Distribution and Characteristics of *Halobates germanus* Population in the Red Sea

Gauri A. Mahadik[1]*, Susana Agusti[1] and Carlos M. Duarte[2]

[1] Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia, [2] Red Sea Research Center and Computational Bioscience Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

We investigated the occurrence of the sea skater *Halobates* spp. from samples collected at a fixed time series station and from six cruises along the north-south extend of the Red Sea during 2016–2018. *Halobates germanus* White, 1883 was the only species found during our study, its distribution ranging between 17° 9′N and 27° 27′N and between 35° 67′E and 41° 49′E. Total *H. germanus* abundance ranged between zero to 158,610 individuals km^{-2} with a considerable temporal (at the fixed station) and spatial (cruises) variation. In general, nymphs of different instar stages dominated the population, followed by females and males. The sex ratio was female-biased, with a higher number of females than males. Presence and prevalence of eggs, exuviae (molts), and early nymphal stages indicate a year round breeding cycle by *H. germanus*. The apparent optimum temperature for *H. germanus* occurrence in the central Red Sea was at 28.2°C, corresponding to peak abundances in spring and fall. Absence of any significant correlation of the abundances with environmental parameters indicate relative resilience of *H. germanus* to changes in environmental conditions.

Keywords: *Halobates*, sea skaters, neuston, abundance, population structure

INTRODUCTION

The surface microlayer of the sea is a highly dynamic and productive area inhabited by highly adapted organisms of the neuston and pleuston communities. The marine water strider or sea skater *Halobates* spp. (Hemiptera, Gerridae) is the only truly oceanic group of insects (i.e., completing their entire life-cycle in the open ocean), with a specialized epineustonic habit (Cheng, 1973, 1985; Andersen, 1991; Andersen and Cheng, 2004). Oceanic *Halobates* species were first discovered during a circumnavigation expedition on board a Russian vessel Rurik between 1815 and 1818, and further studied in the Challenger Expedition, half a century later (Andersen and Cheng, 2004).

Five species of sea skaters *Halobates* namely *H. germanus* White 1883, *H. micans* Eschscholtz, 1822, *H. sericeus* Eschscholtz, 1822, *H. sobrinus* White, 1883, and *H. speldens* Witlaczil, 1886, live permanently in the open ocean, at the air-sea interface (Herring, 1961; Cheng, 1985; Andersen, 1991). Both adults and juveniles spend their entire life on the sea surface, always at some distance from land (Andersen and Cheng, 2004). They prey on other animals of the pleustonic community and are themselves preyed upon by seabirds and pelagic fish (Cheng and Harrison, 1983; Cheng, 1985; Senta et al., 1993; Cheng et al., 2010). Most of the 47 species of *Halobates* that have been described so far are often associated with mangrove ecosystem and many are endemic to specific

islands or island groups (Andersen and Cheng, 2004). The different oceanic species seldom co-occur, and areas of high density rarely overlap (Cheng and Shulenberger, 1976; Ikawa et al., 2004). Typically, only one *Halobates* species is dominant in any particular area and boundaries between ranges are often sharply delineated (Ikawa et al., 2012). Their occurrence is restricted mainly to the warm tropical and subtropical waters, roughly between latitudes 40°N and 40°S, where the winter temperature does not fall much below 20°C (Cheng, 1989; Andersen, 1991; Andersen and Cheng, 2004; Ikawa et al., 2007).

The Red Sea is an unique tropical oligotrophic embayment harboring the most diverse and endemic biota in the world (Dibattista et al., 2016). It is largely a coastal ocean, with a deep (up to 2,800 m) central zone and extensive shallow areas of varied habitats including mangroves, seagrass beds and coral reefs (Bruckner et al., 2011). This narrow desert-enclosed water body is characterized by distinctly high temperatures, high salinity levels of up to 41‰ (Douabul and Haddad, 1970; Âbdallah, 1985) and receives high surface irradiance (Winters and Geesthacht, 2003) year around. A strong latitudinal gradient of temperature extending from the far north (with an annual mean sea surface temperature of 26°C ± 1°C) to the south (with an annual mean sea surface temperature of 31.3°C ± 1.1°C), and a remarkable differences in salinity and primary productivity along this gradient supports a highly diverse and productive ecosystems along the entire coast (Raitsos et al., 2013; Sawall et al., 2015; Chaidez et al., 2017).

