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Marine insects of the Maldives (Heteroptera: Gerridae, Hermatobatidae and Veliidae; Diptera: Chironomidae) with notes on taxonomy, Indo-Pacific distribution, and ecology

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Abstract. Fifty-five samples of marine insects collected in the Maldives between 1998 and 2013 were identified and analysed. Five species previously recorded from the Maldives, namely *Halobates micans* and *H. formidabilis* (Gerridae), *Hermatobates djiboutensis* (Hermatobatidae), *Halovelia convexa* (Veliidae), and *Pontomyia natans* (Chironomidae), are reported here, with numerous new locality records. In addition, the open-ocean *Halobates germanus* was recorded for the first time and the endemic *Halovelia convexa* was found in northern Maldives, extending its previously known distribution.

Key words. Maldives, sea-skater, ocean strider, *Halobates*, *Hermatobates*, *Halovelia*, *Pontomyia*

INTRODUCTION

The Republic of Maldives is situated in the tropical Indian Ocean, southwest of India, along longitude 73°E and between latitudes 7°N and 0.5°S (Fig. 1). The country consists of 26 coral atolls with about 1,200 sandy islets, of which only about 200 are inhabited, although close to 250 more are now developed as tourist resorts. There are stands of sea grasses and mangroves around some of the islets, but these are rather limited in extent.

Although the Maldives has become a popular tourist destination in recent decades, with reef fishes and marine megafauna (such as sharks, rays, and turtles) being particular attractions, much about the country's marine wildlife remains unknown. In particular, little is known about the marine insect fauna. Prior to this study there had been no systematic survey of marine insects, although there had been some reports of mostly limited scope, which are listed below.

Sea-skaters were first reported from Maldives by Herring (1958) from collections of the Danish Carlsberg Foundation's *Dana* Expedition. That expedition passed through the

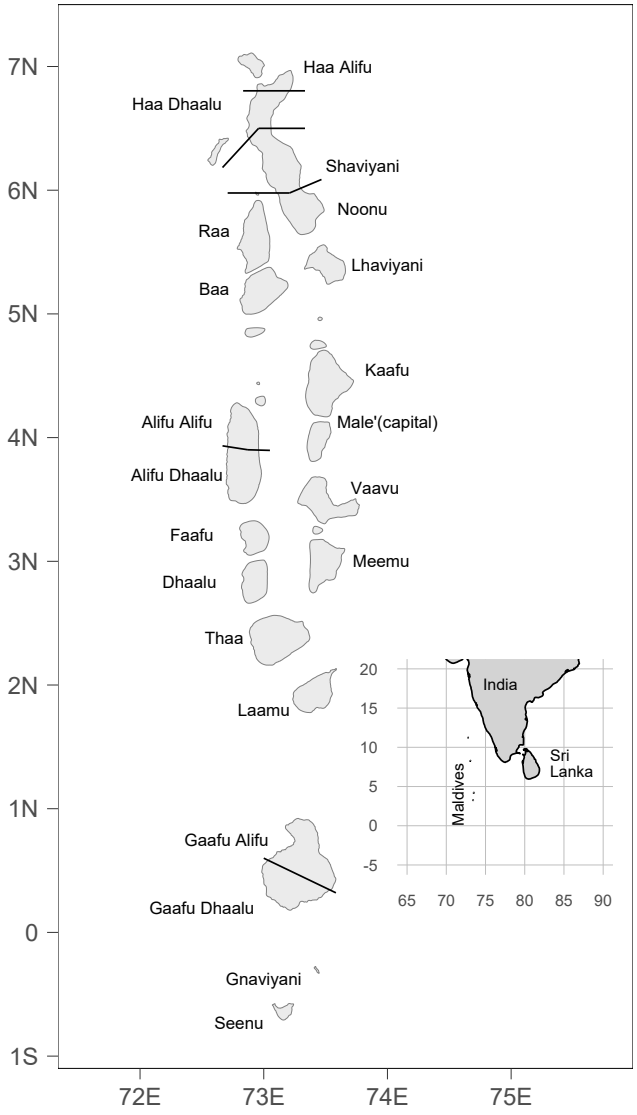

Fig. 1. Location map, with administrative atoll names.

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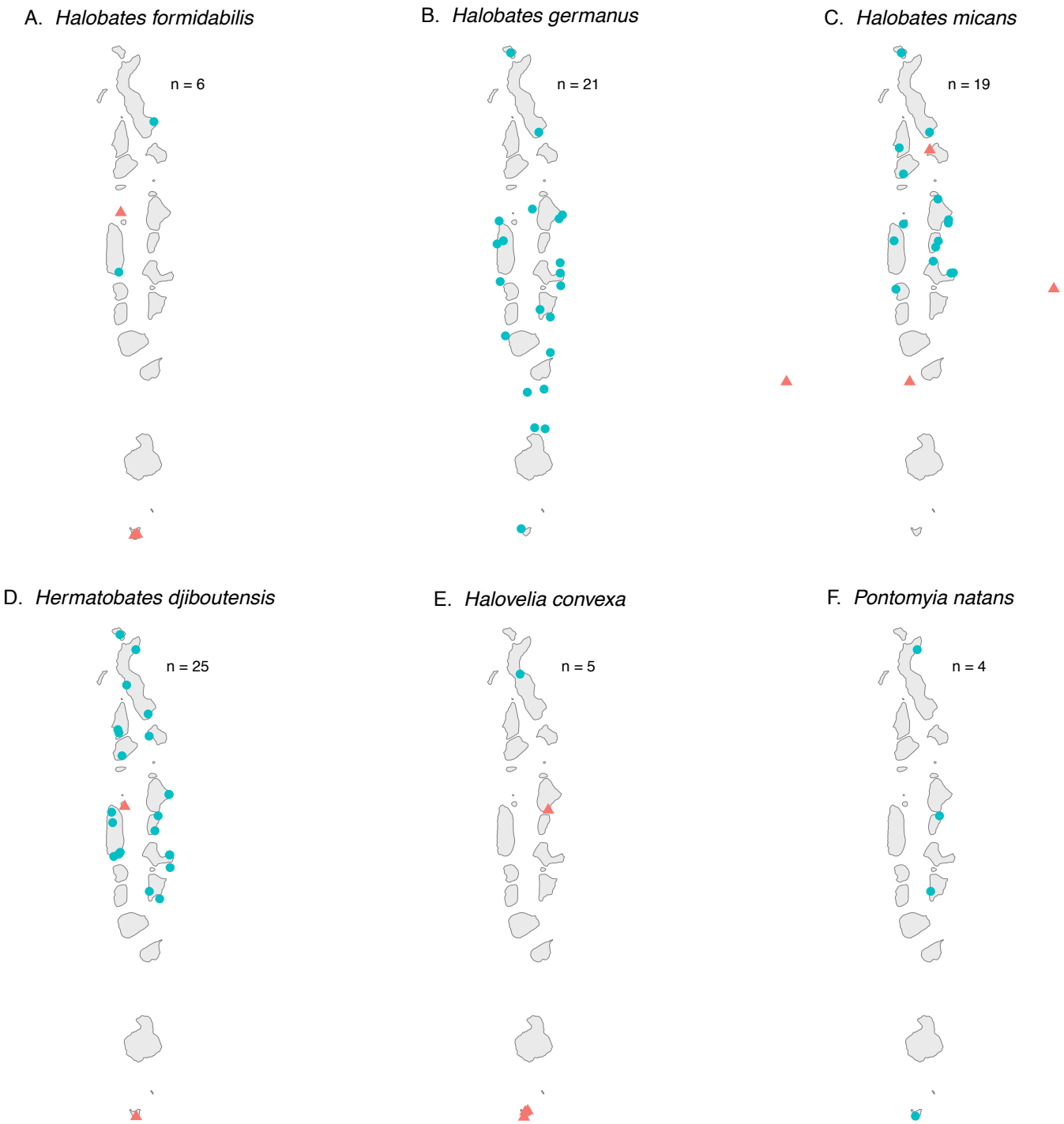

