*Marine Biology Research*, 2012; 8: 915–936

INVITED REVIEW

# Skaters of the seas – comparative ecology of nearshore and pelagic *Halobates* species (Hemiptera: Gerridae), with special reference to Japanese species

TERUMI IKAWA[1]*, HIDEHIKO OKABE[2] & LANNA CHENG[3]

[1]*The University of Morioka, Iwate, Japan,* [2]*National Institute of Advanced Industrial Science and Technology, Tsukuba, Japan, and* [3]*Scripps Institution of Oceanography, University of California San Diego, La Jolla, USA*

**Abstract**

The insects overwhelm all other organisms of the world in species numbers and diversity. However, there are relatively few insects that inhabit the sea. Most of them are confined to the intertidal zone, with only five species of sea skaters, genus *Halobates*, having been successful in colonizing the open ocean. We discuss the ecology of both coastal and pelagic *Halobates* and the closely related genus *Asclepios*, focusing on their distribution ranges and adaptive strategies to marine environments accompanied by brief discussions of their biology. Updated information on the known localities for three species of *Asclepios* and some 40 coastal species of *Halobates* are presented. Many species live in vulnerable coastal habitats exposed to environmental pollution and coastal development. As a case study we trace the historical changes in populations of three Japanese sea skaters, *Asclepios shiranui*, *Halobates matsumurai* and *H. japonicus*, all designated as endangered species. For oceanic *Halobates*, we present an updated distribution map along with global current systems and sea-surface temperatures, examine interactions between distribution ranges and physical factors at the air–sea interface and discuss spatio-temporal variations in populations of each species. Finally, we infer the life history strategy of oceanic *Halobates* through theoretical considerations.

**Key words:** *Marine insects,* Halobates, Asclepios*, endangered species, geographical distribution*

## Introduction

The insects arose during the Silurian–Ordovician period more than 420 Mya (Grimaldi 2009). They evolved over the next 200–300 Mya and succeeded in occupying all conceivable niches in the terrestrial world, surpassing all other organisms in species numbers and diversities. However, relatively few insects have been successful in colonizing the marine environment. Out of more than one million insect species known, only a few thousand belonging to about 20 orders are considered to be marine (Cheng 1976a, 2009; Cheng & Frank 1993). Most of them remained within the intertidal zone. Only five species of sea skaters, in the genus *Halobates* Eschscholtz, 1822, have completely left the shore and advanced into the open ocean (Cheng 1974, 1985). The genus *Halobates* is a member of the Gerridae (Hemiptera: Heteroptera) and contains 46 described species that spend their entire lives in a two-dimensional world at the sea–air interface.

Why there are so few insects in the sea and how only five species of *Halobates* were able to establish themselves in the high seas are intriguing questions that have aroused many discussions and speculations (e.g. Cheng 1976b; Andersen 1991; Ruxton & Humphries 2008). Throughout their evolutionary history the insects have evolved special adaptations for primarily an aerial or terrestrial existence, e.g. wings for long-distance dispersal and complete metamorphoses enabling larvae and adults to exploit different habitats thereby further extending available niches. In order to return to the sea they have to contend with various physical (turbulence, tidal movements, hydrostatic pressure change, depth), physiological (respiration, osmotic regulation) and biological (reproduction, food availability, competition, predation) factors (Cheng 1976b; Ward 1992).

---

*Correspondence: Terumi Ikawa, The University of Morioka, 808 Takizawa, Iwate, 020-0183 Japan. E-mail: trmi@pop02.odn.ne.jp

*Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark*

*(Accepted 6 June 2012; Published online 24 September 2012; Printed 4 October 2012)*

ISSN 1745-1000 print/ISSN 1745-1019 online
http://dx.doi.org/10.1080/17451000.2012.705848

Although various species have been able to overcome each of these obstacles, insects are still poorly represented in the marine environment. It is likely that insects, which evolved more recently, were unable to invade the oceanic realm where crustaceans had so successfully established themselves in the Cambrian some 100 Mya earlier (Cheng 1976b). It is interesting to note that pelagic *Halobates* are the only invertebrates that live entirely at the ocean surface, the only niche left for the insects to invade (Cheng 1985).

In this review, we discuss the ecology of *Halobates* and the closely related genus *Asclepios* Distant, 1915. We give special reference to their distributions and adaptive strategies to their marine habitats. We will treat their biology rather briefly, as this has been covered extensively in several previous reviews (e.g. Cheng 1973a, 1985; Andersen & Cheng 2004).

## Materials and methods

We examined the distributions of all coastal and oceanic *Halobates* species. For coastal species, we compiled known localities for each species and categorized them according to their distribution patterns. For oceanic species we produced an updated map integrated with relevant surface physical factors which may control their distribution ranges. We also evaluated the biology of coastal *Halobates* species in the context of a changing marine environment in which they are increasingly exposed to coastal development and environmental pollution. In this context we made special reference to three endangered Japanese sea skaters by tracing changes in their population and distribution for a period of several decades as examples of stresses affecting coastal species. Finally, we analysed the life-history strategies of oceanic *Halobates* species based on theoretical considerations.

## Coastal sea skaters

### *Overview*

The Gerridae, to which *Halobates* and *Asclepios* belong, are one of the largest families of semi-aquatic Heteroptera with over 700 described species, most of which live in freshwater habitats. At least 80 species belonging to 10 genera are known to live in various brackish or marine habitats (Cheng et al. 2012). A large body of information about *Halobates* and *Asclepios* is available in the literature, but hardly anything is known about the biology of any other species in the remaining eight genera.

Three species of *Asclepios* and some 40 species of *Halobates* are found in coastal areas (Andersen & Cheng 2004). Over 90% of the *Halobates* species live around tropical or subtropical island shores, four are found in temperate coastal waters in Japan, Korea and Australia, and two occur in freshwater rivers in Australia (Andersen & Weir 2004). Two subgenera of coastal *Halobates* can be recognized, *Hilliella* China, 1957 and *Halobates*, based on minor morphological differences (Andersen & Weir 1994). However, we will treat all the species as *Halobates* in this review.

### *Biology and life history*

Most coastal *Halobates* and *Asclepios* known are found in habitats associated with mangrove forests or emergent coastal vegetation, as they depend largely on insects that fall onto the sea surface for food. They catch and feed on floating insects with their piercing and sucking mouthparts. Cannibalism is not uncommon and adults have often been observed to feed on younger nymphs (Andersen & Cheng 2004). They are preyed upon by seabirds and occasionally by marine turtles or surface feeding fish (Cheng et al. 2010).

Hitherto, no attempt has been successful in rearing any sea skaters from eggs to adults in the laboratory. However, through short-term laboratory studies and size measurements of field samples we found that their life histories include the egg stage, five nymphal stages and the adult stage (Cheng & Maxfield 1980; Cheng 1982; Ikawa et al. unpublished data), common to the majority of semi-aquatic Gerridae studied (Cheng 1966). Sea skaters are wingless throughout their life cycle. Nymphs and adults are morphologically alike. Sexes are distinguishable from the fifth nymphal instar for the majority of species (Cheng 1973a), but from the fourth instar for *Halobates japonicus* Esaki, 1924 (Ikawa et al. 2008).

Year-round studies on life cycle were carried out more recently on *Halobates matsumurai* Esaki, 1924 (Figure 1A) and *Asclepios shiranui* (Esaki, 1924) in Japan (Ikawa et al. 2012). They have two or three generations a year and overwinter in the egg stage. In temperate regions of Japan where winter sea-surface temperature (SST) falls below 15°C, diapause would be a prerequisite. Many temperate gerrids overwinter as adults (Spence & Andersen 1992), but egg diapause is known for at least two freshwater gerrids, *Metrobates hesperius* Uhler, 1871 (Taylor 2009) and *Metrocoris histrio* White, 1883 (Ban et al. 1988). Coastal *Halobates* that live in tropical or subtropical waters probably breed all year round (Andersen & Cheng 2004).

In contrast to oceanic species which lay eggs on flotsam, coastal *Halobates* are known to lay eggs only on solid or attached substrates (Foster & Treherne 1986). The eggs of *H. matsumurai* are laid on sandstones along the shore (Figure 1B,C), mostly above mean seawater level (Ikawa et al. 2012). Sandstones on the shore might be the only permanent substrate available in the natural habitat of *H. matsumurai* where the area around the low water mark is mostly sandy. The eggs laid on the sandstones are exposed to solar radiation, wind and storms, and also to predation. As a consequence, the hard eggshell of *H. matsumurai* might have evolved as a special adaptation. Submature eggs in the oviducts are soft, but mature eggs are entirely covered by hard shells (Figure 1B,C; Ikawa et al. 2012). On the other hand, *Halobates fijiensis* Herring, 1958, the only other coastal *Halobates* for which oviposition in the field was known, laid its eggs mainly on sublittoral turtle grass or green algae (Foster & Treherne 1986). Oviposition occurred only during days of extreme low spring tide when these plants were exposed to the air, thus the eggs would remain submerged and protected from overheating and desiccation, and also from wave action.

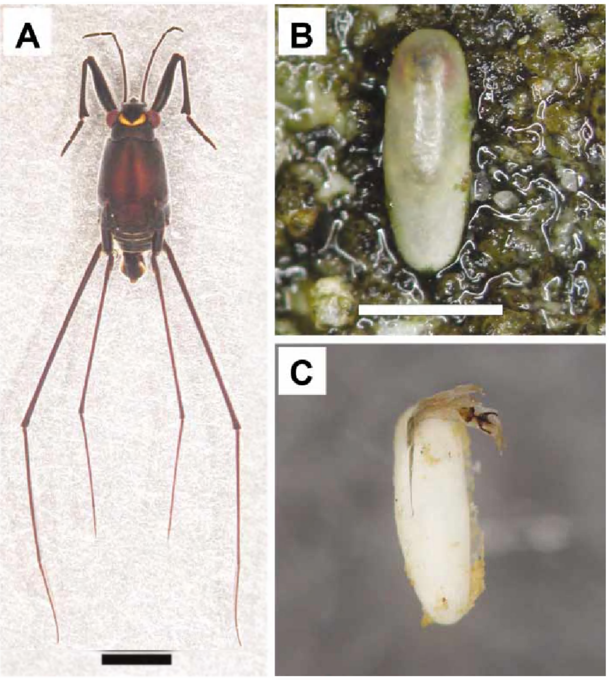


Figure 1. *Halobates matsumurai.* **A**: Adult male. Scale = 2 mm. (Photo by A. Chiba.) **B**: Developing egg showing thick egg shell with red eye-spots and black egg-burster barely showing through. Scale = 1 mm. (Photo by T. Ikawa.) **C**: Egg shell and egg-burster left behind after hatching. (Photo by T. Ikawa.)

### *Life along the seashore*

Adults and nymphs of coastal sea skaters live their entire lives along the shore. They generally remain under overhanging vegetation during mid-day in order to avoid damaging effects from solar radiation (Cheng et al. 1978). During cool autumn days in temperate Japan, they have been observed to skate in the sun (Yone et al. 2004). Adults and older nymphs may occasionally venture into open waters when the sea is calm while younger nymphs kept close to the shore (Cheng 1985).

One of the distinctive behavioural features of coastal sea skaters is the formation of aggregations in which they spend much of their time (Birch et al. 1979). Each aggregation usually consists of similar-sized individuals, presumably to avoid cannibalism (Ikawa 2009). Aggregations of the following species have been observed to maintain constant positions against currents and/or winds: *Halobates robustus* Barber, 1925 (Birch et al. 1979), *Halobates fijiensis* (Foster & Treherne 1986), *Halobates japonicus* (Ikawa et al. 2006, 2007a) and *Halobates mariannarum* Esaki, 1937 (Ikawa 2009) by using environmental cues such as edge of the mangrove (*H. robustus*) or shadows of vegetation on the sea surface (*H. japonicus*). These insects are constantly exposed to local currents, winds or tidal movements. Ebb tides, offshore winds or waves could wash them out to open waters where they cannot survive while onshore winds or shoreward flows may dash them against the bank or leave them stranded on the beach. Thus they need to adjust their positions constantly against changing physical forces. The size, position and composition of aggregations are known to vary according to the tidal cycle. During ebb tide aggregations were maintained close to the mangrove or to the shore and only a small number of individuals were seen in the open water. As the tide rose, aggregations became sparse and less dense, and a considerable number of individuals could be seen in the open water (Birch et al. 1979). These behaviours suggest that it is essential for coastal sea skaters to remain close to the shore especially during ebb tide when chances of being washed out to sea are greater.

### *Habitat preference*

Most coastal species appear to prefer seashores fringed with mangrove or other overhanging vegetation. A survey on the endemic *Halobates robustus* in the Galapagos Islands has found that it occurred around four major islands: Santa Cruz, Santa Maria, Fernandina and Isabella. Individuals were present in large numbers along both sandy and rocky shores fringed with mangroves but were completely absent from shores without any rocky outcrops or mangroves (Birch et al. 1979). Another survey carried out on *Halobates alluaudi* Bergroth, 1893 in the Seychelles found them to be present on Mahé, Praslin, La Digue and the small islet Curieuse, but absent from Cousin and the small islets of Sainte Anne and Cerf. They were found, sometimes in large flotillas consisting of both adults and nymphs, only when mangroves or overhanging trees were present, and were totally absent from islands with only fringing rocks (Cheng 1991). *Halobates matsumurai* and *Asclepios shiranui* differed from other coastal species by living in temperate regions in Japan where there are no mangroves. Surveys carried out around two islands in Japan showed that they occurred only in narrow, protected coves with overhanging vegetation but not along sandy shores exposed directly to the open sea (Ikawa 2010).

