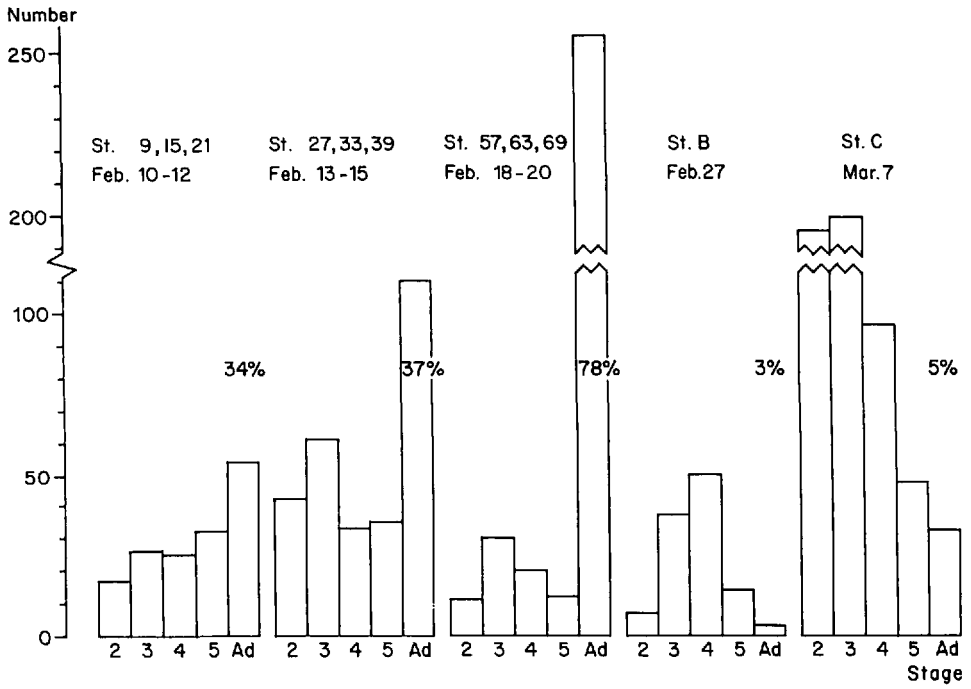

Figure 2. Population structure of *H. germanus* at different (pools of) stations during Feb/March 1985. Night catches only, with total minutes of towing from left to right: 555, 545, 545, 205, 220. Percentages in or above bars for adults indicate those of adults in the total catch. Numbers of first instars not shown because of low catch efficiency.

February 10–12 to February 13–15, and again to February 18–20 (Fig. 2), suggest a development time from fifth instar to adult of about 1 week or less. With some imagination, one can also suppose that the relatively high numbers of second and third instars at the stations sampled from February 13–15 reappear as third and fourth instars at the stations from February 18–20, suggesting again that a stadium takes less than 7 days. However, it is doubtful whether the same population of *H. germanus* was followed with time. Surface currents in February had a velocity of about 30 km per day (Zijlstra et al., 1990). The time needed for the surface water to flow from the area of stations 9, 5, 11 to 27, 33, 39 and subsequently to 57, 63, 69 would then be about 8 + 8 days, whereas R/V TYRO travelled the same distance in only 3 + 5 days. Remarkably, when the vessel returned "upstream" to sample the drogue stations B_2 and C_2 (Fig. 1), the population structures of *H. germanus* were very different from those of the survey stations (Fig. 2). The percentages of adults at B and C was only five or less, and at station C they were accompanied by very high absolute numbers of second and third instars. This points to a highly dynamic population of *H. germanus* in February/March 1985, with large variations in birth and death rates in space and time. Numbers of *H. germanus* in August, and of the other species in February/March, were too low for meaningful comparisons.