Fig. 2. Collection locations of six species of marine insect within the Maldives. A, *Halobates formidabilis*; B, *Halobates germanus*; C, *Halobates micans*; D, *Hermatobates djiboutensis*; E, *Halovelia convexa*; F, *Pontomyia natans*. Circles indicate locations of samples from this study; triangles indicate samples from previously published studies.

archipelago in December 1929 on its round-the-world oceanographic voyage, and sampled at three stations in what are now Maldivian waters. A single species, *Halobates micans* Eschscholtz, 1822, was recorded from all three stations.

Phillips (1959) published a brief record of three species which he collected during his stay in the Maldives in 1958–1959, mostly on Gan in Seenu (=Addu) Atoll (the southernmost island in the Maldives): *Halobates* sp. [subsequently identified as *H. formidabilis* (Distant, 1910)], *Halovelia* sp. [subsequently described as *H. convexa* by Andersen (1989)], and *Hermatobates djiboutensis* Coutiere & Martin, 1901. All three are represented in our collection.

Andersen & Foster (1992) reviewed the sea-skaters of India, Sri Lanka, and the Maldives, noting those recorded by Phillips (1959) and Herring (1961), and adding two new Maldivian locations for *H. formidabilis* and *H. micans*.

Cheng (2004) reported the marine midge *Pontomyia natans* Edwards, 1926 from the Maldives for the first time. Huang et al. (2014) subsequently included Maldivian specimens in their phylogenetic study of *Pontomyia*.

Polhemus & Polhemus (2012), in their review of *Hermatobates*, included one sample and one photograph of *H. djiboutensis* from the Maldives.

We present here notes on the distribution and habitats of six species of marine insects, belonging to two orders (Heteroptera and Diptera), collected between 1998 and 2013.

MATERIAL AND METHODS

The bulk of the material used in this study was collected by Charles Anderson during several excursions between 2002 and 2013. Other samples were collected during short visits to the Maldives by Lanna Cheng (in 1999) and Robert Pitman (in 1998 and 2004), and by Maldivian fisherman Hussein Shaheem (in 2007). Insects were collected by using either a plastic scoop (10 cm diameter) or a plankton net, both by day and at night. Night samples were made by attracting insects to artificial lights. Most samples were euthanised in 5% ethanol and preserved in 4% formaldehyde before later transferring to 70% ethanol, but most *Pontomyia* samples were preserved directly in 70% ethanol.

A location map is provided in Fig. 1, and sampling locations by species are shown in Fig. 2. To provide some objective means of comparing habitat usage among species, we assigned our sampling locations to 5 habitat categories: (1) immediately adjacent to islands; (2) shallow lagoons or reef flats; (3) atoll lagoons; (4) open sea adjacent to atolls; (5) open sea offshore. Each collection site was assigned a habitat score, and means calculated for each species, with the lowest scores indicating more inshore habitats, and the higher scores more offshore.

None of the species sampled are considered to be endangered. All samples were collected with the permission of the Maldivian government Marine Research Centre (MRC), and export was arranged through the MRC (now Maldives Marine Research Institute, MMRI). Most specimens are deposited at the Entomology Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC) (accession numbers ZRC_ENT00052488 to ZRC_ENT00052731). Note that a few individuals were mislaid after identification; these and the earliest samples were not transferred to ZRC.

RESULTS AND DISCUSSION

A total of 55 samples of marine insects were collected between April 1998 and May 2013 (Table 1). Six species belonging to three families of Heteroptera (Gerridae, Hermatobatidae, and Veliidae) and one family of Diptera (Chironomidae) were represented in our samples.

Suborder Heteroptera

Family Gerridae Leach, 1815

Genus *Halobates* Eschscholtz, 1822

Three species of *Halobates* were collected: one coastal species, *H. formidabilis*, and two open-ocean species, *H. germanus* and *H. micans*.

Halobates formidabilis (Distant, 1910)

Halobates formidabilis is the only coastal species of *Halobates* we found in the Maldives. It was first described from the Andaman Sea (Distant, 1910) and also occurs along the coasts of India and Sri Lanka (Andersen & Foster, 1992; Andersen & Cheng, 2004). It is one of the largest of coastal *Halobates* species known, measuring over 5 mm in body length. Both adults and nymphs show distinct colour patterns dorsally (Figs. 3A, 4A, B) and males are easily distinguished from other coastal *Halobates* species by their genitalia (Fig. 4C, D). The male is further characterised by a strongly modified front femur and a prominent spine on the inner margin of its front tibia (Andersen & Cheng, 2004: fig. A45), which is presumably used for holding the female during mating, although little is known about the biology of this species. It was first reported from the Maldives by Phillips (1959) who collected it from Gan Island, Seenu (=Addu) Atoll, in February 1959, reporting it as *Halobates* sp. His samples were subsequently identified as *Halobates formidabilis* by Herring (1961: 241) and confirmed by Andersen & Foster (1992). This species can be easily distinguished from the two open-ocean species of *Halobates* found in the Maldives by its much larger size and completely pale venter (Fig. 3B). It does not appear to be especially common in Maldives (it was found in just 3 of our 55 samples) but is widely distributed. We collected it at the same location as Phillips (1959), i.e., in Seenu (=Addu) Atoll in the south of Maldives, and from two other locations in the middle and north of the archipelago (Fig. 2A). It was only abundant in one sample, from a sheltered lagoon with mangroves, where it possibly breeds (sample 54, Maalhendhoo Island, Noonu Atoll, Table 1). All of our samples, and those of Phillips (1959), were from shallow lagoons or reef flats (Table 2), as expected for this coastal species.