Several studies suggest differences in habitat preference among coastal species. In the coasts of New Guinea and adjacent islands, several species of coastal *Halobates* appeared to have different habitat preference (Polhemus & Polhemus 2006). Polhemus (1990) observed segregation of habitat among three coastal species in Aldabra Atoll. *Halobates poseidon* Herring, 1961 was mostly confined to the mangroves and never beyond 500 m off shore, *H. alluaudi* typically occurred inside the reef crest and almost never beyond 1000 m offshore, while *Halobates flaviventris* Eschscholtz, 1822 was seen mostly beyond the fore reef 500–1000 m offshore. *Halobates flaviventris* is more tolerant to exposed habitats than most coastal species (Cheng 1981; Polhemus 1990). Moreover, *H. flaviventris*, *Halobates princeps* White, 1883 and *Halobates maculatus* Schadow, 1922 have been collected in neuston samples at locations that are more than 150 km from shore (Cheng & Holdway 1983; Cheng et al. 1990). It is perhaps unsurprising, as this would be the necessary means for populations to disperse among islands, within archipelago or an ocean basin. In fact, this would be how pelagic *Halobates* species arose from nearshore ancestors as suggested by DNA analysis (Andersen et al. 2000). However, we are unaware whether any of the extant coastal species is able to survive and reproduce in the open ocean. Further studies on physiology, adaptation and molecular analyses would be necessary before we can determine whether any specimens caught at the high seas are able to adapt to life on the open ocean and on their way to becoming new species.

### *Distribution*

*Asclepios* is clearly an Old World genus, known only from East and Southeast Asia and nowhere else: the type species *Asclepios annandalei* is the most widely distributed species and occurs in India, Malaysia, Singapore, Sri Lanka and Thailand; *Asclepios apicalis* (Esaki, 1924) is found in Taiwan and Vietnam; and *Asclepios shiranui* is known from Japan, China and Korea.

The distribution of coastal *Halobates* is more complex. More than 70% of the known coastal *Halobates* species were recorded from the Indo-Pacific Australasian region, which is probably their centre of diversity. Only two species, *H. hawaiiensis* and *H. robustus*, were recorded from the Pacific Ocean east of the International date line and seven were recorded west of the Indian subcontinent (*H. alluaudi*; *H. formidabilis* Distant, 1910; *H. flaviventris*; *H hayanus* White, 1883; *H. melleus* Linnavuori, 1971; *H. poseidon*; *H. tethys* Herring, 1961). No coastal *Halobates* species is known from any islands in the Atlantic Ocean, although there is an abundance of suitable habitat. Instead, we find species of *Rhagovelia* Mayer, 1865 (*Trochopus* Carpenter, 1898), a member of the Veliidae, in such habitats. Some *Halobates* species are known only from their type localities, some are endemic to islands or island groups, while others are widely distributed and found in locations hundreds of kilometres apart. We do not have sufficient data at present to determine whether some species are truly endemic or restricted to certain islands or island groups. As and when more collections become available, their ranges may be extended. However, based on available data in the literature and various collection records we can make the following generalizations for coastal *Halobates*:

*Endemic.* Species that are possibly endemic and known only from specific islands or discrete oceanic island groups (Table I.1; Figure 2A). Most notable in this category is *Halobates robustus*, which is endemic to the Galapagos Islands (Birch et al. 1979). The remaining species are all known either from the type locality and a few additional locations nearby, or within an island group. Dispersal of these species is likely controlled by local currents, which may serve to restrict their distributions. It is possible that some of the species may have a wider distribution as more collections become available, as evidenced by *H. alluaudi*. This species was described from the Seychelles and was thought to be endemic to the island group (Cheng 1991). However, specimens were later collected during a survey of the remote Aldabra and Cosmoledo atolls, extending its range in the Indian Ocean (Polhemus & Polhemus 1991).

*Regional.* Species distributed along continental shores or among islands within an archipelago (Table I.2; Figure 3A,B). Within this group are several species that are distributed between Australia and Papua New Guinea: *Halobates darwini* Herring, 1961, *Halobates herringi* Polhemus & Cheng, 1982

Table I. Known distributions of coastal *Halobates* species in the Indo-Pacific (no coastal species known in the Atlantic) (QLD, Queensland; NSW, New South Wales; NT, Northern Territories; WA, Western Australia).

**1. Endemic – species that are found only in a restricted region or an oceanic island group (10 spp.)**
*Halobates acherontis* Polhemus, 1982* – Australia (NT).
*Halobates browni* Herring, 1961 – Solomon Is.
*Halobates bryani* Herring, 1961 – Fiji.
*Halobates fijiensis* Herring, 1958 – Fiji.
*Halobates kelleni* Herring, 1961 – Samoa Is. (American and Western).
*Halobates panope* Herring, 1961 – New Caledonia.
*Halobates robinsoni* Andersen & Weir, 2003* – Australia (WA).
*Halobates robustus* Barber, 1925 – Galapagos Is.
*Halobates salotae* Herring, 1961 – Tonga.
*Halobates tethys* Herring, 1961 – Mauritius.
**2. Regional – species that are found in an archipelago, or a sea-basin (16 spp.)**
*Halobates darwini* Herring, 1961 – Australia (WA, NT, QLD), Papua New Guinea.
*Halobates dianae* Zettel, 2001 – Philippines.
*Halobates elephanta* Andersen & Foster, 1992 – Andaman Sea, India (west coast).
*Halobates galatea* Herring, 1961 – Arabian Sea, India (west coast), Sri Lanka.
*Halobates herringi* Polhemus & Cheng, 1982 – Australia (NT, QLD). Indonesia (Irian Jaya).
*Halobates japonicus* Esaki, 1924** – Japan (Honshu, Kyushu, Shikoku, Ryukyu Is.)
*Halobates katherinae* Herring, 1958 – Loyalty Is., New Caledonia, Vanuatu.
*Halobates lannae* Andersen & Weir, 1994 – Australia (WA, NT), Papua New Guinea.
*Halobates matsumurai* Esaki, 1924** – China (Bohai), Japan (Honshu, Kyushu), Korea, Taiwan.
*Halobates melleus* Linnavuori, 1971 – Red Sea.
*Halobates mjobergi* Hale, 1925 – Australia (WA, NT, QLD), Papua New Guinea.
*Halobates murphyi* Polhemus & Polhemus, 1991 – Indonesia (Irian Jaya), Papua New Guinea, Bismarck Arch.
*Halobates nereis* Herring, 1961 – Caroline Is., Papua New Guinea.
*Halobates regalis* Carpenter, 1892 – Australia (WA, QLD).
*Halobates whiteleggei* Skuse, 1891**– Australia (QLD, NSW).
*Halobates zephyrus* Herring, 1961**– Australia (QLD, NSW).
**3. Widespread – species that are found in more than one archipelago or oceanic island group (13 spp.)**
*Halobates alluaudi* Bergroth, 1893 – Kenya, Mozambique, Comoros, Aldabra, Madagascar, Reunion I., Seychelles.
*Halobates calyptus* Herring, 1961 – Philippines, Indonesia (Sulawesi, Maluku Is., Lesser Sunda Is., Irian Jaya), Papua New Guinea, Bismarck Arch., Solomon Islands, Australia (NT).
*Halobates esakii* Miyamoto, 1967 – Thailand, Malaysia, Singapore, Brunei, Indonesia (Maluku Is.)
*Halobates formidabilis* Distant, 1910 – Maldives, India (west coast, east coast), Sri Lanka, Andaman Sea.
*Halobates hawaiiensis* Usinger, 1938 – Hawaiian Is., Kiribati (Christmas I.), Society Is., Tuamotus, Marquesas Is.
*Halobates maculatus* Schadow, 1922 – Indonesia (Sulawesi, Lesser Sunda Is.), Papua New Guinea, Bismarck Arch., Solomon Is.
*Halobates mariannarum* Esaki, 1937 – Mariana Is., Caroline Is., Marshall Is.
*Halobates peronis* Herring, 1961 – Philippines, Bismarck Arch., Solomon Is.
*Halobates poseidon* Herring, 1961 – Kenya, Tanzania, Mozambique, Aldabra, Madagascar.
*Halobates princeps* White, 1883 – Sri Lanka, Nicobar Is., Thailand, Malaysia, Singapore, Philippines, Caroline Is., Indonesia (Sulawesi, Java, Maluku Is., Lesser Sunda Is.), Australia (WA, NT, QLD), Solomon Is., Bismarck Arch., Vanuatu.
*Halobates proavus* White, 1883 – Nicobar Is., Thailand, Malaysia, Singapore, Philippines, Indonesia (Sulawesi, Java, Maluku Is.), Australia (WA, NT, QLD), Papua New Guinea, Solomon Is., Vanuatu.
*Halobates sexualis* Distant, 1903 – Sri Lanka, Malaysia.
*Halobates trynae* Herring, 1964 – Nicobar Is., Thailand, Malaysia, Singapore.
**4. Transoceanic – species that are found in both Pacific and Indian Oceans (2 spp.)**
*Halobates flaviventris* Eschscholtz, 1822 – Somalia, Tanzania, Kenya, Mozambique, South Africa, Aldabra, Comores, Madagascar, Seychelles, India (west coast, south India), Sri Lanka, Nicoar Is., Thailand, Christmas I., Vietnam, Caroline Is., Indonesia (Java, Maluku Is.), Papua New Guinea, Vanuatu.
*Halobates hayanus* White, 1883 – Red Sea, Nicoar Is., Thailand, Malaysia, Singapore, Vietnam, China (South China Sea), Philippines, Indonesia (Sulawesi, Java, Lesser Sunda Is., Maluku Is., Irian Jaya), Papua New Guinea, Australia (WA, NT, QLD).

* species found in freshwater river; ** species found in both subtropical and temperate climate zones

and *Halobates mjobergi* Hale, 1925. Two Australian species, *Halobates zephyrus* Herring, 1961 and *Halobates whiteleggi* Skuse, 1981, are known only from New South Wales and Queensland, while *Halobate elephanta* Andersen & Foster, 1992 and *Halobate galatea* Herring, 1961 are found around the coasts of the Indian subcontinent. The former has also been collected from the Andaman Sea. *Halobates nereis* Herring, 1961 is found in the West Caroline Islands.

*Widespread.* Species distributed within one ocean basin (Table I.3; Figure 4A,B). Most of the species in this group are found in the Pacific Ocean, only three occur in the Indian Ocean (*Halobates alluaudi*, *H. formidabilis* and *H. poseidon*).

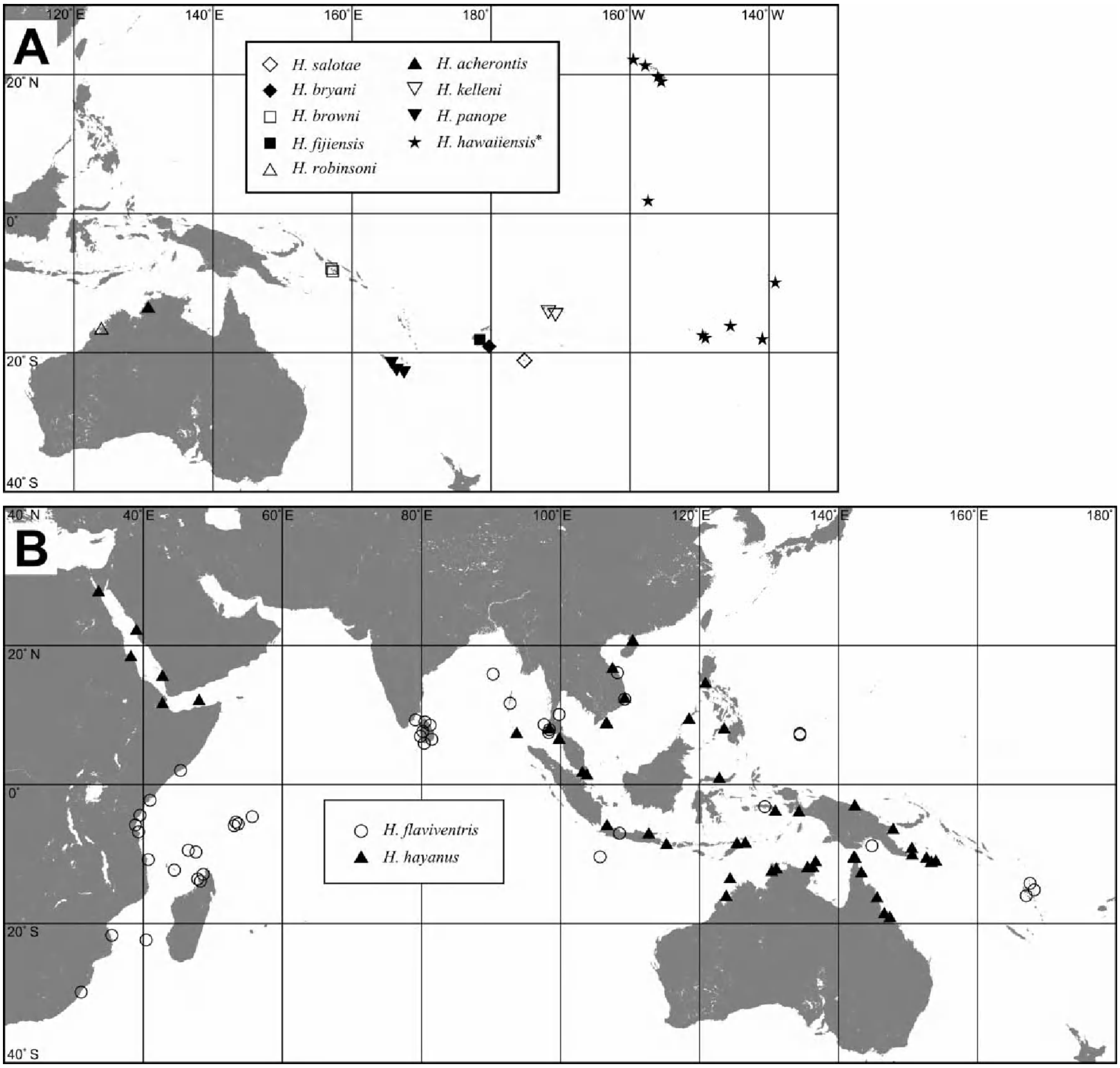


Figure 2. **A**: Distributions of endemic species; *Halobates acherontis*, *H. browni*, *H. bryani*, *H. fijiensis*, *H. kelleni*, *H. panope*, *H. robinsoni*, *H. salotae*; * for ease of map plotting *H. hawaiiensis* with widespread distribution is included in this map while the endemic *H. robustus* to the Galapagos Is. and *H. tethys* to Mauritius are not included. **B**: Distributions of transoceanic species; *H. flaviventris*, *H. hayanus*.

