Mass Oviposition and Egg Development of the Ocean-Skater *Halobates sobrinus* (Heteroptera: Gerridae)[1]

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Abstract: We report the first observation of mass oviposition by the ocean-skater *Halobates sobrinus* White in the eastern tropical Pacific Ocean. We netted, in one scoop, 833 insects and a single egg mass with an estimated 70,000 eggs on a plastic gallon (3.785-liter) milk jug. Evidently anthropogenic debris could provide potentially important oviposition substrates for *Halobates* spp. in the open ocean. Freshly laid eggs incubated at 26–32°C hatched within 8–10 days. Eggs kept at temperatures below 22°C did not hatch even after 20 days.

PELAGIC SPECIES OF the ocean-skater *Halobates* live all their lives at the sea surface. Unlike their coastal congeners, which lay eggs on rocks or roots and branches of mangroves or other plants (Cheng 1985, Foster and Treherne 1986), ocean-skaters must rely on flotsam as oviposition substrates, which include pieces of wood, cork, coal, pumice, plastic, tar, seeds, seaweed, empty mollusk shells (*Spirula* and *Sepia*), seabird feathers, and even dead or dying seabirds (Lundbeck 1914, Herring 1961, Cheng 1985, Andersen and Foster 1992). The most unusual oviposition substrates reported are shells of living heteropods (*Atlanta* spp.), which usually live some tens to a few hundred meters below the sea surface (Seapy 1996). Male atlantids that had come to the surface to swarm were presumably encountered by gravid *Halobates* females, which laid eggs on them. Most of these objects bore only several or a few dozen eggs, but one piece of cork and the tail feathers of a dead common noddy, *Anous stolidus*, were estimated to bear many thousand eggs (Andersen and Polhemus 1976). None of these eggs could be identified to species except by inference from their geographic location in relation to distribution ranges of particular *Halobates* species.

Although we know a lot about the ecology of *Halobates* (Cheng 1985), we still have no idea how these insects find potential mates or suitable oviposition substates in the open ocean. Certain freshwater gerrids are known to use surface ripples for attracting mates (Wilcox and Spence 1986), but this has not been demonstrated in any marine species. A calm water surface would seem to be a prerequisite for ripple communication to function, but such conditions are only sporadic in the open sea. In the Caribbean, males of a related coastal veliid, *Trochopus plumbeus* (Uhler) (Heteroptera: Veliidae), were shown to use surface-dispersible semiochemicals to attract females (Cheng and Roussis 1998). Similar chemical attractants may perhaps be employed by *Halobates*.

The distribution range of each of the five pelagic *Halobates* species is well defined and may cover several thousand square kilometers of tropical ocean surface (Cheng 1989). Theoretical calculations based on oceanic diffusion have shown that mutual encounter rates between individuals, due to ocean turbulence alone, could be as high as 11^{-d} (Ikawa et al. 1998). Whether oceanic diffusion is sufficient to bring the sexes together or whether some other physical or chemical factors are involved has yet to be determined.

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This is the first report on mass oviposition, egg development, and a direct association between *Halobates* adults and an artificial oviposition substrate at the sea surface. The observations were carried out in the eastern tropical Pacific Ocean during two separate legs of a 3-yr survey (1998–2000) on marine mammals undertaken by the Southwest Fisheries Science Center in La Jolla, California.

MATERIALS AND METHODS

Oviposition and egg development were studied on board ship in October 1999 by L.C. *Halobates* females collected by dip net were allowed to lay eggs on moistened filter paper. Pieces of paper bearing about 20 eggs in total were placed in five separate covered containers, immersed in seawater, and kept as follows: 26–32°C (on ship deck), 28–30°C (ocean laboratory), 18–22°C (instrument laboratory), 10–15°C (cold-room), and 4–5°C (refrigerator). Egg development was observed daily until the eggs hatched, or at the conclusion of the expedition 20 days later.

On 31 October 2000, a plastic gallon (3.785-liter) milk jug was sighted by R.L.P., floating on the open ocean about 600 km off the coast of Mexico. As the ship passed within 50 m of the jug we could see that its surface was rendered almost black by a swarm of *Halobates.* As we circled and approached more closely, most of the insects skated away, but by using a long-handled dip net we succeeded in scooping up the jug and catching about 20% of the insects. The jug was found to be almost completely covered by eggs, which we scraped off and preserved in 95% ethanol, together with the insects, for subsequent examination in the laboratory. No fish, crabs, or other animals were found associated with the jug. Ten *Halobates* females were dissected to determine egg numbers in their oviducts.