Halobates germanus White, 1883

Halobates germanus is an Indo-Pacific species. It is widespread in the Indian Ocean and the waters of Southeast Asia but is absent east of longitude 125°W in the Pacific (Andersen & Cheng, 2004; Ikawa et al., 2012). Unlike *H. micans* which occurs in the open ocean far from land, *H. germanus* tends to be found closer to island shores. It is the only pelagic species commonly found in the Red Sea (including the Gulf of Aqaba), the northern Arabian Sea (including the Gulf of Oman), the Bay of Bengal, and the archipelagic waters of Indonesia. It was the most common of the three *Halobates* species collected by us (Table 1, Fig. 2B), and has been previously recorded from adjacent

Table 1. Date, location, habitat, species, collector, and ZRC catalogue number of marine insect samples from the Maldives (note that samples 1–7 and 22 were not transferred to ZRC). Full accession numbers are of the form ZRC_ENT00052XXX. Abbreviations: m = male; f = female; n = nymph; i–iv = nymphal stages 1–4; vm = nymphal stage 5 male; vf = nymphal stage 5 female. Collectors: RP = Robert Pitman; LC = Lanna Cheng; RCA = R. Charles Anderson; HS = Hussein Shaheem.

	Date	Lat./Long.	Island/Atoll	Habitat (Day/Night)	Species	Sample
1	11 April 1998	06°45.6′N 73°10.2′E	Hanimaadhoo Island, Haa Dhaalu Atoll	Island lagoon (anchorage) (N)	*Hermatobates djiboutensis*: 2f *Halobates*: 1 nymph *Pontomyia natans*	RP-98-1
2	12 April 1998	06°11.7′N 73°01.4′E	Medhukumburudhoo, Shaviyani Atoll	Atoll lagoon (N)	*Hermatobates djiboutensis*: 1m, 7f	RP-98-2
3	30 March 1999	04°06.5′N 73°31.5′E	Embudufinolhu, Kaafu (S. Malé) Atoll	Island lagoon (beach) (N)	*Hermatobates djiboutensis*: numerous males and some females *Pontomyia natans*	LC
4	24 February 2002	00°42.0′S 73°09.5′E	Gan Island, Seenu (=Addu) Atoll	Island lagoon (beach) (D)	*Halobates formidabilis*: f, 2vm	RCA-1
5	25 February 2002	00°42.0′S 73°09.5′E	Gan Island, Seenu Atoll	Island lagoon (beach) (D)	*Halobates ?formidabilis* nymphs i, ii	RCA-2
6	24 February 2002	00°42.0′S 73°09.8′E	Gan Island, Seenu Atoll	Island lagoon (beach) (D)	*Halobates ?formidabilis* nymphs i, ii, iii	RCA-3
7	25 February 2002	00°42.1′S 73°09.7′E	South side Gan Island, Seenu Atoll	Island lagoon (10 m from beach) (D)	*Halobates ?formidabilis* nymphs i, ii	RCA-4
8	1 June 2002	05°37′N 73°04′E	Kulhudhufushi, Haa Dhaalu Atoll	Reef flat (D)	*Halovelia convexa*: 8m, 14f, 1n	RCA-5 52488–52510
9	7 October 2002	00°42′S 73°09.2′E	South side of Gan Island, Seenu Atoll	Reef flat (D)	*Halobates ?germanus*: 1 ii	RCA-6 52667
10	28 March 2003	04°30.4′N 73°15.8′E	NW of North Malé, Kaafu Atoll	Open sea, slick line (D)	*Halobates germanus*: 1m, 1f, possibly a mating pair	RCA-7 52632, 52596
11	11 April 2003	04°20.1′N 73°40.3′E	East of North Malé, Kaafu Atoll	Open sea (D)	*Halobates micans*: 2f	RCA-8 52692–3
12	3 March 2004	03°52.2′N 73°28.5′E	Off South Malé, Kaafu Atoll	Open sea (D)	*Hermatobates djiboutensis:* 1f	RCA-9 52511
13	9 March 2004	03°27.6′N 72°49.1′E	Ariadhoo Channel, between Alifu Dhaalu and Faafu Atolls	Open water in channel between atolls. Slick line (D)	*Hermatobates djiboutensis*: 2m, 1f	RCA-10 52512, 52532–3
14	16 March 2004	03°17′N 73°43′E	Watteru Channel, between Vaavu and Meemu Atolls	Open sea	*Halobates germanus*: 2m, 2f *Hermatobates djiboutensis*: 1f	RP-04-1 52633–4, 52597–8, 52513

	Date	Lat./Long.	Island/Atoll	Habitat (Day/Night)	Species	Sample
15	17 March 2004	02°47′N 73°33′E	Off SE Meemu Atoll	Open sea	*Halobates germanus*: 2m, 3f *Hermatobates djiboutensis*: 4m	RP-04-2 52635–6, 52599–601, 53534–7
16	18 March 2004	02°13′N 73°33′E	Off NE Laamu Atoll	Open sea	*Halobates germanus*: 3m, 2f (both mated)	RP-04-3 52637–9, 52602–3
17	19 March 2004	01°38′N 73°27′E	One-and-a-half-degree Channel, south of Laamu Atoll	Open sea	*Halobates germanus*: 2m, 2f, 1vm	RP-04-4 52640–1, 52604–5, 52664
18	20 March 2004	01°01′N 73°18′E	One-and-a-half-degree Channel, north of Gaafu Alifu Atoll	Open sea	*Halobates germanus*: 2m, 2f	RP-04-5 52642, 52717–8, 52606
19	21 March 2004	01°00′N 73°28′E	One-and-a-half-degree Channel, north of Gaafu Alifu Atoll	Open sea	*Halobates germanus*: 3f, 1vf, 1iv	RP-04-6 526079, 52658, 52668
20	21 March 2004	02°54.2′N 73°23.1′E	East of Thuvaru Island, Meemu (=Mulaku) Atoll	Atoll lagoon (30–40 m deep) (N)	*Hermatobates djiboutensis*: 3m, 8f, 1ivm, 1ivf, 1iii *Halobates germanus*: 1iii *Pontomyia natans*: 4m	RCA-11 52538–40, 52561–71, 52670, 52728–30
21	22 March 2004	01°35′N 73°11′E	One-and-a-half-degree Channel, between Laamu and Gaafu Alifu Atolls	Open sea	*Halobates germanus*: 3m, 4f, 2vm, 1iv	RP-04-7 52643–5, 52610–3, 52665–6, 52669
22	23 March 2004	02°29′N 72°50′E	NW of Thaa Atoll	Open sea	*Halobates germanus*: 3m, 6f, 1iv, 1iii	RP-04-8
23	24 March 2004	03°21′N 72°45′E	NW of Faafu Atoll	Open sea	*Halobates germanus*: 1m, 2f (1 mated), 2vf, 5iv	RP-04-9 52646, 52614–5, 52659–60, 52671–5
24	25 March 2004	04°19′N 72°44′E	NW of Alifu Alifu Atoll	Open sea	*Halobates germanus*: 3m, 1f, 1vf	RP-04-10 52647–9, 52616, 52661
25	15 November 2004	04°17′N 73°00′E	South of Velidhoo Island, Rasdhoo, Alifu Alifu Atoll	Over reef (D)	*Halobates micans*: 1m	RCA-12 52699
26	16 November 2004	03°57′N 72°42′E	West of Alifu Alifu Atoll	Open sea, associated with current line (D)	*Halobates germanus*: 1vf	RCA-13 52662
27	28 February 2005	04°16′N 72°57′E	Just south of Rasdhoo, Alifu Alifu Atoll	Open sea, associated with driftline coming off from reef (D)	*Halobates micans*: 1f	RCA-14 52694
28	3 August 2005	04°1′S 73°08.5′E	Gan Island, Seenu Atoll	In disused saltwater swimming pool on west side of island (D)	*Halobates ?germanus*: 2ii, 1iii, 1iv *Pontomyia natans*: 1m 1 winged chronomid, not identified	RCA-16 52676–9, 52725