*Species with trans-oceanic distribution* (Table I.4; Figure 2B). Only two species, *Halobates flaviventris* and *H. hayanus*, belong to this group. They both occur in the Pacific as well as the Indian Oceans. *Halobates flaviventris* probably has the widest range among coastal sea skaters. The original description of this species was cast in doubt and the type specimens have not been located. It was redescribed from specimens collected from Palau by Herring (1961) and is now known from New Hebrides in the western South Pacific through Indonesia to the East African coast in the Indian Ocean (Andersen & Cheng 2004).

### *Endangered Japanese species*

Most sea skaters live in coastal areas and many are now exposed to increasing development and pollution. Unfortunately, we are unable to trace population changes associated with habitat alterations due to lack of long-term studies. The only exceptions are three species in Japan on which we have considerable collection records by professional and amateur entomologists over the years. Furthermore, Japan is the only country in the world that has designated any sea skater as an endangered species.

*Halobates matsumurai*, *Halobates japonicus* and *Asclepios shiranui* are the only known coastal sea skaters in Japan. They were all described by Esaki (1924) and were found along the western or southwestern coasts of Japan in the early days. Following rapid economic growth and industrialization after World War II (~1952–1972) much of their habitats were lost and few specimens were seen in the wild. As a result, *A. shiranui* was designated as an endangered species in the first Red Data Book

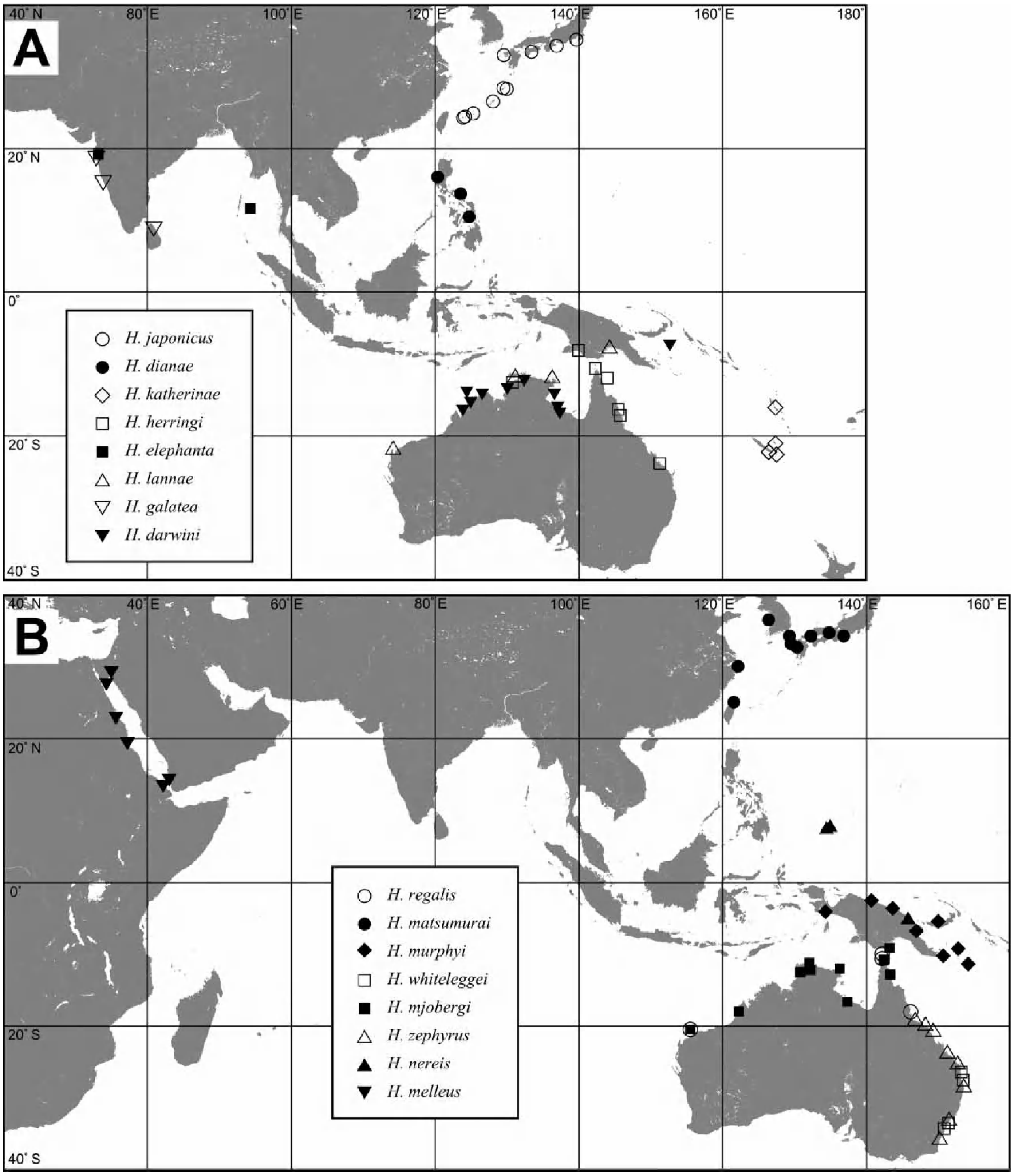


Figure 3. Distributions of regional species. **A**: *Halobates darwini, H. dianae, H. elephanta, H. galatea, H. herringi, H. japonicus, H. katherinae, H. lannae*. **B**: *H. matsumurai, H. melleus, H. mjobergi, H. murphyi, H. nereis, H. regalis, H. whiteleggei, H. zephyrus*.

released by the Japanese government in 1991 (Environment Agency 1991). All three species were later designated as endangered by the Japanese government and/or several local governments (Association of Wildlife Research & EnVision 2007; Ministry of the Environment 2007).

*Asclepios shiranui* was found in waterways of salt farms, estuarine waters and small coves along the westernmost coast of Honshu and the north coast of Kyushu (Figure 5A) until the 1950s (Miyamoto 1961; Hayashi & Miyamoto 2003). Then, its populations began to decline. It became rare and was thought to be extinct. It was rediscovered in the north coast of Kyushu in 1996 (Hayashi & Miyamoto 1997) but was totally extinct in Honshu. Its present distribution is limited to northern Kyushu (Figure 5A).

Until the 1950s, *H. matsumurai* was found in inner bays along the coast of northern Kyushu and western Honshu (Esaki 1924; Miyamoto 1961; Figure 5B). It was rarely seen later and thought to be extinct. It was rediscovered recently in several locations in

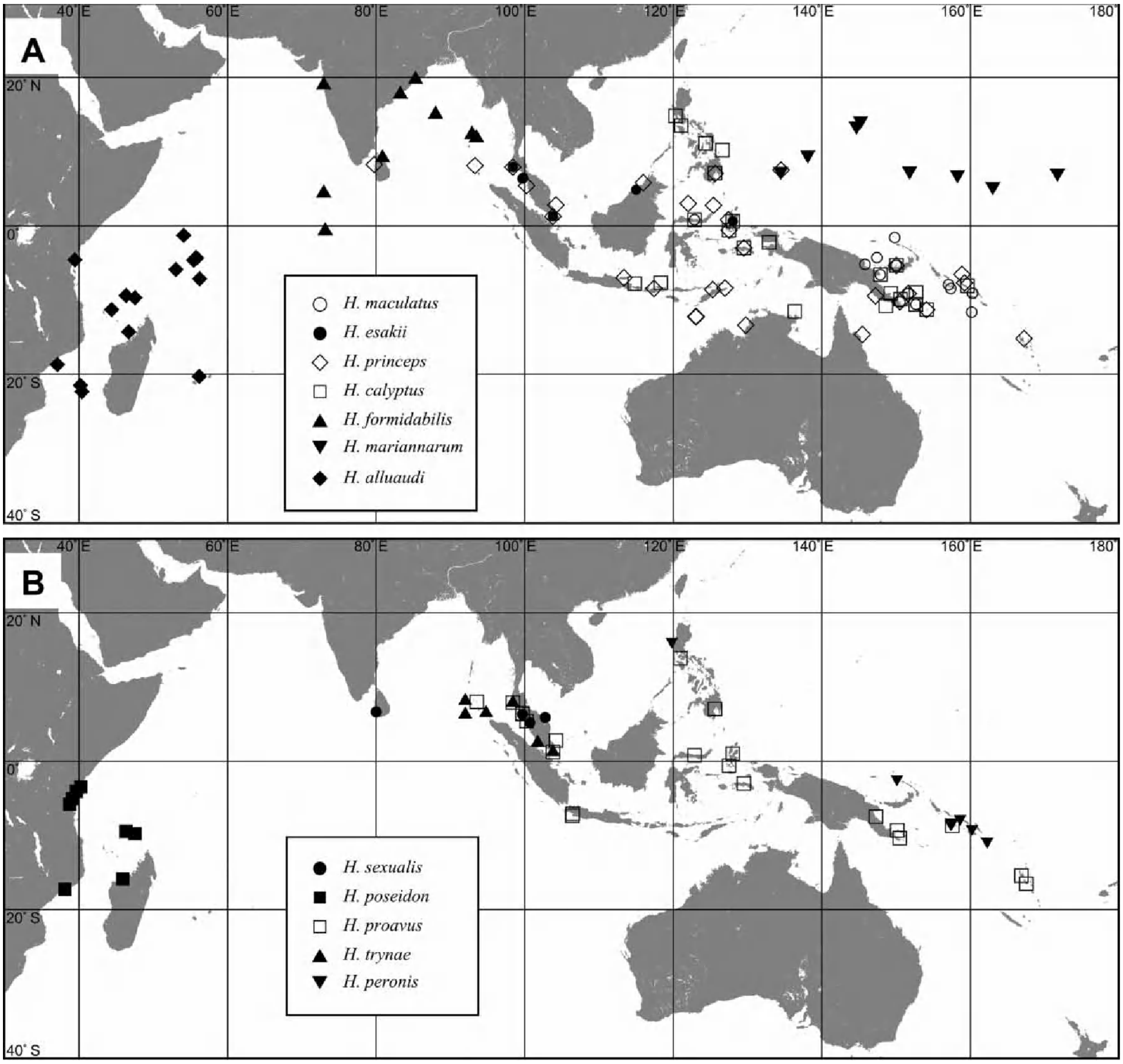


Figure 4. Distributions of widespread species. **A**: *Halobates alluaudi, H. calyptus, H. esakii, H. formidabilis, H. maculatus, H. mariannarum, H. princeps*. **B**: *H. peronis, H. poseidon, H. proavus, H. sexualis, H. trynae*.

Kyushu and Honshu (Miyamoto & Hayashi 1996; Hayashi & Miyamoto 2003).

Japan's post-war high economic growth began in the 1950s. The nationwide rapid industrialization and large-scale coastal development resulted in seawater pollution which was recognized as the main cause of population decline for many species of marine animals and plants, including *A. shiranui* and *H. matsumurai*. Most salt farms along the coast had been abolished due to changes in salt manufacturing processes. It is suspected that the loss or deterioration of waterways of salt farms could also be responsible for the lack of available habitats for *A. shiranui* (Hayashi & Miyamoto 2003).

In the north coast of Kyushu, *A. shiranui* and *H. matsumurai* are often found in the same habitats (Kawachino 2001; Hayashi & Miyamoto 2003). The locations where they occur in different regions share strikingly similar geographic features. They are both found in bays or along jagged coasts of island-studded seas. Even in such areas, they occur only in deep inner coves or bays and not in shores directly exposed to the open sea (Ikawa 2010).