Several studies have explored the planktonic communities of the Red Sea (e.g., Holdway and Maddock, 1983; Bottger Schnack, 1995; Pearman and Irigoien, 2015), however, the knowledge of distribution and occurrence of *Halobates* in the region is sparse. Presence of three species of the genus *Halobates* namely *H. hayanus*, *H. melleus* (synonym: *H. mangrovensis*), and *H. germanus* have been previously reported in the Red Sea and its adjoining waters (Schmidt and Muller, 1973; Cheng, 1985). *H. hayanus* was found near Mersa Halaib (southern Egypt), in the Gulf of Zula and off Aden. *H. germanus* has been recorded frequently from the Gulf of Aden and in the Red Sea. *H. melleus* which lives very close to the shore was found under the mangroves of Nabq (Gulf of Aqaba) and in the Gulf of Zula. Here, we present the distribution, abundance and population structure of *Halobates*, along an extensive area of the Saudi Arabian coast of the Red Sea extending from the mouth of Gulf of Aqaba in the north (28°.03′N) to Jizan in the south (17°.32′N), based on samples collected from a fixed time series and cruise surveys over a period of 2 years.

MATERIALS AND METHODS

Study Sites
Samples were collected from a fixed pelagic time series station (22.3093°N, 38.9612°E) between September 2016 and May 2018 and from several locations along the north-south extent of the Saudi Arabian coast of the Red Sea during six cruises during 2016–2017 (**Figure 1**). The sampling areas were identified along the latitudinal extend of the Red Sea as: the southern Red

Sea (SRS) (between 15°and 20°N), the central Red Sea (CRS) (between 20°and 23.3°N) and the northern Red Sea (NRS) (beyond 23.3°N). The pelagic time series station was located in the off-shore waters of the CRS, nearly 13 km from the coast. The stations surveyed during the cruises extended between 2.5 and 151.4 km away from the land, covering coastal habitats of mangrove, saltmarsh, seagrass meadows, coral reefs, and pelagic open waters. Sea surface temperatures ranged between 24.6 and 32.1°C (28.7 ± 2.41) at the fixed station. At the fixed station, fortnightly sampling frequency yielded 38 samples, while a total of 81 samples were collected during the cruises (**Figure 1**).

Sampling
Sampling was carried out using a 200 µm rectangular neuston net with a 60 cm × 20 cm mouth opening at the fixed station, and a 150 µm net with 50 cm × 15 cm mouth opening for all the cruises. The net was deployed from the side of the vessel to avoid the propellers and was typically towed at the sea surface for 30 min at 2 knots. During the entire towing operation, the net was regularly monitored to ensure that the mouth opening remained 2/3 rd submerged under water. The effective surface area of water sampled was estimated by multiplying the width of the nets and the distance covered during the tows. All samples at the fixed station were collected during day time (mid-day), while sampling during the various cruises was carried out at different times of the day. At the fixed station, temperature and salinity of the sea surface was recorded using an Idronaut Ocean seven 316 Plus profiler. Once aboard, the net was rinsed with seawater and the contents were concentrated into the cod-end jar. The sample was then transferred carefully in labeled storage bottles with the help of a funnel and stored in 96% ethanol.

Identification and Determination of Abundance
The insects were sorted from the rest of the neuston and preserved in 96% alcohol. They were all identified as far as possible to species, sex and developmental stage. The life cycle of *Halobates* includes egg, nymph (N) instars at different stages of development, and the adult stage of female (F) and male (M) (Cheng, 1981). Identification was carried out using the Key for the Identification of *Halobates* Eschscholtz and Related Genera (Hemiptera-Heteroptera: Gerridae) (Andersen and Cheng, 2004). Male specimens were mainly used for species level identification and females were used in absence of males in the samples. All the stages of nymphs were assumed to be of the same species as the adults. Nymphs were further separated into four group as nymph I (1st and 2nd instar stages), nymph II (3nd instar stage), nymph III (4th instar stage) and nymph IV (5th instar stage) according to their body size. Presence of eggs and exuviae (molts) of *Halobates* and occurrence of other insects in the samples was also reported. Identification and counts were performed using a Leica IC80 HD stereoscope microscope.