	Date	Lat./Long.	Island/Atoll	Habitat (Day/Night)	Species	Sample
29	13 May 2006	3°30′N 72°54′E	Dhidhdhoofinolhu, Alifu Dhaalu Atoll	Over shallow seagrass bed adjacent to island (D)	*Halobates formidabilis*: 1f *Hermatobates djiboutensis*: 1f	RCA-17 52584, 52514
30	15 May 2006	3°30′N 72°54′E	Dhidhdhoofinolhu, Alifu Dhaalu Atoll	Island lagoon. Large swarm of sea-skaters seen at about 2000h under lights of over-water restaurant. Returned at 2100h to collect, only a few remaining (N)	*Hermatobates djiboutensis*: 3f, 1i, 1ii, 5iii, 2iv	RCA-18 52515–7, 52572–80
31	14 November 2006	4°27′N 73°42′E	Meerufenfushi Island, Kaafu (N. Malé) Atoll	Island lagoon. From stern of anchored boat, attracted under light (N)	*Hermatobates djiboutensis*: 4m, 5f	RCA-19 52518–21, 52541–4
32	15 November 2006	5°04′N 72°57′E	Centre of Baa Atoll	Atoll lagoon. From stern of anchored boat, attracted under light (N)	*Halobates micans*: 1iv *Hermatobates djiboutensis*: 1m	RCA-20 52715, 52553
33	16 November 2006	5°29′N 72°53′E	Near Maduvveri Island, Raa Atoll	Atoll lagoon. From stern of anchored boat, attracted under light (N)	*Halobates micans*: 1f, 1iv *Hermatobates djiboutensis*: 1m	RCA-21 52695, 52716, 52554
34	23 November 2006	5°44′N 73°22′E	Near Dhigurah Island, Noonu Atoll	Atoll lagoon. From stern of anchored boat, attracted under light (N)	*Halobates micans*: 1m, 1i, 2iii, 2iv *Halobates germanus*: 1f *Hermatobates djiboutensis*: 1m	RCA-22 52700, 52719–21, 52617, 52555
35	24 November 2006	4°40′N 73°30′E	Near Kagi Island, Kaafu (N. Malé) Atoll	Atoll lagoon. From stern of anchored boat, attracted under light (N)	*Halobates micans*: 1m, 1f, 1iv	RCA-23 52701, 52696, 52722
36	January 2007	ca. 7°00′N 72°55′E	Haa Alifu Atoll	Atoll lagoon. From fishing boat, attracted under light (N)	*Halobates germanus*: 331m, 274f, 65vm, 61vf, 6iv (about 10% adults newly moulted; 26% females mated) *H. micans*: 2m, 1f *Hermatobates djiboutensis*: 1f	HS-RCA-24 52727
37	6 June 2007	ca. 4°00′N 72°48′E	Near Fesdu Island, Alifu Alifu Atoll	Atoll lagoon. From fishing boat, big swarm attracted to lights (N)	*Halobates micans*: 1m *Halobates germanus*: 2m, 1i, 1iii *Hermatobates djiboutensis*: 12m, 20f, 1i, 6ii, 3iii, 26iv	HS-RCA-25 522724
38	11 December 2007	5°26′N 72°54′E	Near Maafaru Island, Baa Atoll	Atoll lagoon. On down-wind side of island, just outside reef (?D)	*Hermatobates djiboutensis*: 2m, 1f	RCA-26 52556–7, 52529
39	11 March 2008	4°10′N 72°47′E	Near Velidhoo-Dihiggaa reef, Alifu Alifu Atoll	Shallow lagoon. Collected from stern of boat, under lights (N)	*Hermatobates djiboutensis*: 1iv	RCA-27 52581