*Halobates japonicus* is designated as endangered by two local governments (Association of Wildlife Research & EnVision 2007). Changes in its distribution range are rather ambiguous compared to the other two species and little is known about its habitat preference. It was found along the Pacific coast of Honshu, Shikoku and Kyushu, and in the Nansei Islands (Esaki 1924; Miyamoto 1961; Figure 5C). There were no collections from any locations along the Pacific coast for decades but a few records exist for the Nansei Islands after 1960 (Takara & Azuma 1972; Hayashi & Miyamoto 2005), probably because these remote islands were not as affected by post-war large-scale industrialization as mainland Japan. Recently, large populations of this species

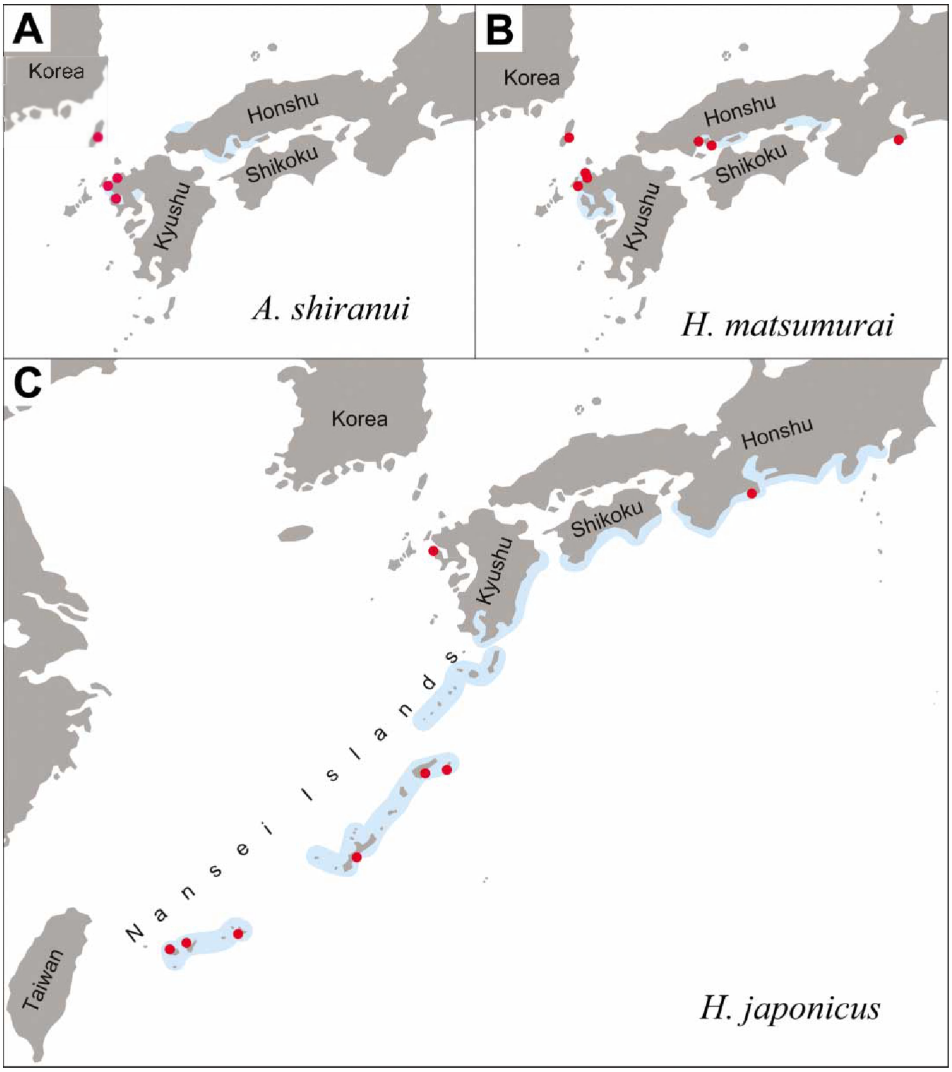


Figure 5. Historical range (blue) and presently known locations (red dots) of Japanese sea skaters. **A**: *Asclepios shiranui*. **B**: *Halobates matsumurai*. **C**: *Halobates japonicus*.

were found in a mangrove-fringed bay in Ishigaki, a remote subtropical island where a series of studies have been carried out (e.g. Ikawa et al. 2008). In Okinawa, the much-populated main island of the Nansei Islands, *H. japonicus* seemed rather rare (M. Moriguchi, personal communication). A small population was observed recently around mangroves in the mouth of Oura River, which is also one of the few remaining habitats in Japan for several endangered species such as dugong, blue coral, etc. (T. Ikawa, personal observation).

Most of the present habitats of the three Japanese sea skaters are in areas conserved by the government as National Parks, Quasi-National Parks, or Important Wetland 500. Starting in the 1930s, the Japanese government designated National Parks or Quasi-National Parks which must have served to preserve habitats for these insects from coastal developments and pollution. 'Important Wetland 500' was designated in 2001 in response to the resolution of the RAMSAR Convention. One wetland in Kyushu was included in 'Important Wetland 500' because the endangered *A. shiranui* and *H. matsumurai* occur there.

Among the three species, the habitat of *A. shiranui* is most restricted, being found only in the northern coast of Kyushu (Figure 5A). *Halobates matsumurai* is found along the coast of northern Kyushu and western Honshu while the range of *H. japonicus* extends for some 1500 km from the Pacific coast of Honshu to the Nansei Islands. Obviously, they can survive only in quiet waters in protected coves, inner bays or jagged shores without coastal development or pollution (Ikawa et al. 2006; Ikawa 2010). Their present distributions are quite restricted compared to that in the 1950s or earlier.

### *Sea skaters and vulnerable marine environments*

Field studies carried out on many tropical islands over the last 30 years (Caroline and Marshall Islands, Cook, Enewetak, Heron, Fiji, Guam, Hawaii, Hong Kong, Magnetic, Moorea, Singapore, Solomons, Tonga, etc.) have confirmed that survival of the majority of coastal *Halobates* species is heavily dependent upon the existence of mangroves or emergent vegetation. Although most of the locations have not been revisited, among those that were visited more recently a considerable decrease or total absence of sea-skater populations were noted (L. Cheng, unpublished). According to the *World Mangrove Atlas* (Spalding et al. 1997), mangrove habitats are largely confined between 30°N or 30°S of the equator with notable extensions in Bermuda (32°20′N), Japan (31°22′N), Australia (38°45′S), New Zealand (38°05′S) and the east coast of South Africa (32°59′S). Destruction of mangrove habitats for industrial or agricultural development has accelerated in many parts of the world in recent years. Although a number of mangrove habitats have been set aside as protected areas, destruction continues in many developing countries where most of the mangrove areas are located. This would be detrimental to the survival of coastal sea skaters. It is essential for us to understand their biology and ecology in order to develop conservation measures to preserve natural habitats for the survival of these unique marine insects before it is too late.

## Oceanic species

### *Overview*

Five species of ocean skaters, *Halobates micans* Eschscholtz, 1822, *Halobates sericeus* Eschscholtz, 1822, *Halobates germanus* White, 1883, *Halobates sobrinus* White, 1883 and *Halobates splendens* Witlaczil, 1886, occupy vast areas of tropical and subtropical oceans (Herring 1961; Scheltema 1968; Cheng 1989; Andersen & Cheng 2004; Figure 6A). Morphological and molecular phylogenetic studies showed that the oceanic way of life has evolved at least twice from coastal life (Andersen 1991; Andersen et al. 2000; Damgaard et al. 2000). Although pelagic *Halobates* share a number of features in common with coastal species, e.g. being completely wingless and confined to the sea–air interface, going through five nymphal instars before reaching the adult stage and probably reproducing throughout the year (Cheng 1973b; Spence & Andersen 1994), they differ from coastal species in several major features which are specifically adapted for their pelagic existence. The most important is undoubtedly their ability to prevent UV damage. Living in the open ocean where no shade can be found, they are exposed to solar radiation throughout the day. Pelagic *Halobates* has a UV-absorbent layer in their cuticle which excludes practically all UV in the biologically damaging wavelengths between 260 and 320 nm (Cheng et al. 1978). Their cuticles were found to contain substantial amounts of mycosporin-like amino acids which protect them from UV damage (D. Karentz & L. Cheng, unpublished data).

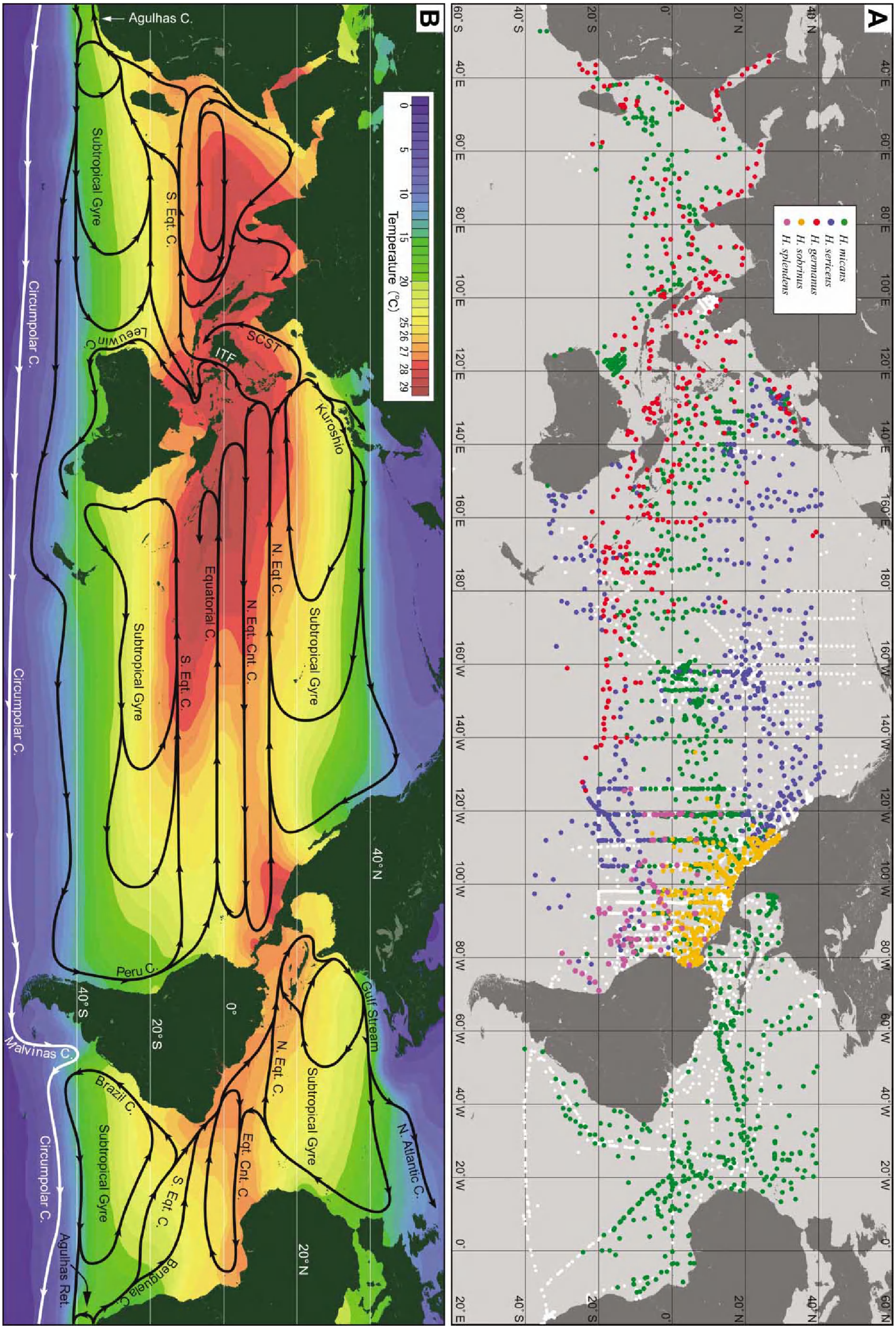
They also differ from coastal species in their feeding habits. Their main prey are small zooplankton organisms trapped at the sea surface, but they may also feed on terrestrial or migratory insects that fall on the sea (Cheng & Birch 1977), whereas coastal species depend entirely on terrestrial insects for food. Unlike coastal species, they lay eggs on floating materials (Cheng 1973a) such as sea shells, bird feathers, tar lumps, nylon ropes, bits of plastics, etc. (Figure 7B,C), because solid, attached substrates are unavailable in the ocean. It is interesting to note that the freshwater gerrid *Metrobates hesperius* has been observed to lay eggs on floating leaves which may serve as a means of dispersal (Taylor 2009).

Compared to coastal species, bodies of nymphs and adults of oceanic *Halobates* are more rounded and the legs are shorter, presumably an adaptation for living on the ocean surface where winds and waves are frequently encountered. Their bodies are covered by a layer of microtrichia which traps air and prevents them from drowning (Cheng 1973c). Hairs on their mid-femur and tibia are also longer and much denser, presumably making them more efficient for long-distance skating on the rough seas (Miyamoto & Senta 1960).

### *Distribution ranges and oceanic pathways*

Ocean skaters are found roughly between latitudes 40°N and 40°S of all three major oceans (Figure 6A), an area larger than the total land area of the world. Thus, they have the widest distribution range among the Insecta. In this section we examine how

Figure 6. **A**: Distributions of oceanic *Halobates*, showing negative sampling stations (white dots) as well as positive ones (*H. micans*, green dots; *H. sericeus*, blue dots; *H. germanus*, red dots; *H. sobrinus*, orange dots; *H. splendens*, purple dots). **B**: Generalized global current system superimposed on annual mean sea-surface temperature. Abbreviations are used for Agulhas Retroflection (Agulhas Ret.), Equatorial Counter Current (Eqt. Cnt. C.), Indonesia Throughflow (ITF), North Equatorial Counter Current (N. Eqt. Cnt. C.), North Equatorial Current (N. Eqt. C.), South China Sea Throughflow (SCST), South Equatorial Current (S. Eqt. C.).