Data and Statistics Analysis
We have included the data from both positive and negative tows for the estimation of total abundances (F + M + N). Abundance
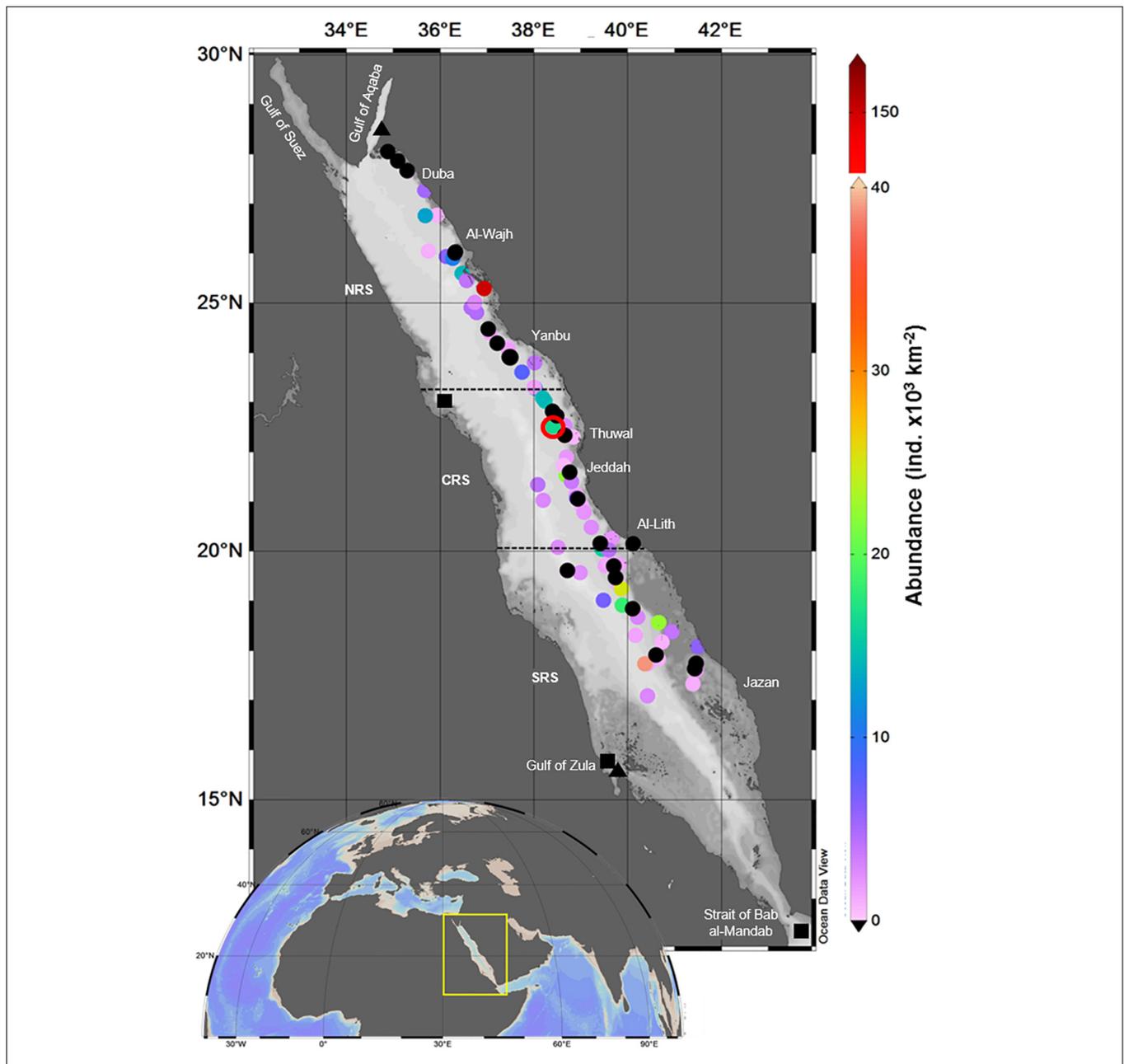
FIGURE 1 | Sampling locations (colored dots, time series station outlined in red) and corresponding abundance of *Halobates germanus* (individuals × 10^3 km^{-2}) in the Red Sea during 2016–2018. The regions of the northern Red Sea (NRS), the central Red Sea (CRS), and the Southern Red Sea (SRS) are delineated with black dash lines. Abundance values are represented according to the color palette on the right. Note the difference in the scale bar. Black dots correspond to locations with negative tows (absence of *H. germanus* in the samples). Abundance at the time series station is the average of 38 samples. Previously reported occurrence of other two species, *H. melleus* (black triangle) and *H. hayanus* (black square) is also shown.