	Date	Lat./Long.	Island/Atoll	Habitat (Day/Night)	Species	Sample
40	15 March 2008	3°59.7′N 73°30.4′E	Near Gulhi Island, Kaafu (S. Malé) Atoll	Island lagoon. Collected from stern of boat, under lights (N)	*Halobates micans*: 2m, 1vm, 1vf, 1iii	RCA-28 52702–3, 52714, 52710, 52723
41	16 March 2008	3°54.0′N 73°27.9′E	Near Guraidhoo Island, Kaafu (S. Malé) Atoll	Island lagoon. Collected from stern of boat, under lights (N)	*Halobates micans*: 1m, 1vf	RCA-29 52704, 52711
42	20 March 2008	3°29.1′N 73°42.6′E	Near Fotheyo Finolhu Vaavu Atoll	Atoll lagoon. Collected from stern of boat, under lights (N)	*Hermatobates djiboutensis*: 1f	RCA-30 52530
43	21 March 2008	3°29.1′N 73°42.5′E	Near Fotheyo Finolhu Vaavu Atoll	Atoll lagoon. Collected from stern of boat, under lights (N)	*Halobates micans*: 2m, 1f *Halobates germanus*: 1m, 3f *Hermatobates djiboutensis*: 2m, 2iv (1 newly moulted)	RCA-31 52705–6, 52697, 52650, 52618–20, 52558–9, 52582–3
44	24 March 2008	4°27.0′N 73°41.9′E	Meerufenfushi Island, Kaafu (N. Malé) Atoll	Island lagoon. Collected from stern of boat, under lights (N)	*Hermatobates djiboutensis*: 8m, 7f	RCA-32 52545–52, 52522–8
45	29 March 2008	3°29.0′N 73°42.4′E	Near Fotheyo Finolhu Vaavu Atoll	Atoll lagoon. Collected from stern of boat, under lights (N)	*Halobates germanus*: 7m, 10f, 1vf	RCA-33 52651–7, 52621–30, 52663
46	2 April 2008	4°21.1′N 73°41.4′E	Meerufenfushi/Dhiffushi Kaafu (N. Malé) Atoll	Island lagoon. Collected from stern of boat, under lights (N)	*Halobates germanus*: 2iv	RCA-34 52680–1
47	27 April 2009	4°24.8′N 73°44.6′E	Meerufenfushi/Dhiffushi, Kaafu (N. Malé) Atoll	Outside atoll.Collected on current line out at sea (D)	*Halobates germanus*: 1f	RCA-35 52631
48	5 May 2009	0°41.2′S 73°08.6′E	Gan Island, Seenu (=Addu) Atoll	Collected from disused seawater swimming pool at west end of island (D)	?freshwater gerrid, not identified: 1n	RCA-36 52726
49	7 May 2009	0°35.7′S 73°05.1′E	Hithadhoo Island, Seenu (=Addu) Atoll	Collected near beach in shelter of half-submerged log on shallow lagoon (NE) side of island (D)	*Halobates germanus*: 9i, 2ii	RCA-39 52682–91, 52731
50	13 October 2010	3°29.4′N 73°44.8′E	Near Fotheyo Island, Vaavu Atoll	Open sea. Collected from current line, to east of island and outer atoll reef (D)	*Halobates micans*: 1vf	RCA-40 52712
51	6 October 2012	3°40.5′N 73°25.5′E	Fulidhoo Island, Vaavu Atoll	Island lagoon. Floating at surface (D)	*Halobates micans*: 1 cast skin	RCA-41
52	11 February 2013	3°31.6′N 72°55.3′E	Dhigurah Island, Alifu Dhaalu Atoll	Island lagoon (N)	*Hermatobates djiboutensis*: 1m	RCA-42 52560
53	13 February 2013	3°13.7′N 74°49.8′E	Near Minimasgali Island, Faafu Atoll	Reef lagoon (N)	*Halobates micans*: 3m, 1f, 1vf	RCA-43 52707–9, 52698, 52713

	Date	Lat./Long.	Island/Atoll	Habitat (Day/Night)	Species	Sample
54	5 May 2013	5°54.1′N 73°27.5′E	Maalhendhoo Island, Noonu Atoll	Shallow, sheltered lagoon with mangrove (D)	*Halobates formidabilis*: 2m, 1vm, 1vf, 6iv, 1iii	RCA-44 52585–95
55	6 May 2013	5°22.8′N 73°22.9′E	Dhidhdhoo Island, Lhaviyani Atoll	Island lagoon (N)	*Hermatobates djiboutensis*: 1f	RCA-45 52531

Table 2. Habitat categories for six species of marine insect (excludes samples of uncertain identity and habitat, and of cast exoskeletons): (1) immediately adjacent to islands; (2) shallow lagoons or reef flats; (3) atoll lagoons; (4) open sea adjacent to atolls; (5) open sea offshore.

Species	n	Habitat score range	Habitat score mean
Pontomyia natans	4	1–2	1.5
Halobates formidabilis	6	1–2	1.6
Halovelia convexa	5	2	2.0
Hermatobates djiboutensis	25	1–5	2.7
Halobates micans	16	2–5	3.5
Halobates germanus	23	1–5	3.7

waters (Cheng, 1989), on which basis Andersen & Foster (1992) included Maldives within the range of this species. However, our specimens appear to be the first records of *H. germanus* actually from Maldivian waters. It is easily distinguished from *H. formidabilis* by its much smaller size (Fig. 5A) and the structure of the male genitalia (Fig. 5B, C).

Halobates micans Eschscholtz, 1822

Halobates micans is the only cosmopolitan species of *Halobates* and is widely distributed in the warm tropical and subtropical oceanic waters of the Atlantic, Pacific, and Indian Oceans (Herring, 1961; Cheng, 1989). It has only occasionally been found in the relatively shallow waters of the Sunda Shelf (Andersen & Cheng, 2004), including the waters around Singapore and peninsular Malaysia (Tran et al., 2015). In Maldivian waters, this species has been collected further offshore than any other marine insect species (Herring, 1961; Fig. 2C).

Family Hermatobatidae Poisson, 1965

Genus *Hermatobates* Carpenter, 1892

The genus *Hermatobates* was first described by Carpenter in 1892 based on a single male collected from coral reefs at Mabuiag Island in the Torres Strait. The genus is exclusively marine and was considered to include some of the rarest marine insects. Prior to 1977, the nine species described at that time were represented by a total of just 14 type specimens in all the world's museums, and females of only two species (*H. hawaiiensis* China, 1956 and *H. singaporensis* Cheng, 1976) were known (Cheng, 1976). After its natural habitat was discovered by Cheng (1977) it is not uncommon to find them in intertidal zones of tropical islands in large numbers (Foster, 1989; Andersen & Weir, 2000; Polhemus & Polhemus, 2006). This genus was originally included in the Gerridae but has now been elevated to its own family (Andersen & Polhemus, 1976). Polhemus & Polhemus (2012) published a comprehensive review of the family