A
● *H. micans*
● *H. sericeus*
● *H. germanus*
● *H. sobrinus*
● *H. splendens*
40° E
60° E
80° E
100° E
120° E
140° E
160° E
180°
160° W
140° W
120° W
100° W
80° W
60° W
40° W
20° W
0°
20° E
60° N
40° N
20° N
0°
20° S
40° S
60° S
B
Temperature (°C)
0
5
10
15
20
25
26
27
28
29
Agulhas C.
Subtropical Gyre
S. Eqt. C.
Leeuwin C.
ITF
SCST
Kuroshio
Circumpolar C.
N. Eqt. C.
Equatorial C.
N. Eqt. Cnt. C.
Subtropical Gyre
S. Eqt. C.
Subtropical Gyre
Circumpolar C.
Peru C.
Gulf Stream
Malvinas C.
N. Eqt. C.
Subtropical Gyre
Brazil C.
Subtropical Gyre
Circumpolar C.
N. Atlantic C.
Eqt. Cnt. C.
S. Eqt. C.
Benguela C.
Agulhas Ret.
40° N
20° N
0°
20° S
40° S

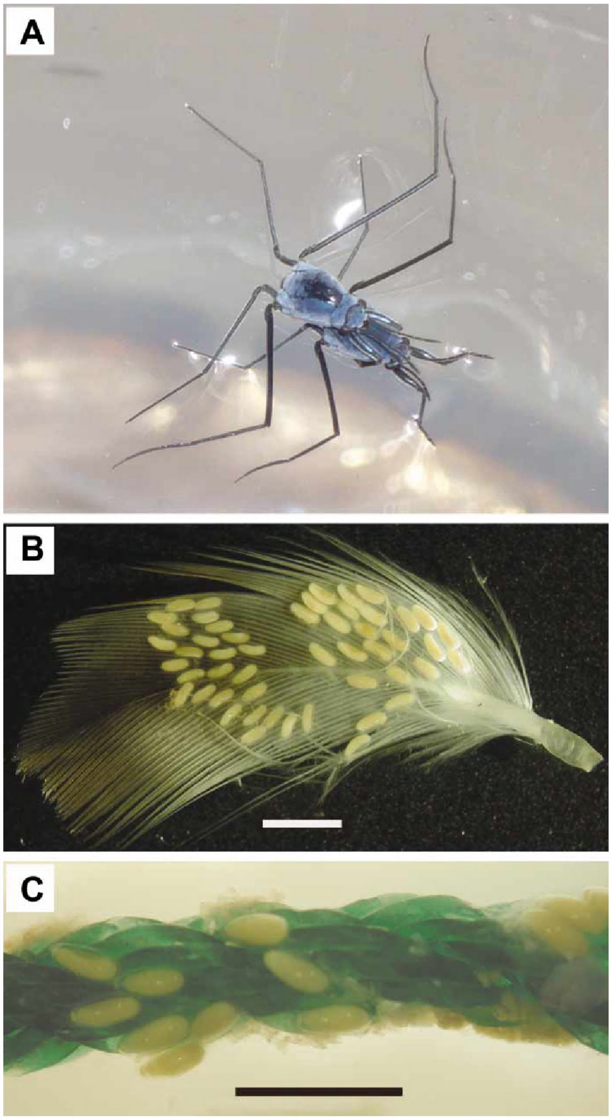


Figure 7. **A**: Mating pair of *Halobates micans*. (Photo by M. Sasaki) **B**: Eggs of oceanic *Halobates* on seabird feather. Scale = 2 mm. (Photo by S. Koyachi) **C**: Eggs of oceanic *Halobates* on nylon rope. Scale = 2 mm. (Photo by S. Koyachi)

the range of each species may be influenced by physical factors such as SST, ocean circulation and prevailing winds, and how far and where *Halobates* could skate with or against such forces. A newly constructed map (Figure 6A) is presented and potential oceanic pathways for their long-range dispersal are discussed.

Although ocean skaters are known to occupy tremendously wide areas of the major oceans, certain regions are seldom surveyed or even visited by oceanographic cruises. Thus, there is always some uncertainty in determining limits of their distribution ranges. To recognize the true distribution ranges, we need to have negative as well as positive surface tow records covering the entire World Ocean, which is, of course, impossible. We were able to obtain considerable data sets from all available sources for the central and eastern North Pacific, but data are largely lacking from many other regions, especially the central South Pacific and central South Indian Oceans. In our map we have included both positive and negative tow records from all available data sets, whereas only positive tows were used for compiling previous distribution maps (Cheng 1974, 1989; Andersen & Cheng 2004).

### *Distribution of* Halobates micans

*Halobates micans* (Figure 7A) is the only cosmopolitan species living in all three major oceans and is also the only species found in the Atlantic Ocean. It occupies the warm equatorial region, but has different latitudinal ranges in each ocean basin. In the North Atlantic it has been found at ca. 40°N, the highest latitude recorded. However, this may not be its northern limit, because we do not have data beyond 40°N (Figure 6A). The Gulf Stream which branches at about 38°30′N and 44°W (Mann 1967) could possibly carry individuals further north in its northward branch, the North Atlantic Current (Figure 6B). Ring-like eddies shed from the Gulf Stream (Saunders 1971) could also facilitate further dispersal of *H. micans* northwards in warm core rings or southwards into the Sargasso Sea in cold core rings. Thus, the Gulf Stream, combined with other surface currents would be able to transport *H. micans* within the North Atlantic Subtropical Gyre.

Within the equatorial Atlantic *H. micans* could be dispersed westward by the Equatorial Current and the trade winds or eastward by the Equatorial Counter Current. However, there is a conspicuous gap off the northeastern coast of Brazil (ca. 0–10°N and 30–60°W) where it is absent, as evidenced by many negative tows (Figure 6A). This region is characterized by frequently observed patches of low-salinity surface waters (Hu et al. 2004) resulting from freshwater discharged from the Amazon and Orinoco Rivers which have the largest rate of discharge in the World (Berner & Berner 1987).

In the South Atlantic, especially south of 20°S, our data are insufficient for determining conclusive boundaries. It is likely that *H. micans* extends to ca. 40°S only along the South American coast. This extension could be attributed to the west boundary Brazil Current that flows along the coast of Brazil (Figure 6B). Cool water carried along the coast of Argentina by the Malvinas Current northward until it reaches the Brazil Current could act as a barrier for dispersal of *H. micans* further south.

In the central and eastern South Atlantic *H. micans* is probably limited to ca. 20°S. In fact, none was caught in 68 tows along a cruise track from Rio de la Plata (38°S) to Cape Town (34°S) (Cheng & Shultz-Baldes 1981). The SST in the eastern South Atlantic is lower compared to the western South Atlantic (Figure 6B), owing to the Benguela Current which carries cold water around the Cape of Good Hope and the west African coast. Combined with strong northward winds (Hellerman & Rosenstein 1983; Josey et al. 2002) it would be difficult for *H. micans* to penetrate southward. Thus, in the South Atlantic it is confined mainly within the South Equatorial and Equatorial Counter Currents with an extension along the Brazil Current.

In the Pacific Ocean *H. micans* is largely confined within a zone between latitudes 15°N and 15°S, bounded by the North and South Equatorial and the Equatorial Counter Currents (Figure 6A). This is much narrower than that in the Atlantic. We do not think SST alone is responsible for this narrower distribution as there were no notable differences between the two areas (Figure 6B). Its absence is likely due to the presence of another species, *H. sericeus*, in higher latitudes. Within this zone, the North and South Equatorial and Equatorial Counter Currents as well as trade winds could facilitate trans-Pacific migration of *H. micans*. Beyond this zone its range extends northwards to ca. 25°N along the North American coast, and to ca. 30°N along the Japanese coast. The latter was attributed to the strong Kuroshio Current that flows northeastward from the Philippines.

In the Indian Ocean our data are limited, especially from the South Indian Ocean and the Arabian Sea. *Halobates micans* is mainly found between 8°N and 10°S, the narrowest zone among three oceans. SST is unlikely to form any barrier because it is quite high in most parts of the Indian Ocean (Figure 6B). The Agulhas Current could be responsible for the southern range extension of *H. micans* along the African coast and the Leuween Current for its presence along the Australian coast (Figure 6A).

It should be noted that around the Malay Archipelago, collections of *H. micans* are quite limited compared to *Halobates germanus*. In the Sulu, Celebes and Java Seas and the Bay of Thailand only *H. germanus* has been collected (Figure 6A). In the Banda Sea both species were caught but most of the specimens were *H. germanus* (Cheng et al. 1990).

### *Distribution of* Halobates germanus

*Halobates germanus* occurs in the Indian and the western and central Pacific Oceans (Figure 6A). In the Indian Ocean, it is found in the Arabian Sea, the Bay of Bengal, and Central and South Indian Ocean as far as 10°S. The southern extension along the African coast could be attributed to the Agulhas Current, as is also the case for *Halobates micans*. It also occurs in the Red Sea, the Gulfs of Aden, Oman and the Andaman Sea where *H. micans* has never or rarely been caught. In the Pacific Ocean, *H. germanus* is found off the coasts of Melanesia, Micronesia and Polynesia but not the Hawaiian Islands. It is absent east of 125°W as evidenced by numerous negative data. This longitude is also the easternmost location of Polynesia, where strong westward winds blow (Hellerman & Rosenstein 1983; Josey et al. 2002). Strong winds and lack of island coasts might prevent *H. germanus* from invading the eastern Pacific. In contrast to other species it appears to prefer areas close to islands or margins of continents. It was also frequently collected in many areas of marginal seas and straits in the Malay Archipelago, suggesting its stronger affinity to coastal environments. Moreover, several adults were collected, skating among aggregations of the coastal *Halobates japonicus* in an inner bay of Nansei Islands (Ikawa et al. 2008).

### *Distribution of* Halobates sericeus

*Halobates sericeus* is only found in the Pacific Ocean where it has an amphi-tropical distribution with populations living north (10–40°N) and south (10–40°S) of the equatorial zone occupied by *H. micans* (Figure 6A). As a considerably wide area (20–40°S and 120–170°W) in the South Pacific has rarely been surveyed, we could not determine whether it is really absent in this area. It appears to live within the subtropical gyres in the North and South Pacific Ocean and can thus be expected to circulate widely with currents in the gyres.

### *Distributions of* Halobates sobrinus *and* Halobates splendens

*Halobates sobrinus* and *H. splendens* have relatively narrow distribution ranges confined to the eastern tropical Pacific Ocean (Figure 6A). *Halobates sobrinus* occupies an area between ca. 5°S–30°N and ca. 120–80°W off the coast of Mexico and Central America within the Intertropical Convergence Zone where the water is quite warm (Figure 6B) and the wind stress is very low (Hellerman & Rosenstein 1983; Josey et al. 2002).

*Halobates splendens* occurs off the coast of Central and South America, between ca. 30°S–10°N and ca. 120–70°W (Figure 6A). Off the Peru coast, SST and salinity are lower during upwelling. This species must have adapted to this annual fluctuations in temperature and salinity. There are no distinct recursive winds or currents in this region (Figure 6B; Hellerman & Rosenstein 1983; Josey et al.

Table II. Average densities of *Halobates* in various oceanic regions.

| Species | Region | Average density (km$^{-2}$) | Reference |
|---|---|---|---|
| *Halobates micans* | Eastern Atlantic Ocean | $4.3 \times 10^4$–$2.1 \times 10^5$ | Cheng & Schulz-Baldes (1981) |
| | Caribbean Sea | $2.4 \times 10^3$–$7.0 \times 10^3$ | Stoner & Humphris (1985) |
| | Gulf of Mexico | $3.9 \times 10^4$ | Cheng & Wormuth (1992) |
| | Eastern Pacific Ocean | $5.9 \times 10^3$ | Cheng & Shulenberger (1980) |
| | Western Pacific Ocean (west of Mariana Islands) | $3.0 \times 10^3$ | Ikawa et al. (2002) |
| | Western Pacific Ocean (off the Japanese coast) | $1.1 \times 10^4$ | Ikawa et al. (2004) |
| | East China Sea | $7.2 \times 10^3$ | Ikawa et al. (2004) |
| | Banda Sea | $2.0 \times 10^3$ | Cheng et al. (1990) |
| | Indian Ocean (off the Australian coast) | $1.4 \times 10^4$–$2.8 \times 10^4$ | Ikawa et al. (2007b) |
| *Halobates sericeus* | Eastern Pacific Ocean | $1.2 \times 10^3$ | Cheng & Shulenberger (1980) |
| | Western Pacific Ocean (west of Mariana Islands) | $7.0 \times 10^3$ | Ikawa et al. (2002) |
| | Western Pacific Ocean (off the Japanese coast) | $2.4 \times 10^2$, $2.4 \times 10^3$ | Ikawa et al. (2004) |
| | East China Sea | $1.5 \times 10^4$ | Ikawa et al. (2004) |
| *Halobates germanus* | Western Pacific Ocean (off the Japanese coast) | $1.2 \times 10^3$, $4.1 \times 10^3$ | Ikawa et al. (2004) |
| | East China Sea | $9.9 \times 10^3$, $1.2 \times 10^4$ | Ikawa et al. (2004) |
| | Banda Sea | $3.1 \times 10^3$, $1.5 \times 10^4$ | Cheng et al. (1990) |
| *Halobates sobrinus* | Eastern Pacific Ocean | $2.6 \times 10^3$ | Cheng & Shulenberger (1980) |
| *Halobates splendens* | Eastern Pacific Ocean | $8.2 \times 10$ | Cheng & Shulenberger (1980) |

2002). Consequently, *H. splendens* is continuously exposed to northwestward winds and currents. This might account for its low density compared to the other three species (*H. micans*, *H. sericeus* and *H. sobrinus*) which can be found in the same area (Cheng & Shulenberger 1980; Table II).

### *Trans-oceanic and intra-oceanic migration pathways*

There exist three possible trans-oceanic pathways that would allow gene flow among populations of *Halobates micans* and/or of *Halobates germanus*. First, *H. micans* could be transported by the Agulhas Current from the Indian Ocean to the South Atlantic Ocean. This current flows southward along the African coast and turns to the east from the tip of South Africa, forming the Agulhas Retroflection (Figure 6B). Rings shed from the latter are injected into the South Atlantic Ocean (Gordon 2003) and may carry *H. micans* with them. Second, the poleward Leeuwin Current (Cresswell & Golding 1980) which flows along the west coast of Australia and continues along its south coast to the Tasman Sea (Ridgway & Condie 2004) could be a carrier from the Indian Ocean to the Pacific Ocean (Figure 6B). *Halobates micans* collected off the west Australian coast down to ca. 35°S might suggest this possibility. Third, *H. micans* and *H. germanus* could migrate from the western Pacific Ocean via the Indonesia Throughflow (Lukas et al. 1996) or the South China Sea Throughflow (Qu et al. 2005) to the Indian Ocean (Figure 6B). In fact, *H. germanus* is frequently found in many areas of marginal seas and straits in the Malay Archipelago (Figure 6A). On the other hand, collection records suggest rather limited migration of *H. micans* from the western Pacific into the Indian Ocean (Figure 6A). There seems to be no direct pathway between the Atlantic and the Pacific Oceans because two cold currents, the Peru and the Malvinas that flow northwards along the western and eastern South America, would prevent them from migrating southward (Figure 6B). In addition, the Drake Passage would be too cold and too rough for *Halobates* to skate through.