Data on relative population densities and species composition of *Halobates* and other surface organisms were obtained from samples collected during the expedition by two operators using long-handled dip nets. We used two 500-W lamps suspended over the side of the ship at night to attract and illuminate the animals. Each net had an opening 75 cm in diameter, with a depth of 100 cm, and was mounted on a wooden handle 8 m long. We sampled for 1 hr each night, after sunset, while the ship was at station. Samples collected were then sorted into major animal taxa and preserved in 70% ethanol in separate vials. *Halobates* collected were counted, identified to species, and separated into adults by sexes, and development stages.

RESULTS AND OBSERVATIONS

When provided with moistened filter papers, female *Halobates sobrinus* were observed to lay eggs in rapid succession (1 to 2 sec^{-1}) in batches of various numbers (1, 1, 3, 3, 3, 4, 6, 8, 8, 8, 9, 10, 11, 13, 29). The eggs were glued firmly to the substrate, and most, if not all, of the eggs laid by a single female were oriented in the same direction. Newly laid eggs were translucent and creamy white or pale olive green. They turned orange by the third day and reddish orange by the fifth day. Bright red eyespots and dark brown outlines of developing appendages became clearly visible on day 5.

Temperature was found to be important in controlling rate of egg development. Eggs kept on deck and in the ocean laboratory (26–32°C) hatched in 8 to 10 days. None of the eggs kept at lower temperatures (below 24°C) hatched even after 20 days, when the experiment was terminated at the end of the cruise leg.

We caught 833 insects in association with the plastic jug. They were all identified as adults of a single species, *Halobates sobrinus* White. Females were somewhat more abundant (62%) than males. About 6% of the females had just mated, as indicated by the slightly parted halves of the gonocoxa (ventrite of first genital segment). In nonmated females the two halves are closely appressed.

The rectangular egg mass scraped from the jug measured about 4 by 6 cm. The eggs had been laid in a random fashion, without any obvious orientation, and were glued to the jug or to one another. They were oval, resembling miniature rice grains, and measured about 0.8 mm long by 0.4 mm wide. The total egg mass, some 15 egg layers thick,

TABLE 1

Halobates Species, Total Number of Adults and Nymphs, and Location of Dip Net Samples Taken during a 3-day Period within a 500-km Radius of the Egg-Bearing Gallon Jug (Sample no. 0)

Date 2000	Sample No.	*Halobates* Species	Total Insects	Total Adults	Total Nymphs	Latitude °N	Longitude °W
31 Oct. (Jug site)	0	*sobrinus*	833	833	0	10° 08′	94° 56′
30 Oct.	1	*sobrinus*	194	165	29	12° 47′	92° 12′
30 Oct.	2	*sobrinus*	124	117	7	11° 29′	93° 33′
		micans	12	12	0		
31 Oct.	3	*sobrinus*	109	97	22	10° 40′	94° 25′
		micans	3	3	0		
31 Oct.	4	*sobrinus*	134	123	11	09° 47′	95° 43′
01 Nov.	5	*sobrinus*	56	53	2	09° 00′	94° 56′
		micans	1	1	0		
01 Nov.	6	*sobrinus*	3	3	0	07° 58′	97° 34′
		micans	4	4	0		

was estimated to contain about 70,000 eggs. The eggs were all creamy white and judged to be at about the same developmental stage, no more than 3 days old. Of the 10 females collected with the jug that we dissected, 1 carried no eggs, and the other 9 contained from 6 to 20 eggs (6, 6, 8, 9, 10, 12, 12, 16, 20), with an average of 10 per female. We estimate that the jug must have been used by at least 7000 females.

Results of *Halobates* samples collected during a 3-day period and within a 500-km radius of the jug sighting are presented in Table 1. Two species were collected and identified: *H. sobrinus* and *H. micans*. Although both species co-occurred in four of the six samples collected, *H. sobrinus* was obviously the dominant species responsible for laying the eggs reported here.

During the entire 3-yr expedition (1998–2000) we collected only about 20 other items of floating debris (none exceeded 3 by 4 cm) with 2–30 *Halobates* eggs attached: pieces of styrofoam, plastic, mollusk shells, twigs, and feathers of seabirds. We also found a freshly dead brown booby (*Sula leucogaster*) with several hundred eggs attached to the tail feathers.