values are individuals caught per standard tow reported as number of individuals km^{-2} (ind. km^{-2}). Abundance estimates are conservative given the net avoidance behavior exhibited by *Halobates.* For reporting the percentages of each developmental stage in the entire population, we have used the values only from the positive tows with nymphs (26 and 44 positive tows, at the fixed station and the cruise survey, respectively). Values are presented as mean ± standard error. Each data point represents

at least one net tow or the mean of several net tows of comparable sampling efficiency. Seasons were categorized as spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

Sex ratio was estimated as the number of males per 100 females (M:F) and a chi-square test was used to verify departures from a 1:1 sex ratio. Abiotic parameters such as temperature, salinity, chlorophyll *a* and oxygen were tested by linear correlation to

analyze if any of them could explain the variability of *Halobates* distribution. Also, Pearson's correlation was used to assess whether there is a correlation between the abundance and the distance from the coast. One-way analysis of variance (ANOVA) was used to test for differences in the abundance and percentage values. Significant differences were recorded at $p < 0.05$. Data and statistical analyses were carried out using Microsoft® Excel 2013. Multivariate analysis was performed using R.

RESULTS

Distribution and Abundance

During this study, a total of 119 samples were collected across the different locations along the Saudi Arabian coast of the Red Sea. Individuals were recorded up to 17°.09′N in the SRS, however, no individuals were recorded north of 27° 27′N in the NRS, the longitudinal range of their occurrence was between 35° 67′ and 41° 49′E (**Figure 1**). Although there was no correlation between the abundance and the distance of sampling locations from the coast (Pearson's correlation coefficient, $r = -0.04$, $p > 0.05$), no individuals were found in samples collected at stations within 6.0 km from the coast, irrespective of the habitats.

A total of 464 individuals of *Halobates* were caught from the 91 positive tows. In general, during the survey, 23.5% of the tows did not yield any insects. Also, for the positive tow, the number of insects caught per tow varied greatly with catches ranging from 1 to 220 individuals (**Table 1**). The population of *Halobates* was exclusively of *H. germanus* White, 1883, individuals (**Figure 2**). At the fixed station, the abundance ranged between 2,030 and 86,200 ind. km^{-2}, with a mean value of 16,250 ± 2,640 ind. km^{-2} (**Figure 3**). Out of the 38 samples, 18% of the samples did not have any sea skaters and 7.89% of samples had only exuviae but no sea skaters. For the cruise samples, the total abundance ranged broadly between 630 and 158,610 ind. km^{-2}, with a mean of 6,180 ± 2,050 ind. km^{-2}, with 25.92% of the 81 samples had no individuals or exuviae present (**Table 1**). There was no significant difference in the abundance with latitude, the mean abundance values being similar in the NRS, CRS and SRS (ANOVA, $p = 0.43$).