In spite of the existence of potential trans-oceanic pathways, results of DNA analysis suggest limited gene flow among populations of *H. micans* or *H. germanus* from different oceans (Andersen et al. 2000). Transit through the three potential trans-oceanic pathways would not have been frequent enough to achieve complete mixing of different populations. However, these pathways could certainly carry ocean skaters to some extent, allowing gene flow and preventing allopatric speciation.

We do not know to what extent the northern and southern populations of *H. sericeus* are able to cross the equatorial zone occupied by *H. micans*. Results from molecular analyses suggest very limited gene flow between the two populations (Andersen 2000; Leo et al. 2012). However, specimens collected close to the equator in the central and eastern Pacific Ocean (about 165–145°W, 130°W, 110°W, 80°W in Figure 6A) suggest that it could penetrate into the habitat of *H. micans*. In fact, along the northern and southern ranges of *H. sericeus*, prevailing trade winds are known to converge towards the equator, thus able to carry the insects across. Cheng (1997) suggested that trans-equatorial migration was possible during seasonal weakening of zonal currents. Therefore, if migration is limited between northern and southern populations, there must exist some other factors to keep the two populations apart. Higher SST in the equatorial zone may not be a barrier because *H. sericeus* appears to have a high temperature tolerance (Ikawa et al. 2002). Lower salinity might be a possibility because in general *H. sericeus* is found in saltier waters in subtropical gyres and has been found to shift its distribution towards the equator following the salinity front (Ikawa et al. 2002). Biological competition with *H. micans* is another possibility (Cheng 1985).

### *Do distribution ranges overlap?*

The distribution map (Figure 6A) presented here is compiled from various collection records accumulated over many years. We found large areas of overlap in the following three regions: (1) eastern tropical Pacific Ocean (4 species; *Halobates micans*, *H. sericeus*, *H. sobrinus* and *H. splendens*); (2) western Pacific Ocean (ca. 10–35°N) between the westernmost area of the North Equatorial Current and the Kuroshio (3 species; *H. micans*, *H. sericeus* and *H. germanus*); (3) Indian Ocean between ca. 10°S and 10°N (2 species; *H. micans* and *H. germanus*).

In the eastern tropical Pacific Cheng & Shulenberger (1980) showed that even though two or more species were occasionally collected in the same net, usually only one species dominated numerically. Thus, areas of high density of each species did not overlap. In the westernmost areas of the North Pacific Equatorial Current, results of three cruises conducted in different years revealed that *H. micans* was predominant in two cruises. However, it was almost completely replaced by *H. sericeus* during the third cruise (Ikawa et al. 2002). The southward shift of salinity front related to the El Nino event (Kimura et al. 2001) might have been responsible for transporting *H. sericeus* southwards with saltier water moving from the north. In the Indian Ocean, distribution overlap would also be uncommon. During the circumnavigational cruise of 'Operation Drake', no tow contained both species. *Halobates germanus* was caught only in the Gulf of Aden and the Red Sea while *H. micans* occurred exclusively in the open stretch of the ocean (Cheng & Holdway 1983). In the eastern South Indian Ocean, a total of 1190 individuals sampled in 221 tows contained no *H. germanus* but were all *H. micans* (Ikawa et al. 2007b). Seasonal variations of winds and currents in the Indian Ocean might cause seasonal shifts in the distribution of *Halobates* (Ikawa et al. 2007b), generating apparent overlaps in the map.

### *Co-occurrence and spatio-temporal variations*

So far, the only region where two or more species are known to co-occur in comparable densities is along the Kuroshio Current between the southeastern East China Sea and the southern Pacific coast of Japan (Ikawa et al. 2004). In the North Pacific, *Halobates micans* and *H. germanus* are usually found south of the habitat zone of *H. sericeus* (Figure 6A). The Kuroshio originates east of the Philippines and flows across the habitats of both *H. micans* and *H. germanus*, possibly transporting them to the north. Eddies generated by frontal disturbances of the Kuroshio (Kimura et al. 1997) may provide heterogeneous environments for these species to coexist in a narrow area (1000–6000 m$^2$) that can be covered by a single net tow. However, *H. micans* and *H. germanus* may not be carried totally passively within the Kuroshio. Each species appears to have its own habitat preference. Higher numbers of *H. micans* were found along the Pacific coast of Japan where the main stream of the Kuroshio flows while *H. germanus* was more abundant within the branch of the Kuroshio in the East China Sea. This difference could be caused by the difference in volume transport between the main stream of the Kuroshio and its branch. *Halobates micans* appeared to be more closely associated with warm waters of the Kuroshio than *H. germanus*.

Temporal changes in species composition in the East China Sea were possibly due to different temperature preferences among the three species (Ikawa et al. 2004). In the East China Sea, when the SST was lowest (23.2°C), the most common insects caught were *H. sericeus*. When SST was intermediate (27.6°C), *H. sericeus* was predominant followed by *H. germanus* while *H. micans* was most abundant followed by *H. germanus* when SST was highest (28.9°C). *Halobates micans* appeared to be abundant in this area and off the Japanese coast only during the summer when SST was quite high (T. Ikawa, unpublished data), suggesting that it is least tolerant to low SST.

Most ocean skaters are caught in warm waters where SST is above 20°C; a few collected in cooler waters have been considered strays (Andersen & Cheng 2004). In fact, the distribution of *H. micans* was found to be limited by the 21°C winter isotherm in the Atlantic Ocean (Scheltema 1968). They were rarely caught off the south coast of Japan during winter when SST falls below 20°C except in the main stream of the Kuroshio (Miyamoto & Senta 1960; T. Ikawa, unpublished data).

Oceanic *Halobates* were thought to reproduce all year round (Cheng 1973a; Spence & Andersen 1994). Most females sampled off the Japanese coast in autumn were gravid. Many eggs were also found on floating materials and some were obviously ready to hatch (T. Ikawa, unpublished data). Their numbers decreased toward winter and we do not know where the females or eggs went. In May, population began to recover, *H. sericeus* being the earliest to be caught in any numbers (T. Ikawa, unpublished data). Thus, the abundance of *Halobates* appears to fluctuate seasonally not only in this region but probably also in other areas where SST falls below 20°C in winter. The 20°C isotherm shifts annually ca. 1000 km along the meridian (see Figure 6.4 in Open University 1989). We can therefore expect the northern or southern limits of *H. sericeus* in the Pacific or of *H. micans* in the Atlantic to shift seasonally about 1000 km northwards in boreal summer and southwards in boreal winter.

### *Theoretical aspects of population structure and life-history strategy*

Physical forces, such as winds or currents, must play decisive roles in determining the population structure and life history of ocean skaters that live exclusively at the air–sea interface. Hitherto, the only theoretical study on the influence of any physical factor on *Halobates* was that by Ikawa et al. (1998). They considered oceanic diffusion as an integrated effect of all physical forces. In the following three sections, we delve further into the effects of oceanic diffusion on ocean skaters, discuss theoretical inferences with results from DNA analysis (Andersen et al. 2000), and illuminate their unique adaptive strategy to live at the ocean surface.

### *Oceanic diffusion operating on a patch of ocean skaters*

The term diffusion usually refers to molecular diffusion. Oceanic diffusion, however, is quite different from molecular diffusion (Okubo 1980). First, molecular diffusion is microscopic, caused by thermal movements of molecules. Oceanic diffusion, on the other hand, is caused by turbulence that consists of various-sized eddies. The worldwide prevailing winds and tide-generating forces give energy to large-scale eddies, and this energy is transferred to smaller eddies. Because these eddies carry rather high energy, oceanic diffusion is much more powerful than molecular diffusion. Second, while diffusivity, i.e. diffusion coefficient, is constant in molecular diffusion, it increases with the scale of the phenomenon in oceanic diffusion because more numbers of larger eddies are involved with the increase of the scale. This means oceanic diffusion operates more powerfully as the scale of phenomena increases. Therefore, oceanic diffusion must greatly influence ocean skaters that have wide distribution ranges across the ocean.

Based on the empirical data, Okubo (1971, 1974) constructed two kinds of oceanic diffusion diagrams, i.e. horizontal variance versus diffusion time and the diffusivity versus the scale of diffusion. This is formalized as (Ikawa et al. 1998)

$$\sigma^2 = 5.15 \times 10^{-5} t^3, \qquad (1)$$

where $\sigma^2$ (cm$^2$) is the horizontal variance of a diffused dye patch and $t$ (s) is the time after its release on the ocean (Okubo 1971). Equivalently, the diffusivity $K_a$ (cm$^2$ s$^{-1}$) is given as

$$K_a = 9.3 \times 10^{-3} \sigma^{4/3}. \qquad (2)$$

We set $1.5\sigma$ as the radius of a *Halobates* patch, because 67.5% of the population is included within this radius, provided the distribution is two-dimensional Gaussian. Then, our calculations show that oceanic diffusion could increase the radius of a *Halobates* patch as much as 3500 km in 120 days (Ikawa et al. 1998). This distance is equivalent to about one-fourth of the maximum distribution range of *Halobates micans* in the Pacific Ocean. Starting from the egg stage, ocean skaters could live for more than 4 months (Cheng 1985; L. Cheng, unpublished data). Then, individuals could probably be carried across the Pacific Ocean within the time required for several reproductive cycles. It also means a high rate of gene flow is possible within a major ocean basin where there are no geographical barriers. However, gene flow might be restricted between major oceans where continents or island chains could act as physical barriers for dispersal. These predictions were supported by the analyses of mitochondrial DNA sequences of oceanic *Halobates* (Andersen et al. 2000). Haplotype lineages of *H. micans* from Pacific, Atlantic and Indian Oceans were significantly different from one another. Similarly, limited gene flow was suggested between *H. germanus* populations from Pacific and Indian Oceans. Thus, gene flow among populations of different ocean basins is limited. However, there is no correlation between nucleotide divergence and geographical distance of *H. micans* or *H. germanus* within each ocean basin.

### *Mutual encounter due to random movements and oceanic diffusion*

How do ocean skaters find conspecifics or mates in the vast ocean once they are scattered by storms and winds? *Halobates* are often observed to form dense aggregations (Cheng 1985). Their local distribution patterns analysed from sampling data are not uniform but clumped (Cheng & Shulenberger 1980; Ikawa et al. 2002). However, little is known about the mechanism of aggregation or mating of sea skaters. They may find conspecifics by chemicals as demonstrated in a coastal veliid *Rhagovelia* (*Trochopus*) (Cheng & Roussis 1998) and suggested in the coastal *Halobates hawaiiensis* (Tsoukatou et al. 2001), or by detecting surface ripples as shown in a freshwater *Gerris* Fabricius, 1794 (Gerridae) (Wilcox 1979). Ignoring these aggregative factors, conservative estimates of mutual encounter rates can be obtained by two different ways, i.e. by active random movements or by passive oceanic diffusion (Ikawa et al. 1998).

For estimating encounter rate due to random movements, the following conservative values are assumed: speed of motion $= 0.1\ \mathrm{m\ s^{-1}}$ (Cheng 1985); time for activity $\mathrm{day}^{-1} = 8$ h (L. Cheng, unpublished data); distance that a skater can scan visually $= 0.1$ m (L. Cheng, unpublished data). Then, encounter $\mathrm{day}^{-1}$ ($f_r$) due to random movements when the population density $\rho$, is

$$f_r = 5.8 \times 10^{-4}\rho. \qquad (3)$$

On the other hand, if ocean skaters are carried only by oceanic diffusion, the frequency of mutual encounter $f_0$ (times $\mathrm{day}^{-1}$) is obtained as

$$f_0 = 2.4\rho^{1/3}. \qquad (4)$$

The most interesting aspect with this calculation is the dependency of mutual encounter rate on population density $\rho$, especially when $\rho$ becomes very low. By oceanic diffusion, mutual encounter rate is proportional to one-third power of population density $\rho$. Consequently, a decrease in encounter rate with a decrease in $\rho$ is not as steep as a linear decrease expected in the case of random movements. As is shown in Table II, the estimated densities of *Halobates* in various regions of the ocean fluctuated from $8.2 \times 10\ \mathrm{km}^{-2}$ to $2.1 \times 10^5\ \mathrm{km}^{-2}$. When the density is $10\ \mathrm{km}^{-2}$, $10^3\ \mathrm{km}^{-2}$ or $10^5\ \mathrm{km}^{-2}$, we obtained encounter rates of $f_r = 6 \times 10^{-3}$, 0.6 and 60, and $f_0 = 5$, 24 and 111, respectively. These calculations suggest that by oceanic diffusion alone an individual may be able to find a mate even after it has been carried away for a long distance into regions where densities are very low. Thus oceanic diffusion could be responsible for bringing individuals living far apart closer and result in high rates of gene flow within an ocean basin. These calculations do not contradict the results of DNA analyses but suggest that populations of *Halobates* in a given ocean basin are not substructured. There remain possibilities that more extensive and precise DNA and morphological analyses might reveal limited gene flow in an ocean basin. Then ocean skaters would presumably require some means of maintaining their local aggregations against oceanic diffusion.

As mentioned in previous sections, densities and distributions of ocean skaters could undergo drastic fluctuations annually and seasonally. It would be vital for them to develop means to re-aggregate or to find mates under low densities. Oceanic diffusion which acts to carry *Halobates* apart could also enhance encounters among dispersed populations. Riding on oceanic diffusion would be one of their tactics to survive at the ocean surface.

### *Adaptive significance of distribution range*

One of the most notable features of distribution pattern of oceanic *Halobates* is their wide extension without distinct discontinuities (Figure 6A). We examine the adaptive significance of such vast distribution areas and infer life-history strategies that enabled ocean skaters to survive on the high seas by using the mathematical model constructed by Skellam (1951) and Kierstead & Slobodkin (1952).