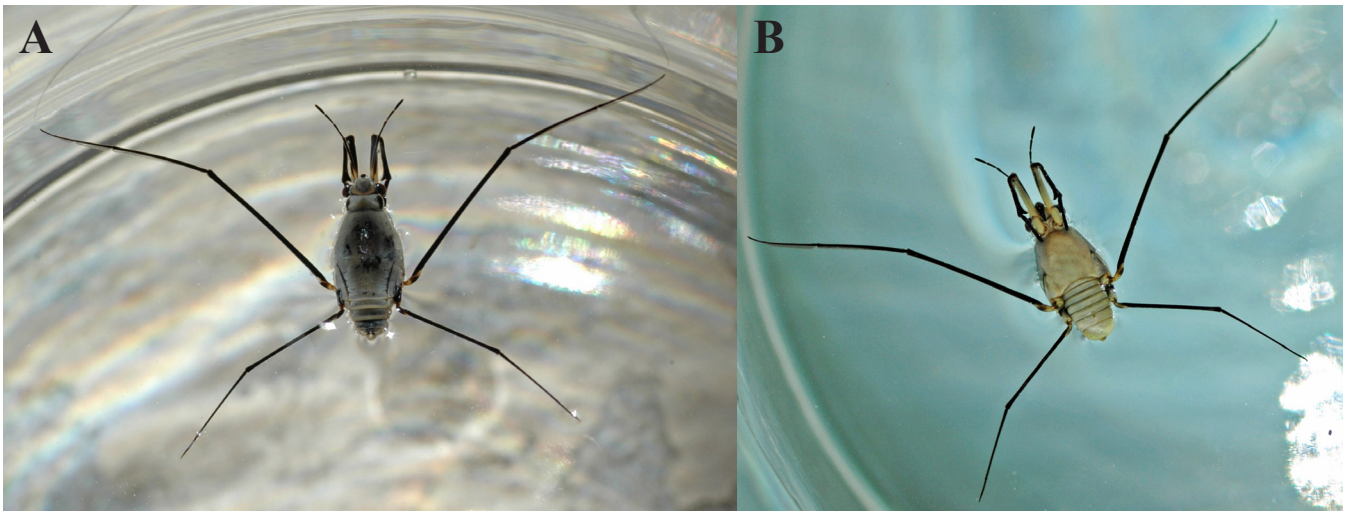

Fig. 3. *Halobates formidabilis*. 5th instar nymph, live individual, Dhidhdhoofinolhu Island, Alifu Dhaalu Atoll, 13 May 2006; not measured, approximate length 5 mm. A, dorsal view; B, ventral view, note uniform pale colouration.

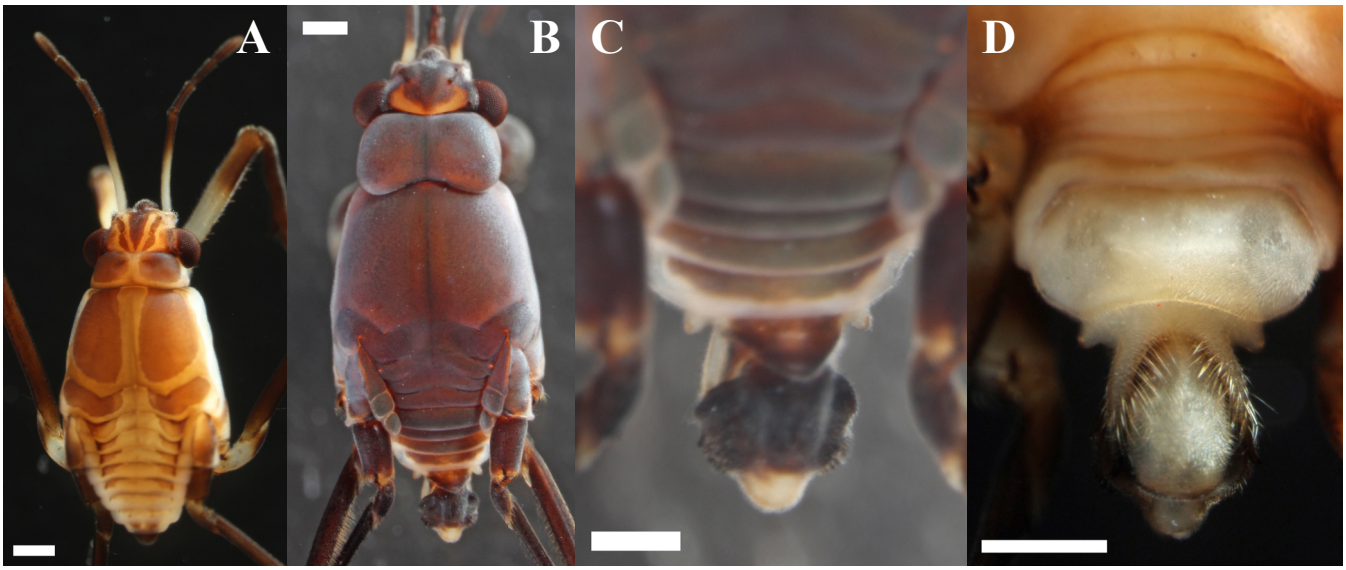

Fig. 4. *Halobates formidabilis*. Specimens from Maalhendhoo Island, Noonu Atoll, 5 May 2013. Scale bars = 0.5 mm. A, 5th instar nymph, dorsal view, showing colour pattern (length = 4.2 mm); B, adult male, dorsal view (length = 5.6 mm); C, male genitalia, dorsal view (genital segment length = 2.0 mm); D, male genitalia, ventral view (genital length = 1.4 mm).

with descriptions of two new species and a key to all 12 recognised species. Another species, from China, was added by Luo et al. (2019).

Hermatobates djiboutensis Coutière & Martin, 1901

Hermatobates djiboutensis is confined to the Red Sea and western Indian Ocean and is not found in Southeast Asia (Polhemus & Polhemus, 2012). It is the only species of this genus found in the Maldives, where it was first collected by Phillips (1959) and was the most frequently collected marine insect in our samples (Table 1). We collected it from inside the atolls, both in island and atoll lagoons, but not immediately adjacent to islands (Tables 1, 2; Fig. 2D). We assume that this species' habitat and behaviour do not differ from those of other *Hermatobates* species elsewhere: they live and hide in crevices of intertidal rocks or stone walls at high tide, coming out to feed only at low tide. If they are prevented from returning to air-filled cavities when the tide turns, they are able to skate freely over the sea surface for long periods of time. Specimens caught by us are presumably those that have strayed from their typical inshore habitats (Cheng & Leis, 1980; Cheng & Schmidt, 1982). This species is known to be highly attracted to light at night and it is not uncommon to catch dozens of specimens using night lights (e.g., samples 30 and 37, Table 1). For this species, 84% of the specimens in our Maldives samples were taken at night using lights, the highest percentage for any of the species we collected. Adult males can be easily distinguished from adult females. In the male, the meso- and metanota are completely fused and extended posteriorly to cover part of the abdomen (Fig. 6A), and the genital segments are modified ventrally (Fig. 6B). In the female, some of the abdominal segments can be clearly seen between lateral lobes of the metanota (Fig. 6D), and the genital segments are not modified (Fig. 6D). Furthermore, the male front leg is highly modified,