DISCUSSION

Egg development in *Halobates sobrinus* is evidently temperature dependent. All eggs kept above 25°C hatched within 10 days, but those kept below 22°C did not hatch even after 20 days. We were unable to determine whether eggs kept at lower temperatures would remain viable or eventually hatch because the experiment had to be terminated. In its natural habitat, *H. sobrinus* is found only in waters above 20°C and is abundant in areas where seawater temperatures range between 24 and 28°C (Cheng and Shulenberger 1980). We do not know how many eggs an adult female can produce in her lifetime. *Halobates* adults have been kept alive in the laboratory for over a month and may live for 2 months or more in their natural habitat (Cheng 1985). Although females have laid an average of only 10 eggs per session in our study, they can carry up to 30 eggs or more in their oviducts (Cheng 1985). It is likely that they can mature eggs in batches as needed or when food becomes available (Cheng and Frank 1993). *Halobates* appears to have adopted a strategy of slow growth and prolonged longevity to survive at the ocean surface (Ikawa et al. 1998).

Ocean-skaters have well-developed eyes and in daylight presumably locate their prey as well as mates and oviposition substrates by sight. However, because they are confined to a two-dimensional, featureless habitat at the sea-air interface, with their bodies raised only about 1 mm or so above the sea surface, it seems that it would be difficult for them to see potential mates amid ocean waves except when the sea is calm. A relatively large floating object, such as a gallon jug, could presumably be more easily seen from many meters away and could thus possibly serve as a "beacon" to guide wandering *Halobates* to aggregate, mate, and lay eggs. The fact that in one scoop we netted 833 insects (which we estimated to represent only 20% of the insects originally present) along with the jug suggests that the insects had been somehow attracted to the jug. In contrast, our dip net samples taken nearby on the same day yielded only 97 adult *H. sobrinus* in 2 hr of sampling (Table 1, sample 3). It is possible that females can retain mature eggs until suitable substrates or favorable environmental conditions for egg development are encountered. If the gallon jug was the only suitable substrate available, it would, out of necessity, be used by all gravid females in the surrounding area.

Whether there are potential evolutionary benefits or adaptive advantages for mass oviposition is unclear. Although aggregation of adults may help to improve their chances of finding a suitable mate, it may also facilitate their detection and predation by seabirds, which are the main predators of *Halobates* (Cheng and Harrison 1983). On the other hand, when a dense flotilla of the coastal species *Halobates robustus* (endemic to the Galápagos Islands) was approached by seabirds, agitated and accelerated activities of individuals were seen to confuse the predators, causing them to lose the prey (Treherne and Foster 1981). Such "schooling" or herding behavior for reducing predation pressure is well known for many organisms, including even an aquatic plant (Moore 2001). Thus mass oviposition and more-or-less synchronized hatching of eggs may increase the chances of survival of young *Halobates* nymphs.

Although *H. sobrinus* and *H. micans* cooccur in the eastern tropical Pacific Ocean, they may not share the same ecological niche, because the areas where each occurs in abundance are almost completely separate (Cheng and Shulenberger 1980). Specimens of both species were collected by dip net in the vicinity of the jug (Table 1), but adults of *H. micans* were found in rather low numbers (1–12) compared with *H. sobrinus* (up to 194), which was the only species associated with the egg-bearing jug. It is evident that *H. sobrinus* was very abundant in this area. The highest population density for this species reported in the eastern tropical Pacific was 10,000 km^{-2} (Cheng and Shulenberger 1980).

We do not know whether a mass oviposition on the scale we observed is exceptional. On the same day, within 10 km of the jug sighting, we passed another floating object of similar size, surrounded by another dark swarm of *Halobates*, but we were unable to stop the ship to sample it. During our 3-yr study period in the eastern tropical Pacific, we often saw large pieces of debris, but we never observed breeding swarms of *Halobates* associated with them. Although we collected *Halobates* at over 90% of all stations (150–200 per year) during our 3-yr survey in the eastern tropical Pacific, we found less than 20 pieces of egg-bearing flotsam, suggesting that there may be a shortage of suitable oviposition substrates in the open ocean. The fact that the gallon jug had been used by no less than 7000 females indicates that suitable substrates may indeed be rare and may be limiting *Halobates* reproduction. Thus, input of anthropogenic debris might promote increases in population of these enigmatic ocean insects.

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