All organisms have thresholds of tolerances for environmental conditions surrounding them. For an aquatic species with restricted physiological tolerances, areas of suitable water could be limited and oceanic turbulence could act to carry individuals away into unsuitable areas. Therefore, to keep a stable distribution range, there should be a balance between intrinsic growth rate and loss due to diffusion into unsuitable areas. The mathematical expression for this is

$$K(\partial^2\rho/\partial x^2 + \partial^2\rho/\partial y^2) + r\rho = 0 \text{ inside of } \Omega, \text{ and}$$
$$\rho = 0 \text{ outside of } \Omega, \qquad (5)$$

where $\rho$ ( $x, y, t$) is population density as a function of space and time, $r$ is growth rate (instantaneous rate of population increase), $K$ is diffusivity and $\Omega$ is the region suitable for *Halobates* to reproduce.

The steady-state patch size for zonal and circular patch is given by

$$L = \pi(K/r)^{1/2} \text{ and } R = 2.4048(K/r)^{1/2}, \qquad (6)$$

where $L$ is the width of the zonal patch and $R$ is the radius of the circular patch, respectively. Under the influence of oceanic diffusion, diffusivity $K$ in equation (6) should depend on the scale of phenomena, i.e. $L$ or $R$. Thus, instead of $K$, we use a diffusivity $K_a$ from equation (2). Then, expected growth rate is given by (Ikawa et al. 1998),

$$r_z = 0.0212L^{-2/3} \text{ and } r_c = 0.0313R^{-2/3}, \qquad (7)$$

where $r_z$ is growth rate for zonal and $r_z$ for circular patch, respectively.

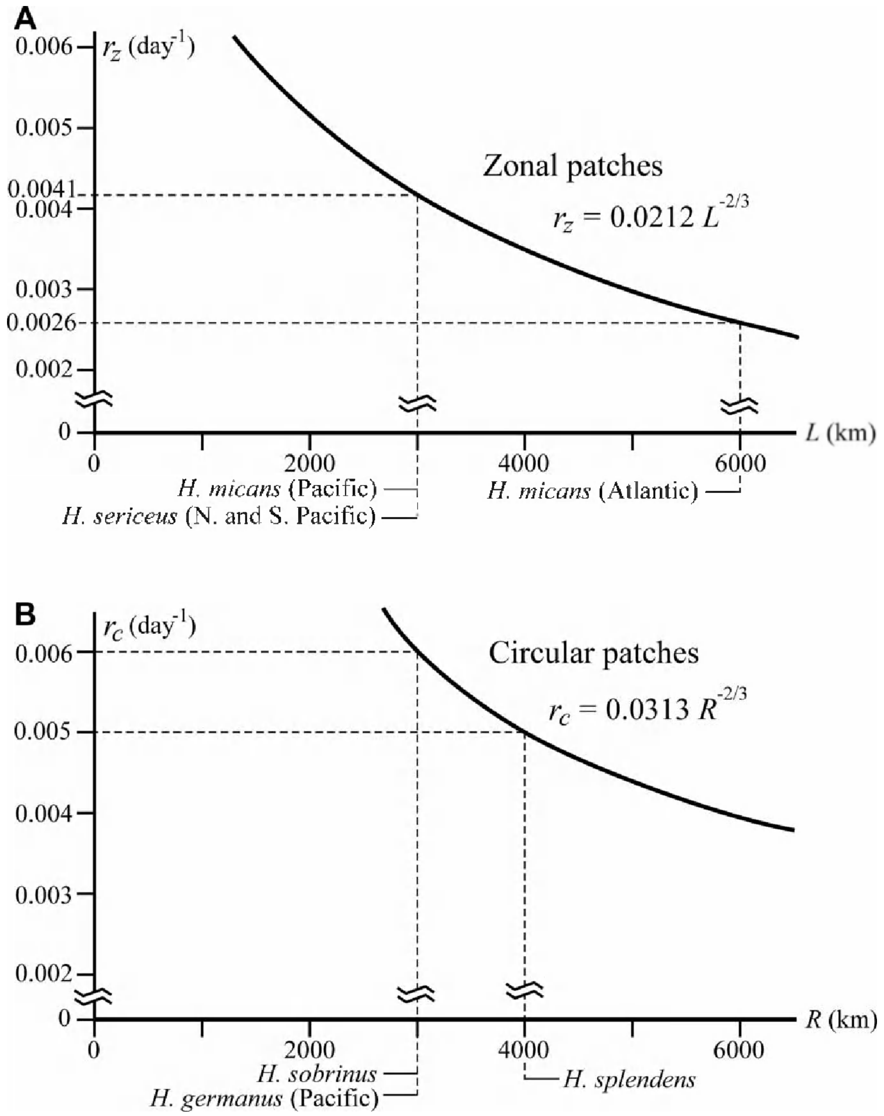


Figure 8. Relationship between estimated growth rate and patch size of oceanic *Halobates* spp. for **A**: Zonal patches, **B**: Circular patches.

The distributions of *Halobates micans* and *H. sericeus* can be treated as zonal patches since their eastern and western boundaries are continental coasts and they are only able to expand towards the north and south. On the other hand, the distributions of *H. sobrinus*, *H. splendens* and *H. germanus* in the Pacific Ocean appear to form circular patches (Ikawa et al. 1998; Figure 6A). In Figure 8A,B are shown relationships between $r_z$ and $L$, and between $r_c$ and $R$, and habitat ranges of *Halobates* species as estimated in Figure 6A. Because growth rate is proportional to $-2/3$ power of habitat size, it increases drastically with the decrease in patch size, i.e. much higher growth rates would be required to keep smaller patches stable.

The estimated growth rates of *Halobates* are from 0.0026 day$^{-1}$ (*H. micans* in the Atlantic Ocean) to 0.0060 day$^{-1}$ (*H. sobrinus* and *H. germanus*). These values are rather low by comparison with 0.33 day$^{-1}$ for the spotted alfalfa aphid *Therioaphis maculata* Buckton, 1899 (Ito 1975), 0.12 day$^{-1}$ for the flower beetle *Tribolium confusum* Jacquelin Du Val, 1863 and 0.014 day$^{-1}$ for the spider beetle *Ptinus fur* Linnaeus, 1758 (Pianka 1978). However, it would be appropriate to assume low growth rates for *Halobates* considering their relatively long life span (at least 4 months) and long oviposition period (more than 1 month) (Cheng 1985; L. Cheng, unpublished data). The calculations by equation (7) show that low values of $r$ can be realized only when the patch size is a few thousand kilometers in width or diameter. For *Halobates*, it is improbable that small-sized stable patches of less than 1.0 km in diameter could exist, because the corresponding growth rates would have to be more than 0.85 day$^{-1}$, an unrealistically high value for these insects.

Turbulence is thought to be one of the major factors for excluding most insects from the open ocean (Ward 1992). One plausible strategy to successfully survive in rough environments is to reproduce quickly, with high growth rates, early maturity and short life span. Then, once ocean skaters find a suitable habitat, they might be able to aggregate, mate and reproduce quickly. However, the mathematical model and field observations infer a quite different life-history strategy. Ocean skaters have rather low growth rates and long life spans. This life-history strategy could have been selected due to their extremely harsh and unpredictable environment. On the ocean surface, strong winds and storms might occur too frequently to allow them to form a stable local aggregation and to complete even one generation. With high growth rate and short life span, the possibilities would be low for ocean skates to survive and reassemble in a local patch after they are scattered by storms. However, a long life span and long oviposition period would give them better chances to find conspecifics, food and suitable habitats to regroup and reproduce even after they are dispersed over long distances. Although they have been observed to form local aggregations, such flotillas would be unstable and destroyed frequently by storms and winds. Riding on oceanic turbulence, ocean skaters would repeatedly disperse, regroup and reproduce during their long life span, making their whole distribution range as one stable patch, i.e. as a freely exchanging gene pool. This prediction is supported by the results of DNA analyses (Andersen et al. 2000). Thus, to occupy vast regions in all three major oceans is their vital strategy for surviving in the high seas.

## Concluding remarks – strategy shift from the shore to the ocean

The life of coastal sea skaters is characterized by a strong affinity to the shore where they depend on terrestrial insects falling on the sea surface for food, rocks or plants for egg-laying, and overhanging vegetation for shade, etc. Away from the shore, they cannot survive. Their life is thus inseparable from the shore and they must always move against tidal currents, winds or waves that act to carry them away. The life of pelagic skaters is, by contrast, totally different. They spend their entire lives on the ocean surface where water and air are moving unceasingly in all directions. Their life-history strategy is not to avoid oceanic turbulence but to skate with it as long as they live. During their long life span they can find mates even after they have been dispersed far away from their place of birth, treating the vast tropical ocean basin as one gene pool. To extend their distribution range fully over the broad expanse of the water would be their optimal strategy to successfully colonize the open ocean. DNA analysis suggests that the oceanic way of life evolved twice independently in *Halobates*; their coastal ancestors that were washed away from the shore managed somehow to adapt to life on the open ocean (Andersen et al. 2000). It is fascinating trying to understand how the drastic shift in life-history strategy from total dependence on the shore to the surf-riding life could have been realized.

## Acknowledgements

This article was written during the turmoil and tragedy of the earthquake/tsunami that hit eastern Japan (where TI and HO live) on 11 March 2011. We express heartfelt thanks to Dr F. Uiblein for his understanding and to overseas as well domestic friends and colleagues for extending concerns and encouragements. We are indebted to many colleagues who have collected samples for us over the years and for providing us with sampling data. There are too many to mention individually. In particular, we wish to thank Dr A. D. Tran for providing unpublished collection data of coastal species; Mr A. Kawakubo, Mr Y. Nozoe and other members of Saikai Pearl Sea Resort for participating in field studies of Japanese sea skaters; TI's students for assistance in studies of both coastal and oceanic species; A. Townsend for help in accessing historical station data at SIO; and Drs R. L. Pitman and M. Schulz-Baldes for supplying original cruise data; S. Hoshizaki for insightful discussions; and two anonymous reviewers for their valuable comments. We wish to dedicate this article to the memory of three departed colleagues: Dr R. A. Lewin who supported us with his profound academic knowledge and as our dearest friend all through his life; Dr A. Okubo who inspired us with his great insight in mathematical biology and physical oceanography; and Dr M. Tsuchiya who led us to the fascinating world of interplay between physical and biological phenomena.

Land mask (3′ grid) in Figures 2–4 and 6 has been derived from land cover image provided by GSI, CEReS, Collaborating Organizations (http://www.iscgm.org/gmd/download/sample_image_dl.html). Global sea-surface temperature data (1°grid) in Figure 6B have been adopted from World Ocean Atlas 2009, NOAA National Oceanographic Data Center (http://www.nodc.noaa.gov/OC5/WOA09/woa09data.html).

## References

Andersen NM. 1991. Marine insects: Genital morphology, phylogeny and evolution of sea skaters, genus *Halobates*

(Hemiptera: Gerridae). Zoological Journal of the Linnean Society 103:21–60.

Andersen NM, Cheng L. 2004. The marine insect *Halobates* (Heteroptera: Gerridae): Biology, adaptations, distribution and phylogeny. Oceanography and Marine Biology, An Annual Review 42:119–80.

Andersen NM, Cheng L, Damgaard J, Sperling FAH. 2000. Mitochondrial DNA sequence variation and phylogeography of oceanic insects (Hemiptera: Gerridae: *Halobates* spp.). Marine Biology 136:421–30.

Andersen NM, Weir TA. 1994. The sea skaters, genus *Halobates* Eschscholtz (Hemiptera: Gerridae), of Australia: Taxonomy, phylogeny and zoogeography. Invertebrate Taxonomy 8: 861–909.

Association of Wildlife Research, EnVision 2007. Search System of Japanese Red Data. http://www.jpnrdb.com/index.html and http://www.jpnrdb.com/search.php?mode=map&q=07150360721 (accessed 26 March 2012). (in Japanese)

Ban Y, Shigeaki S, Ishikawa M. 1988. Life history of the water strider *Metrocoris histrio* B. White (Hemiptera: Gerridae) in Aichi Prefecture, Japan. Verhandlungen ders Internationalen Vereinigung für Limnologie 23:2145–51.

Berner EK, Berner RA. 1987. Global Water Cycle: Geochemistry and Environment. Englewood Cliffs, NJ: Prentice-Hall. 397 pages.

Birch MC, Cheng L, Treherne JE. 1979. Distribution and environmental synchronization of the marine insect, *Halobates robustus*, in the Galápagos Islands. Proceedings of the Royal Society of London Series B 206:33–52.

Cheng L. 1966. Studies on the biology of the Gerridae (Hem., Heteroptera) II. Entomologists' Monthly Magazine 102:273–82.

Cheng L. 1973a. *Halobates*. Oceanography and Marine Biology, An Annual Review 11:223–35.

Cheng L. 1973b. The ocean-strider *Halobates* (Heteroptera: Gerridae) in the Atlantic Ocean. Oceanology 13:564–70.

Cheng L. 1973c. Marine and freshwater skaters: Differences in surface fine structures. Nature 242(5393):132–33.

Cheng L. 1974. Notes on the ecology of the oceanic insect *Halobates*. Marine Fishery Review 36:1–7.

Cheng L, editor. 1976a. Marine Insects. Amsterdam: North-Holland. 581 pages.

Cheng L. 1976b. Insects in marine environments. In: Cheng L, editor. Marine Insects. Amsterdam: North-Holland, p 1–4.

Cheng L. 1982. *Halobates* from Micronesia, with notes on keeping *H. mariannarum* alive in the laboratory. Micronesica 17:97–106.

Cheng L. 1985. Biology of *Halobates* (Heteroptera: Gerridae). Annual Review of Entomology 31:111–35.

Cheng L. 1989. Factors limiting the distribution of *Halobates* species. In: Ryland JS, Tyler PA, editors. Reproduction, Genetics and Distribution of Marine Organisms. Fredensborg: Olsen and Olsen, p 357–62.

Cheng L. 1991. The endemic sea-skater *Halobates alluaudi* Bergroth, 1893 (Hemiptera: Gerridae) in the Seychelles. Raffles Bulletin of Zoology 39:161–68.