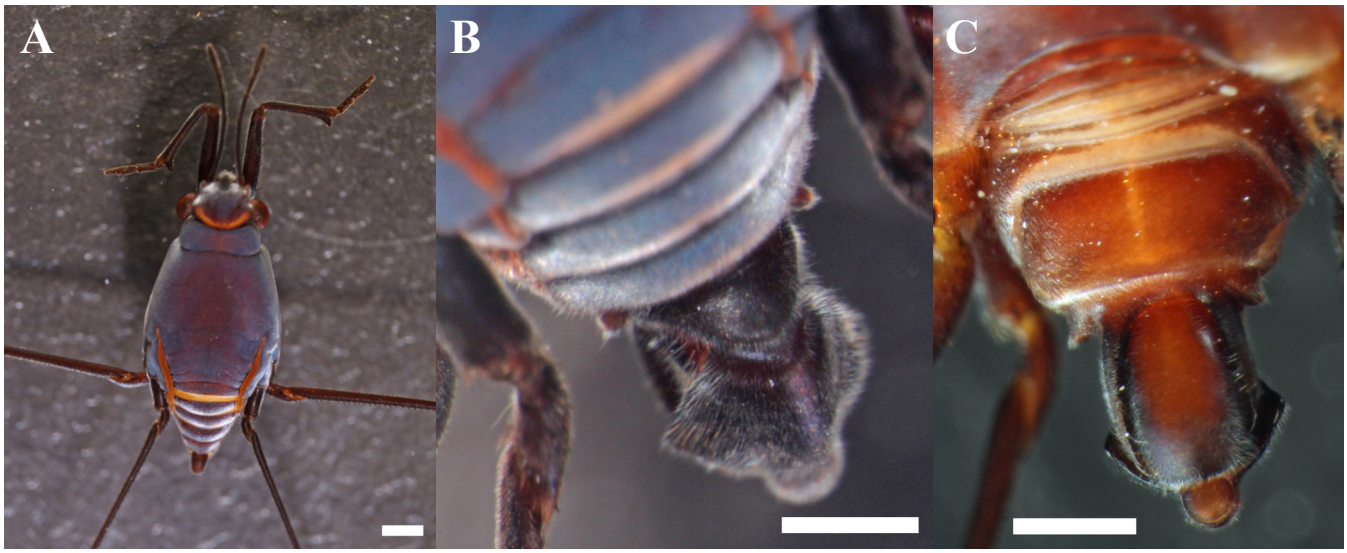

Fig. 5. *Halobates germanus*. Specimens collected inside Haa Alifu Atoll at night, January 2007. Scale bar = 0.5 mm. A, adult female, dorsal view (body length = 3.7 mm); B, male genitalia, dorsal view (genital segment length = 1.9 mm); C, male genitalia, ventral view (genital length = 1.5 mm).

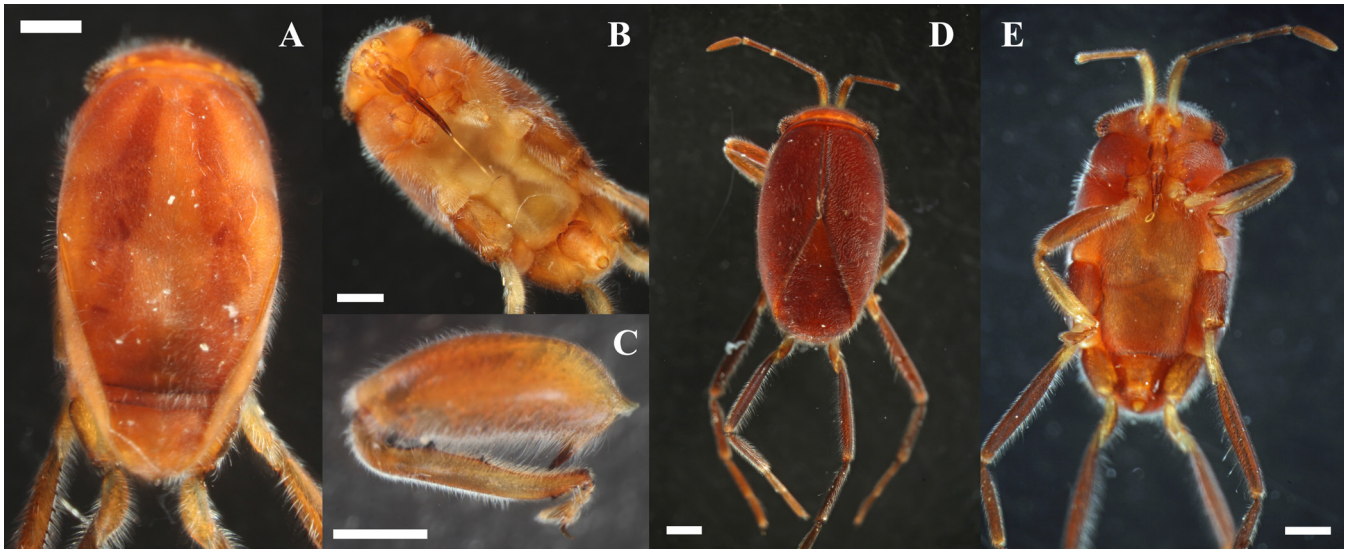

Fig. 6. *Hermatobates djiboutensis*. Specimens from Meerufenfushi Island, Kaafu (North Malé) Atoll, 14 November 2006. Scale bar = 0.5 mm. A, male, dorsal view; B, male ventral view (length ca. 3.8 mm); C, male front leg showing teeth and tubercles on tibia (length of femur ca. 0.8 mm); D, female, dorsal view (length ca. 3.6 mm); E, female, ventral view.

with small teeth and tooth-like tubercles along the inner margin of the tibia (Fig. 6C); these are presumably used for grasping the female during mating.

Family Veliidae Brullé, 1836

Genus *Halovelia* Bergroth, 1893

The Veliidae is a large family with 57 known genera and more than 800 described species worldwide. It is a family of small aquatic bugs with most adults measuring less than 3 mm in body length. Most are found in freshwater. *Halovelia* is an exclusively marine genus with more than 50 described species, commonly found among intertidal rock pools around tropical islands (Andersen, 1989).

***Halovelia convexa* Andersen, 1989**

Halovelia convexa is a tiny marine bug, with adults measuring about 2 mm in body length. It appears to be endemic to the Maldives (Andersen, 1989). Specimens were first reported by Phillips (1959) from Seenu (=Addu) Atoll, as *Halovelia* sp. It was subsequently described as *Halovelia convexa* by Andersen (1989) based on Phillips' Seenu material and additional specimens, also collected by Phillips, from Dhoonidhoo Island, Kaafu (North Malé) Atoll, in 1958. We collected *Halovelia convexa* only once (Table 1, sample 8), in June 2002, from rocky pools on the reef flat at low tide, 20 m or more from the beach at the southern end of Kulhudhfushi Island, Haa Dhaalu Atoll in the north of Maldives. There were many mating pairs. The habitat was very similar to that in Seenu Atoll described by Phillips

(1959): "clear weedless pools left by the receding tide on the outer aspects of the reef, often 200 feet [60 m] or more from the shore". Although known from rather few samples, *H. convexa* is widely distributed throughout the Maldives (Fig. 2E). Within the genus *Halovelia*, *H. convexa* is part of the *H. malaya*-group, which occurs from the western Indian Ocean to the Solomon Islands, and probably originated in Southeast Asian waters (Andersen, 1989).