Relation to Plankton Biomass.—The increase in mean density of *H. germanus* from 3.1 in August 1984 to 15.3 per 1,000 m^2 in February/March 1985 contrasts with the changes observed in the plankton biomass of the photic zone. Both chlorophyll concentrations (Gieskes et al., 1988) and displacement volumes of

Table 4. Densities of *H. germanus* grouped into three categories according to the upper 5 m chlorophyll concentrations [chl]. Density expressed as number per 1,000 m^2; averages of night tows only (15 tows for 1984, 14 tows for 1985)

	Chlorophyll (mg m^{-3})		
	≤0.1	0.1–0.5	>0.5
August 1984			
Mean density	X	5.1 (N = 8)	0.9 (N = 7)
Density range	X	0–28.4	0–4.2
Feb/March 1985			
Mean density	18.2 (N = 7)	12.5 (N = 7)	X
Density range	0–71.7	0.7–20.6	X

zooplankton (Schalk, 1987; Baars et al., 1990) decreased by a factor of two to three from the cruise in the upwelling season to the cruise in the oligotrophic season. For comparison with *Halobates* densities, we used the chlorophyll concentrations [chl] measured just beneath the surface at the neuston stations as an indicator for the intensity of upwelling and/or the degree of oligotrophy. During the August cruise, when [chl] was always above 0.1 $mg \cdot m^{-3}$, most *H. germanus* were caught at stations with the lowest surface chlorophyll concentrations (Table 4). Even for February/March, when the mean surface [chl] was much lower than in August, there was a tendency for the highest densities to be associated with the lowest [chl]. Neither of the intraseasonal comparisons in Table 4 is statistically significant. However, if we pool the cruises, *H. germanus* density appears inversely related to surface [chl] (Spearman's rank correlation coefficient $r_s = -0.50$, N = 29, $P < 0.01$). As *H. germanus* is carnivorous (Cheng, 1985), the inverse relation with chlorophyll, if true, must be indirect and invites a search for biomass changes in potential prey organisms. Most appropriate in this respect would be a closer examination of the pleuston and neuston catches in our own samples, but these have not yet been sorted and counted.

Discussion

The neuston sampling during the Snellius II Expedition provided a substantial contribution to our knowledge of the distribution patterns of *Halobates* in eastern Indonesian waters. There had been earlier major cruises in the area, but results on *Halobates* were never published (Siboga Expedition 1899–1900) or the sampling had primarily focused on deep waters (Snellius Expedition 1929–1930). Delsman (1926) described the development and hatching of *Halobates* eggs collected in the Java Sea, but he did not try to identify the species. From Cheng and Holdway (1983) and the present study we presume that *H. germanus* was involved. This widespread oceanic species in the Indian and western Pacific Oceans (Cheng, 1973c; 1985; 1989) predominated in our catches, both in the SE monsoon and in the NW monsoon. During the cruise in the latter season, densities increased five-fold. The other open-ocean species, the cosmopolitan *H. micans,* was caught only in the NW monsoon. In the Indo-Pacific region *H. micans* is known to occur at stations further out to sea than *H. germanus* (Cheng and Holdway, 1983). Comparing August 1984 with February/March 1985, the increase of *H. germanus* and the appearance of *H. micans* are somehow related to the reversed direction of the surface currents and/or to the increasing degree of oligotrophy. In August, in the middle of the SE monsoon, the surface layer driven westwards out of the eastern Banda Sea is replaced by upwelling of deeper water in the Aru Basin and

by surface water from the shallow Arafura Sea. Presumably, no large populations of open-oceans *Halobates* exist in this shelf sea, and a supply of specimens from the Coral Sea would be limited by the relative narrowness of the Torres Strait. In February/March, at the end of the NW monsoon, the eastward surface current from the Java Sea, via the Flores Sea into the Banda Sea, is mainly fed by Pacific Ocean surface water via the South China Sea and the Strait of Macassar, but Indian Ocean surface water reaches the eastern Banda Sea via the Timor Sea (Wyrtki, 1961).

Besides differences in the origin and course of the surface water, in the Banda Sea the main difference between the two monsoons is the oligotrophy during the NW monsoon. From the present analysis, it is suggested that the density of *H. germanus* (and maybe also of *H. micans*) is highest in oligotrophic conditions. This may be due to a lower rate of loss out of the study area caused by wind-driven upwelling conditions and/or higher birth and development rates. For the latter we obtained two indications. The relative abundances both of juvenile stages and of cast skins of *H. germanus* were much higher for February/March than for August. The development rate in February was perhaps only 7 days or less per stadium, twice as fast as that reported for *H. mariannarum* (kept at 20–23°C), a coastal species found in Micronesia (Cheng, 1981). Since during our sampling period the average sea-surface temperature was 29.6°C, and since temperature is known to influence the rates of development of insects, such an acceleration is to be expected, providing food conditions are not limiting. In *H. micans* in the Atlantic Ocean, abundance increased with temperature in the range 20–25°C, but above 25° other (unknown) factors apparently became important as well (Cheng and Schulz-Baldes, 1981).