Life Cycle Components and Population Structure of *H. germanus*

The populations of *H. germanus* at the fixed station and the cruise survey were composed of nymphs at different stages of development (**Figures 2A–E**), adults (**Figures 2F,G**), eggs (**Figure 2H**), and exuviae (**Figure 2I**). Both at the fixed station and during the cruises surveys, nymphs were dominant and represented 87.2 ± 16.8 and 57.6 ± 4.5% of the total population, respectively, followed by females and males (**Figures 4A, 5A**). Exuviae were found in 55.2% of the fixed station samples and 28.4% of the cruise samples (**Figures 4A, 5A**). Eggs, mostly attached to floating *Sargassum* pneumatocyst (**Figure 2H**), were found in all seasons; in 7 tows at the fixed station (February, March, September, and November) and in 10 cruise samples, collected in the months of March, April, July, and November. Nymphs including instar 1st, 2nd, 3rd, 4th, and 5th were identified across different samples. In general, the 1st and 2nd instar were more abundant and together comprised 49.9 ± 10.0 and 48. 7 ± 4.7% of the total nymph population at the fixed station and for the cruises, respectively. The abundance of nymphs declined with increasing instars, percentage contribution of the 5th instar being the least at the fixed station and for the cruise stations (**Figures 4B, 5B**).

Seasonal variations were observed in the population structure at the fixed station as well as in the samples collected during the cruises, although the difference were not significant. At the fixed station, nymphs dominated the population in all seasons except during summer when the population was exclusively of females (**Figure 4A**). During the remaining seasons, the sex ratio was also female-biased, with highest value of 0.33 during winter. Abundance of exuviae was highest during spring, followed by fall and showed a sharp decline during summer and winter (**Figure 4A**).

For the cruise samples, adults and nymphs were present in the population during all the seasons despite the seasonal changes in their composition (**Figure 5A**). The population structure was similar during spring and winter, with the highest percentage of nymphs followed by males and females and a sex ratio of 0.53 and 0.55, respectively. During summer, nymphs

TABLE 1 | Overview of neuston sampling in the Red Sea during 2016–2018.

No.	Year	Sampling period	No. of tows (no. of tows with *Halobates* including exuviae)	Min–max number of individuals caught per tow	Total (female + males + juveniles) caught during the cruise	Abundance ind. × 10³ km⁻² (mean ± SE)
1	2016	September 20–27	16 (7)	1–3	16	0.74 ± 0.24
2	2016	November 6–9	7 (5)	1–23	61	5.65 ± 2.23
3	2016	November 21–December 1	14 (12)	1–34	68	4.47 ± 1.84
4	2017	March 1–13	18 (12)	1–36	101	3.76 ± 1.74
5	2017	March 31–April 6	7 (6)	1–61	85	8.19 ± 5.16
6	2017	July 9–21	19 (18)	1–220	366	13.76 ± 8.13
Time series	2016–2018	September 2016–May 2018	38 (31)	1–96	333	16.25 ± 2.64