Order Diptera

Family Chironomidae Newman, 1834

Genus *Pontomyia* Edwards, 1926

The midge genus *Pontomyia* is exclusively marine, with three known species widely distributed along island shores of the Indo-Pacific and an un-assigned species from the Atlantic Ocean (Huang et al., 2014). *Pontomyia* are unique marine midges with their larval life spent entirely underwater among submerged plants or algae. The males have modified wings but are completely flightless, while the females are larviform, completely wingless and almost entirely legless. Adults lack functional mouthparts and do not feed after emergence (Huang & Cheng, 2011). They have one of the shortest known adult life spans, with males living from 1–3 hours and females dying shortly after mating and egg-laying (Cheng & Collins, 1980).

Pontomyia natans Edwards, 1926

Pontomyia natans was first reported from the Maldives by Cheng (2004). In addition to the two samples reported by Cheng (2004; also listed in Table 1 as samples 1 and 3), two other samples are reported here (numbers 20 and 28); all were collected from shallow lagoons or small bays adjacent to islands. *Pontomyia natans* has the lowest habitat score (i.e., was the most inshore) of any of the marine insect species in our study (Table 2). Although we have data from only four samples, their timings do suggest the possibility that *P. natans* shows both annual seasonality and lunar periodicity in its reproduction. Our marine insect samples were collected in every month of the year except July (Table 1), and yet three of our four *P. natans* samples were collected between 21 March and 11 April, suggesting the possibility of reproductive seasonality; late March and early April is the calm inter-monsoon period when the northeast monsoon season gives way to the southwest monsoon. In addition, all four samples were collected close to the new or full moon, suggesting the possibility of adult emergence and reproductive activity in the Maldives being closely correlated with lunar cycles (Table 3) and the tides, as has been reported for other *Pontomyia* species (Cheng & Collins, 1980; Neumann, 1986; Soong et al., 1999). This is in contrast to the situation for *P. natans* in Taiwan, where it showed no clear pattern of emergence in relation to moon phase (Soong et al., 1999). Note that due to a misprint in Cheng (2004: 56), species names were transposed, and in referring to the Taiwanese study the text should have read: "Adults of *P. oceana* emerged only during new moon or full moon periods while those of *P. natans* emerged almost every night during the study period". Despite its tiny adult size and apparently limited ability to disperse, this species is widely distributed from the Maldives to Samoa; within Southeast Asia it has so far only been recorded from Pulau Tioman, Malaysia, as well as from Christmas Island (Huang & Cheng, 2011; Huang et al., 2014). However, a phylogenetic study revealed that larval specimens of *Pontomyia* from Puerto Rico in the Atlantic were nested within the *P. natans* clade (Huang et al., 2014); further study of this unexpected result is ongoing.

Table 3. Dates of collection of *Pontomyia natans* relative to moon phase.

Sample no.	Date collected	Date of Full or New Moon
1	11 April 1998	Full, 11 April 1998
3	30 March 1999	Full, 31 March 1999
20	21 March 2004	New, 20 March 2004
28	3 August 2005	New, 5 August 2005

CONCLUDING REMARKS

Prior to this study, five species of marine insect had been recorded from the Maldives. All five were collected during this study, and an additional species, *Halobates germanus*, was collected for the first time. Despite the lack of prior records, *H. germanus* appears to be the most common marine insect in Maldivian waters, having been collected more often than any other *Halobates* and in greater numbers than any other species. The lack of previous samples of *H. germanus* may in part be due to earlier sampling having been carried out either far offshore (*Dana* Expedition) or close to atolls and islands, while the preferred habitat of *H. germanus* appears to be intermediate waters.

Habitats of the marine insects collected during this study broadly agreed with existing knowledge. Known coastal or inshore species (*Halobates formidabilis*, *Halovelia convexa*, and *Pontomyia natans*) were only found in shallow lagoons, adjacent to islands or on reef flats (Table 2). *Halovelia convexa* was only found over reef flats and was the only species that was not collected with any other species. The two most commonly collected species were *Hermatobates djiboutensis* (occurring in 25 of 55 samples) and *Halobates germanus* (23 of 55). These two were also found in the widest range of habitats, from waters directly adjacent to islands to the open sea. However, *H. djiboutensis* was most frequently found in open waters inside atolls, while *H. germanus* occurred most frequently in open waters outside the atolls. Finally, *H. micans* was the only species not collected immediately adjacent to islands. It was the only species found far offshore in the *Dana* Expedition samples (Herring, 1961) and the only species that did not co-occur with any of the three inshore species. This is to be expected

since it is a truly open-ocean species, unlike *H. germanus* which tends to occur rather closer along continental and island shores (Cheng, 1989; Cheng et al., 2012).

The known distributions of these six marine insect species in and around the Maldives are shown in Fig. 2A–F. It appears that all six may occur throughout the archipelago. This is apparent even for species that have only been recorded a few times (*H. formidabilis*, *H. convexa*, and *P. natans*). More intriguing is the possibility that two species (*H. djiboutensis* and perhaps also *H. micans*) may be more common among the northern and central atolls of the Maldives than in the south. This might be explained by differences in oceanography between the south of the Maldives compared with the north and centre, the south being more under the influence of Equatorial currents, while the north and central atolls are more affected by seasonally reversing monsoon currents. These differences are known to affect the distribution and abundance of other marine species in the Maldives, for example tunas and reef manta rays, *Mobula alfredi* (Anderson et al., 1998, 2011). However, it seems equally possible that this is simply a reflection of the relative lack of sampling in and around the southern atolls (with the exception of Seenu Atoll). Further sampling in Laamu and Huvadhoo (= Gaafu Alifu and Gaafu Dhaalu) Atolls should resolve this issue.

Nothing is known about predation on marine skaters in Maldivian waters, although seabirds have been noted as key predators elsewhere (Cheng & Harrrison, 1983; Cheng, 1985; Cheng et al., 2010). From Sri Lankan waters, adjacent to the Maldives, Henry (1971: 338) found a "mass" of *Halobates* in the stomach of a Bridled Tern (*Onychoprion anaethetus*) which he dissected. Seabirds including the Bridled Tern, other Terns (*Sterna* spp.) and Noddies (*Anous* spp.) are seasonally abundant in the Maldives (Anderson & Shimal, 2020) and are likely to be significant predators of marine skaters there.

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