Abundance and quality of food seem to be among the most intriguing key factors in the population dynamics of open-ocean *Halobates*. From the present data, one gets the impression that *Halobates* is probably a specialized predator of organisms belonging to oligotrophic habitats. In this respect it is a pity that there has been no quantitative analysis of *Halobates* abundance in relation to the abundance of separate taxonomic groups of pleuston and neuston in the same catches. The present study suffers from the same omission.

Our findings, presented in Table 4, invite re-examination of *Halobates* records from other areas with continuous or seasonal upwelling. As in the Banda Sea, monsoon upwelling is known from the northwest Indian Ocean (Somalia, Oman), the Bay of Bengal and the Gulf of Thailand. Records of *H. germanus* in these areas are scanty, but 90% fall within the NE and NW monsoon (Cheng, 1973c), and thus seem to corroborate our hypothesis. During the SE (or SW) monsoon, catches were mainly in the oligotrophic, equatorial part of the Indian Ocean. During the part of the sailing track of the EYE OF THE WIND from Kenya along the coast of Somalia into the Red Sea in August 1980, 52 *H. micans* (and 1 *H. germanus*) were caught 3°N and 82 *H. germanus* around 12°N in the Gulf of Aden; no *Halobates* was caught in between, in the Somali upwelling zone from 5–10°N (Cheng and Holdway, 1983). However, since no data on chlorophyll concentrations were collected it was not possible to make analyses comparable to those presented in Table 4. For the upwelling area off West Africa, a comparison of the surface chlorophyll map (Margalef, 1971) with *H. micans* catches during the same cruise (Cheng, 1974) reveals that no specimens were caught in the upwelling plume proper (chl > 1 mg·m^{-3}). More detailed data from the EASTROPAC area, including the Peru upwelling zone, and from the distribution maps presented in Cheng and Shulenberger (1980) indicate that none of the four open-ocean species of the eastern Pacific occurs in the narrow upwelling zone

along the Peruvian coast. *H. sericeus,* confined to the central water masses of the North and South Pacific and the only species occurring at sea surface temperatures around 18°C, does not approach within 1,000 km of Peru, although it has been caught close to the coast at many other places in the Pacific.

Finally, we have to discuss our catches of two coastal species, *H. flaviventris* and *H. princeps* (Cheng, 1985). Although our sampling program was limited to offshore sites, we caught one specimen of each in the SE monsoon (using single nets) compared with a total of more than 100 (using two nets) in the NW monsoon. These two species often occurred together, and both were caught even at station 15, about 150 (Banda Islands) to 200 (Ambon) km from the nearest shore (Fig. 1). The population structure of *H. flaviventris,* a species widely distributed among the islands of the western Pacific and the Indian Oceans (Cheng, 1985), was dominated by final instars and adults. This is not really surprising since only adults and older nymphs of such coastal *Halobates* venture out to sea, younger nymphs being generally confined to protected areas among mangroves or other coastal vegetation close to shore (Birch et al., 1979).

H. princeps appeared to be rarer than *H. flaviventris* (Table 2). It is the biggest of the four species found in our survey, being one of the largest coastal species in this genus (Herring, 1961). The adults measure over 6 mm in body length, whereas those of the other three range from 4 to 4.5 mm. Despite its large size, this species is poorly known, and although it has been reported from several islands in the Indo-Malaysian region as well as from Micronesia, very few specimens have ever been collected (Herring, 1961; Cheng, 1981; 1985; Cheng and Holdway, 1983). It may be more agile than its smaller cousins and thus can better avoid being caught.

We will conclude by remarking that the complex topography, the monsoon regime, and the variety of *Halobates* species around eastern Indonesia provide excellent opportunities for more detailed studies of the ecology, behavior and biogeography of these interesting marine insects.

Acknowledgments

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