Sampling period, total number of tows performed during each cruise (number of positive tows), range for number of individuals caught during different tows for each cruise (min–max), total number of individuals caught during the cruise (sum of adults and nymphs) and abundance of individuals per unit area (mean ± standard error).
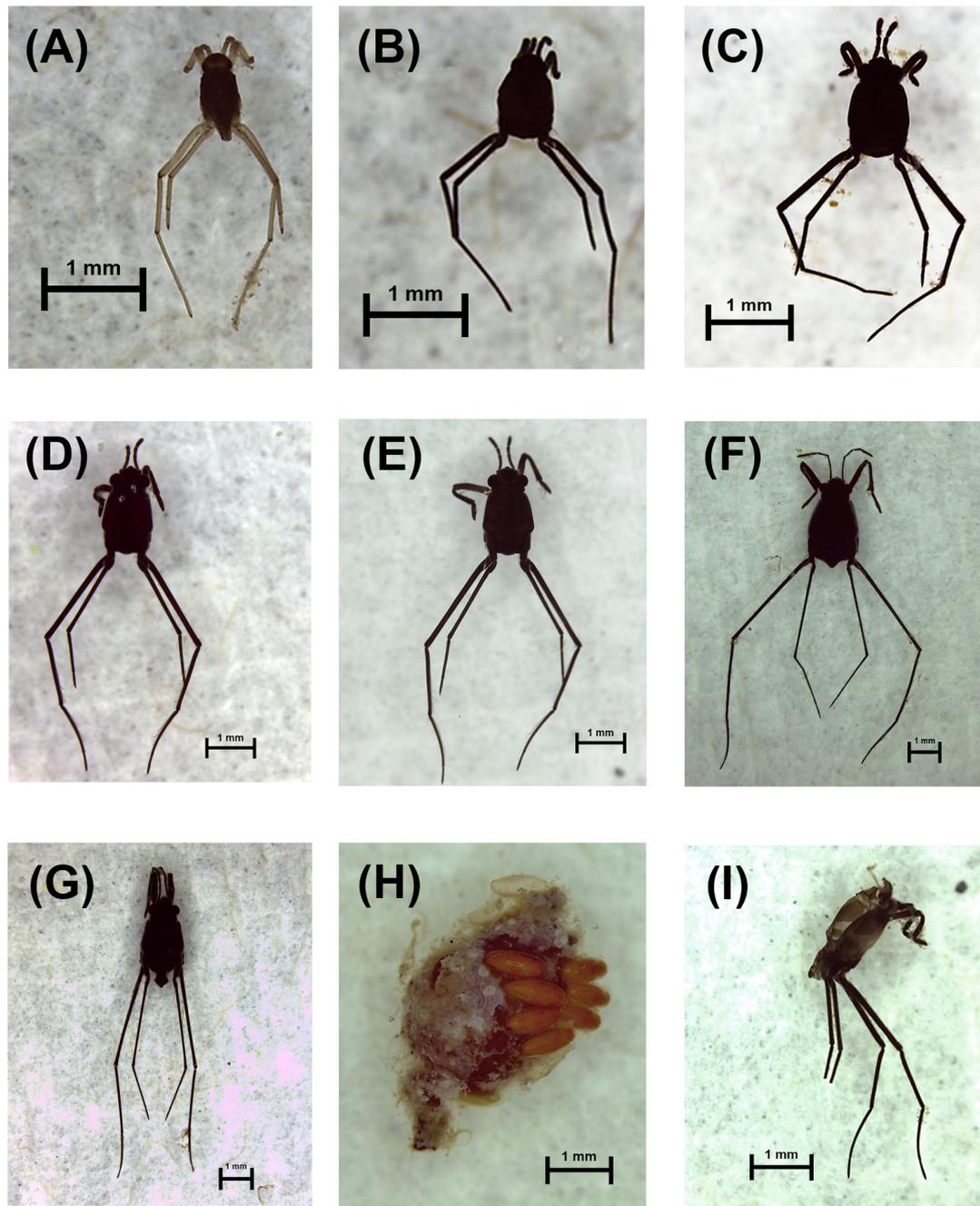
FIGURE 2 | Different stages of life cycle of *Halobates germanus*. **(A–E)** 1st to 5th instar stages, **(F)** adult female, **(G)** adult male, **(H)** eggs on *Sargassum* spp. pneumatocyst, and **(I)** exuviae. All scale bars = 1 mm.

still dominated the population, but the percentage of females was higher than that of the males, resulting in a female-biased sex ratio of 0.40. The fall population was dominated by females (67.5%), followed by the nymphs and males. The sex ratio during fall was therefore highly female biased (0.11). Occurrence of exuviae co-occurred with the nymph population, with the highest and lowest number of exuviae found during summer and fall, respectively. During spring and winter, similar

to the population structure, the number of exuviae was also similar (**Figure 5A**).