Cheng L. 1997. Disjunct distributions of *Halobates* (Hemiptera: Gerridae) in the Pacific Ocean. Pacific Science 51:134–42.

Cheng L. 2009. Marine insects. In: Resh VH, Carde RT, editors. Encyclopedia of Insects. 2nd edition. San Diego, CA: Academic Press, p 600–04.

Cheng L, Baars MA, Oosterhuis SS. 1990. *Halobates* in the Banda Sea (Indonesia): Monsoonal differences in abundance and species composition. Bulletin of Marine Science 47:421–30.

Cheng L, Birch MC. 1977. Terrestrial insects at sea. Journal of Marine Biological Association, UK 57:995–97.

Cheng L, Damgaard J, Garrouste R. 2012. The sea-skater *Halobates* (Heteroptera: Gerridae) – Probable cause for extinction in the Mediterranean and potential for re-colonization following climate change. Aquatic Insects 34(Suppl 1):47–58.

Cheng L, Douek M, Goring DAI. 1978. UV absorption by gerrid cuticles. Limnology and Oceanography 23:554–61.

Cheng L, Frank JH. 1993. Marine insects and their reproduction. Oceanography and Marine Biology, An Annual Review 31:479–506.

Cheng L, Holdway P. 1983. *Halobates* collected during the circumnavigational expedition Operation Drake. Zoological Journal of Linnean Society 78:187–98.

Cheng L, Maxfield L. 1980. Nymphs of two sea-skaters, *Halobates robustus* and *H. micans* (Heteroptera: Gerridae). Systematic Entomology 5:43–47.

Cheng L, Roussis V. 1998. Sex attractant in the marine insect *Trochopus plumbeus* (Heteroptera: Veliidae): A preliminary report. Marine Ecology Progress Series 170:283–86.

Cheng L, Shulenberger E. 1980. Distribution and abundance of *Halobates species* (Insecta: Heteroptera) in the eastern tropical Pacific. Fishery Bulletin 78:579–91.

Cheng L, Schulz-Baldes M. 1981. Frequency and population composition of *Halobates micans* (Heteroptera: Gerridae) from the central and South Atlantic Ocean. Meteor Forschungsergebnisse, Reihe D – Biologie 33:17–21.

Cheng L, Spear L, Ainley DG. 2010. Trophic importance of marine insects (Heteroptera: Gerridae, *Halobates* spp.) to eastern tropical Pacific seabirds. Marine Ornithology 38:91–95.

Cheng L, Wormuth J. 1992. Are there separate populations of *Halobates* in the Gulf of Mexico? Bulletin of Marine Science 50:307–19.

Cresswell GR, Golding JT. 1980. Observations of a south-flowing current in the southeastern Indian Ocean. Deep-Sea Research 27:449–66.

Damgaard J, Andersen NM, Cheng L, Sperling FAH. 2000. Phylogeny of sea skaters, *Halobates* Eschscholtz (Hemiptera, Geridae), based on mtDNA sequence and morphology. Zoological Journal of the Linnean Society 130:511–26.

Esaki T. 1924. On the genus *Halobates* from Japanese and Formsan coasts (Hemiptara: Gerrida). Psyche 31:112–19.

Environment Agency. 1991. The Threatened Species of Japan – Invertebrates. Tokyo: Japan Wildlife Research Center. 271 pages. (in Japanese)

Foster WA, Treherne JE. 1986. The ecology and behaviour of a marine insect, *Halobates fijiensis* (Hemiptera: Gerridae). Zoological Journal of the Linnean Society 86:391–412.

Gordon A. 2003. The brawniest retroflection. Nature 421: 904–05.

Grimaldi D. 2009. Fossil record. In: Resh VH. Carde RT, editors. Encyclopedia of Insects. 2nd edition. San Diego, CA: Academic Press, p 396–403.

Hayashi M, Miyamoto S. 1997. Rediscovery of *Asclepios shiranui* (Heteroptera, Gerridae) from northern Kyushu, Japan. Japanese Journal of Entomology 65:438–39.

Hayashi M, Miyamoto S. 2003. Distribution and habitat of *Asclepios shiranui*, with distributional notes on some other coastal marine skaters (Heteroptara: Gerridae and Veliidae) in northern Kyushu, Japan. Rostria 51:1–20. (in Japanese with English summary)

Hayashi M, Miyamoto S. 2005. Hemiptera. In: Kawai T, Tanida K, editors. Aquatic Insects of Japan: Manual with Keys and Illustrations. Kanagawa: Tokai University Press, p 291–378. (in Japanese)

Hellerman S, Rosenstein M. 1983. Normal monthly wind stress over the world ocean with error estimates. Journal of Physical Oceanography 13:1093–104.

Herring JL. 1961. The genus *Halobates* (Hemiptera: Gerridae). Pacific Insects 3:223–305.

Hu C, Montgomery ET, Schmitt RW, Muller-Karger FE. 2004. The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: Observation from space and S-PALACE floats. Deep Sea Research II 51: 1151–71.

Ikawa T. 2009. Preliminary study of age structure of the sea skater *Halobates mariannarum* Esaki (Gerridae: Hemiptera). Journal of Morioka University 27:27–33.

Ikawa T. 2010. Survey of Kuroshima and Takashima, two major islands of Kujukushima as habitats of the threatened marine insects, *Halobates matsumurai* Esaki and *Asclepios shiranui* Esaki (Hemiptara: Gerridae). Journal of Morioka University 27:27–33.

Ikawa T, Nozoe Y, Yamashita N, Nishimura N, Ohnoki S, Yusa K, et al. 2012. Life histories of two sympatric endangered species of marine insects *Halobates matsumurai* and *Asclepios shiranui* (Hemiptera: Gerridae). Psyche 261071. 7 pages.

Ikawa T, Okabe H, Hoshizaki S, Kamikado T, Cheng L. 2004. Distribution of the oceanic insects *Halobates* (Hemiptera: Gerridae) off the south coast of Japan. Entomological Science 7:350–57.

Ikawa T, Okabe H, Hoshizaki S, Suzuki Y, Fuchi T, Cheng L. 2002. Species composition and distribution of ocean skaters *Halobates* (Hemiptera: Gerridae) in the western Pacific Ocean. Entomological Science 5:1–6.

Ikawa T, Okubo A, Okabe H, Cheng L. 1998. Oceanic diffusion and the pelagic insects *Halobates* spp. (Gerridae: Hemiptera). Marine Biology 131:195–201.

Ikawa T, Okabe H, Aoki M, Watanabe M 2007a. A field experiment of motion picture analysis of aggregations of the sea skater *Halobates japonicus* Esaki (Hemiptera: Gerridae). Journal of Morioka University 24:49–58. (in Japanese with English summary)

Ikawa T, Onodera S, Okabe H, Hosizaki S, Cheng L. 2007b. Occurrence and density of *Halobates micans* (Hemiptera: Gerridae) in the eastern South Indian Ocean. Entomological Science 10:213–15.

Ikawa T, Susa K, Watanabe M 2006. Preliminary study of aggregations and reproductive organs of the sea skater *Halobates japonicus* Esaki (Hemiptera: Gerridae). Journal of Morioka University 23:103–08. (in Japanese with English summary)

Ikawa T, Watanabe M, Aoki M, Okabe H 2008. Consecutive daily sampling of aggregations of the sea skater *Halobates japonicus* Esaki (Hemiptera: Gerridae). Journal of Morioka University 25:31–37. (in Japanese with English summary)

Ito Y 1975. Animal Ecology I. Tokyo: Kokinshoin. 226 pages. (in Japanese)

Josey SA, Kent EC, Taylor PK. 2002. Wind stress forcing of the ocean in the SOC climatology: Comparisons with the NCEP–NCAR, ECMWF, UWM/COADS, and Hellerman and Rosenstein datasets. Journal of Physical Oceanography 32: 1993–2019.

Kawachino Y. 2001. New localities of *Asclepios shiranui* and *Halobates matsumurai* in Nagasaki Prefecture. Transaction of Nagasaki Biological Society 53:26. (in Japanese)

Kierstead H, Slobodkin LB. 1953. The size of water masses containing plankton bloom. Journal of Marine Research 12:141–47.

Kimura S, Inoeu T, Sugimoto T. 2001. Fluctuation in distribution of low-salinity water in the North Equatorial Current and its effect on the larval transport of the Japanese eel. Fisheries Oceanography 10:51–60.

Kimura S, Kasai A, Nakata H, Sugimoto T, Simpson J, Cheok JVS. 1997. Biological productivity of meso-scale eddies caused by frontal disturbances in the Kuroshio. ICES Journal of Marine Science 54:179–92.

Leo SST, Cheng L, Sperling FAH. 2012. Genetically separate populations of the ocean-skater *Halobates sericeus* (Heteroptera: Gerridae) have been maintained since the late Pleistocene. Biological Journal of the Linnean Society 105:797–805.

Lukas R, Yamagata T, McCreary JPJ. 1996. Pacific low-latitude western boundary currents and the Indonesian throughflow. Journal of Geophysical Research 101:12209–16.

Mann CR. 1967. The termination of the Gulf Stream and the beginning of the North Atlantic Current. Deep-Sea Research 14:337–59.

Ministry of the Environment. 2007. The revised red list of the insects of Japan. 12 pages retrieved from http://www.env.go.jp/press/press.php?serial=8648 (accessed 26 March 2012). (in Japanese)

Miyamoto S. 1961. Gerridae. Insecta Japonica. Series 1, Part 3. Tokyo: Hokuryukan. 2 + 40 pages. (in Japanese)

Miyamoto S, Hayashi M. 1996. Discovery of *Halobates matsumurai* (Heteroptera: Gerridae) from Tsushima Is., Kyushu. Japanese Journal of Entomology 64:110.

Miyamoto S, Senta T 1960. Distribution, marine condition and other biological notes of marine waterstriders, *Halobates* spp., in the south-western sea area of Kyushu and western area of Japan Sea. Sieboldia 2:171–86. (in Japanese with English summary)

Okubo A. 1971. Oceanic diffusion diagrams. Deep Sea Research 18:789–802.

Okubo A. 1974. Some speculations on oceanic diffusion diagrams. Rapports et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer 167:77–85.

Okubo A. 1980. Diffusion and Ecological Problems: Mathematical Models. Berlin: Springer-Verlag. 254 pages.

Open University. 1989. Ocean Circulation. Oxford: Pergamon Press. 238 pages.

Pianka ER. 1978. Evolutionary Ecology. 2nd edition. New York, NY: Harper and Row. 397 pages.

Polhemus DA. 1990. Heteroptera of Aldabra Atoll and nearby islands, western Indian Ocean, Part 1. Marine Hetertoptera (Insecta): Gerridae, Veliidae, Hermatobatidae, Saldidae and Omaniidae, with notes on ecology and insular zoogeography. Atoll Research Bulletin 345:1–16.

Polhemus DA, Polhemus JT. 1991. Distributional data and new synonymy for species of *Halobates* Eschscholtz (Heteroptera: Gerridae) occurring on Aldabra and nearby Atolls, Western Indian Ocean. Journal of the New York Entomological Society 99:217–23.

Polhemus DA, Polhemus JT. 2006. The marine Heteroptera (Insect) of eastern New Guinea and adjacent archipelagoes. Denesia 19:927–82.

Qu T, Du Y, Meyers G, Ishida A, Wang D 2005. Connecting the tropical Pacific with Indian Ocean through South China Sea. Geophysical Research Letters 32:L24609. 4 pages.

Ridgway KR, Condie SA, 2004. The 5500-km-long boundary flow off western and southern Australia. Journal of Geophysical Research 109:C04017. 18 pages.

Ruxton GD, Humphries S. 2008. Can ecological and evolutionary arguments solve the riddle of the missing marine insects? Marine Ecology 29:72–75.

Saunders PM. 1971. Anticyclonic eddies formed from shoreward meanders of the Gulf Stream. Deep-Sea Research 18:1207–19.

Scheltema RS. 1968. Ocean insects. Oceanus 14:8–12.

Skellam JG. 1951. Random dispersal in theoretical populations. Biometrika 38:196–218.

Spalding M, Blasco F, Field C, editors. 1997. World Mangrove Atlas. Okinawa. Japan: The International Society for Mangrove Ecosystem. 178 pages.

Spence JR, Andersen NM. 1994. Biology of water striders: Interactions between systematics and ecology. Annual Review of Entomology 39:101–28.

Stoner AW, Humphris SE. 1985. Abundance and distribution of *Halobates micans* (Insecta: Gerridae) in the northwest Atlantic. Deep-Sea Research 32:733–39.

Takara T, Azuma S. 1972. Fauna of Iriomote Island, Ryukyus. II. List of the insects (2) Order Hemiptera (Heteroptera). The Science Bulletin of the Faculty of Agriculture, University of the Ryukyus 19:99–121. (in Japanese)

Taylor SJ. 2009. Concurrent phenologies of three semiaquatic bugs (Heteroptera: Gerridae, Veliidae) on a small river in central Illinois, USA. Psyche 2009:562471. 5 pages.

Tsoukatou M, Cheng L, Vagias C, Roussis V. 2001. Chemical composition and behavioural responses of the marine insect *Halobates hawaiiensis* (Heteroptera: Gerridae). Zeitschrift für Naturforschung 56:597–602.

Ward JV. 1992. Aquatic Insect Ecology. 1. Biology and Habitat. New York, NY: John Wiley and Sons. 438 pages.

Wilcox RS. 1979. Sex discrimination in *Gerris remigis*: Role of a surface wave signal. Science 20:1325–27.

Yone F, Matsuo T, Kawakubo A, Saijo F, Mori Y 2004. Distribution of coastal sea skaters in southern Kujukusima. Transaction of Nagasaki Biological Society 57:1–9. (in Japanese)

*Editorial responsibility: Tom Fenchel*