Environmental Parameters at the Fixed Station

At the fixed station, the temperature recorded ranged between 24.4 and 32.1°C (mean ± SE: 28.7° ± 0.4°C). Salinity ranged
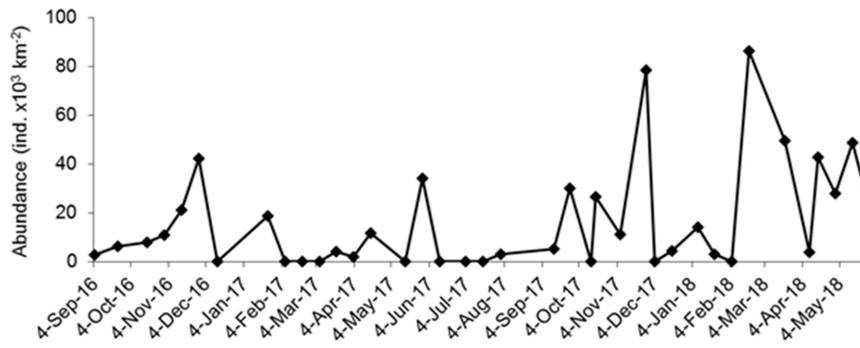
FIGURE 3 | Variation in the abundance (individuals × 10³ km⁻²) of *Halobates germanus* population (females, males, and nymphs) at the fixed station in central Red Sea during 2016–2018.
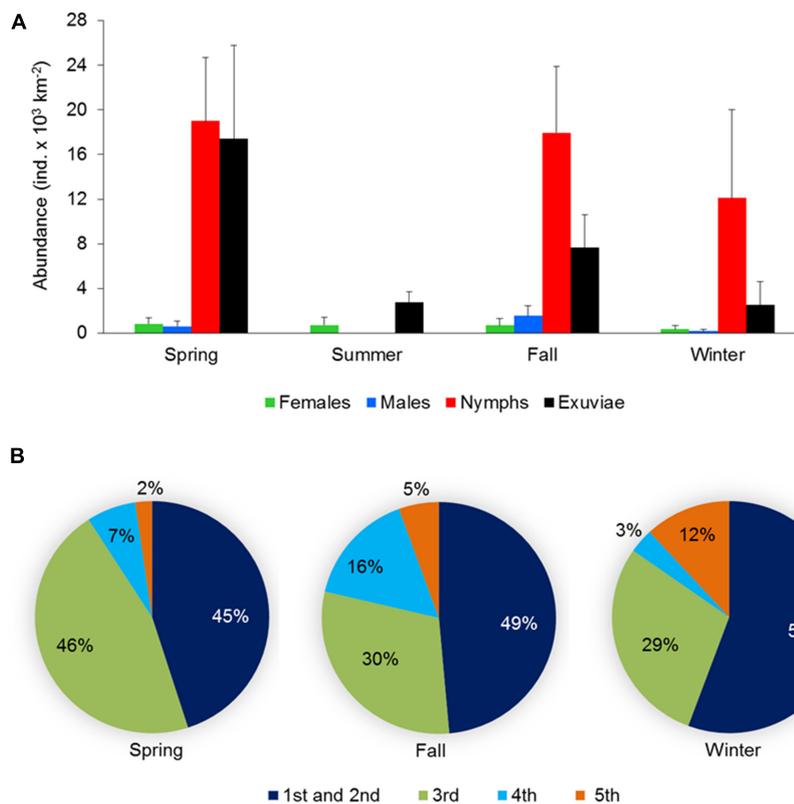

FIGURE 4 | (A) Abundance and population structure (females, males, and nymphs) and exuviae of *Halobates germanus* during different seasons and **(B)** relative contribution of different instar stages to the total nymph population observed at the fixed station in central Red Sea during 2016–2018. Error bars indicate standard error of the mean.

from 37.9 to 40.9 PSU (mean ± SE: 39.3 ± 0.1). Oxygen at the surface ranged between 4.2 and 6.4 ppm (mean ± SE: 5.4 ± 0.1 ppm). Chlorophyll *a* values varied significantly ranging between 0.1 and 0.8 µg L⁻¹ (mean ± SE: 0.4 ± 0.0). Temperature and salinity showed a similar trend with higher values during summer and fall, and relatively lower values during spring and winter. Oxygen was inversely related to the temperature. Chlorophyll *a* was higher during winter and lowest during summer.

There was no significant correlation of the abundance of *H. germanus* (total, adults and nymphs) with temperature ($r^2 = 0.01$, $p = 0.57$), salinity ($r^2 = 0.00$, $p = 0.77$), or chlorophyll *a* ($r^2 = 0.11$, $p = 0.09$) (**Figure 6**). However, there was a parabolic relationship between the abundance of *H. germanus* and sea surface temperature, suggesting a narrow temperature range for *H. germanus*, with an apparent optimum temperature estimated as 28.2° C (**Figure 7**).
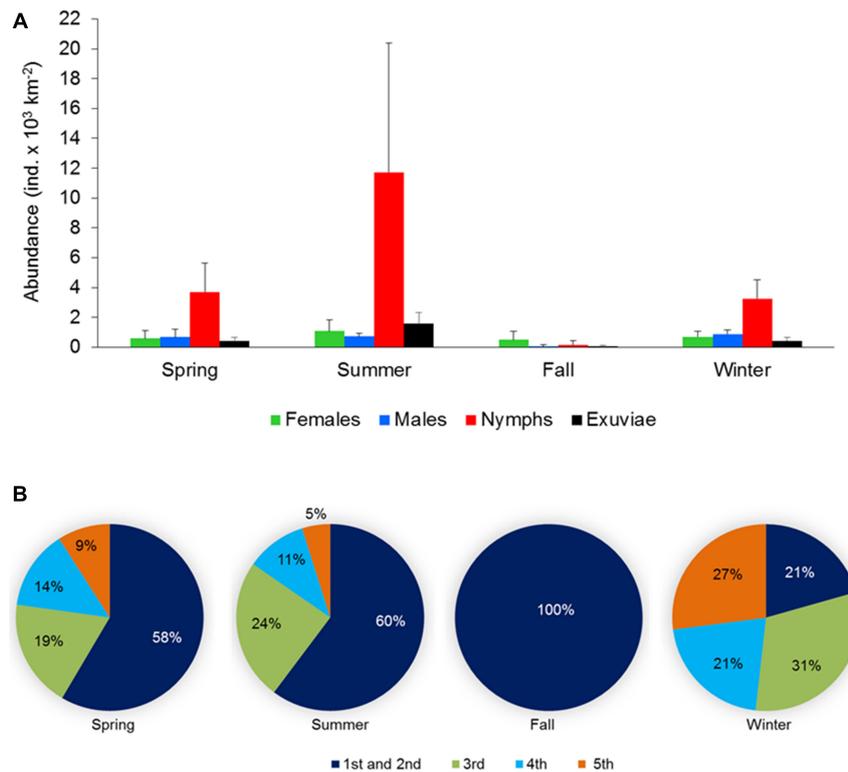
FIGURE 5 | (A) Abundance and population structure (females, males, and nymphs) and exuviae of *Halobates germanus* and **(B)** relative contribution of different instar stages to the total nymph population during different season observed at different locations surveyed during the cruises along the north-south extend of the Red Sea during 2016–2018. Error bars indicate standard error of the mean.
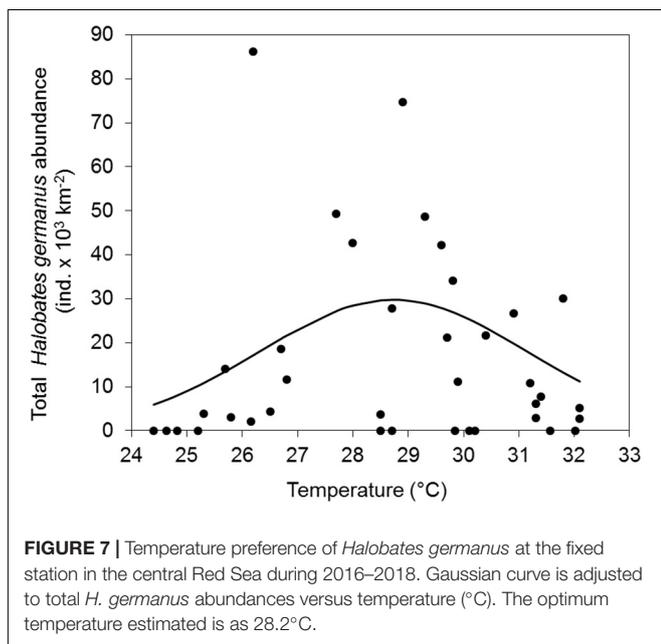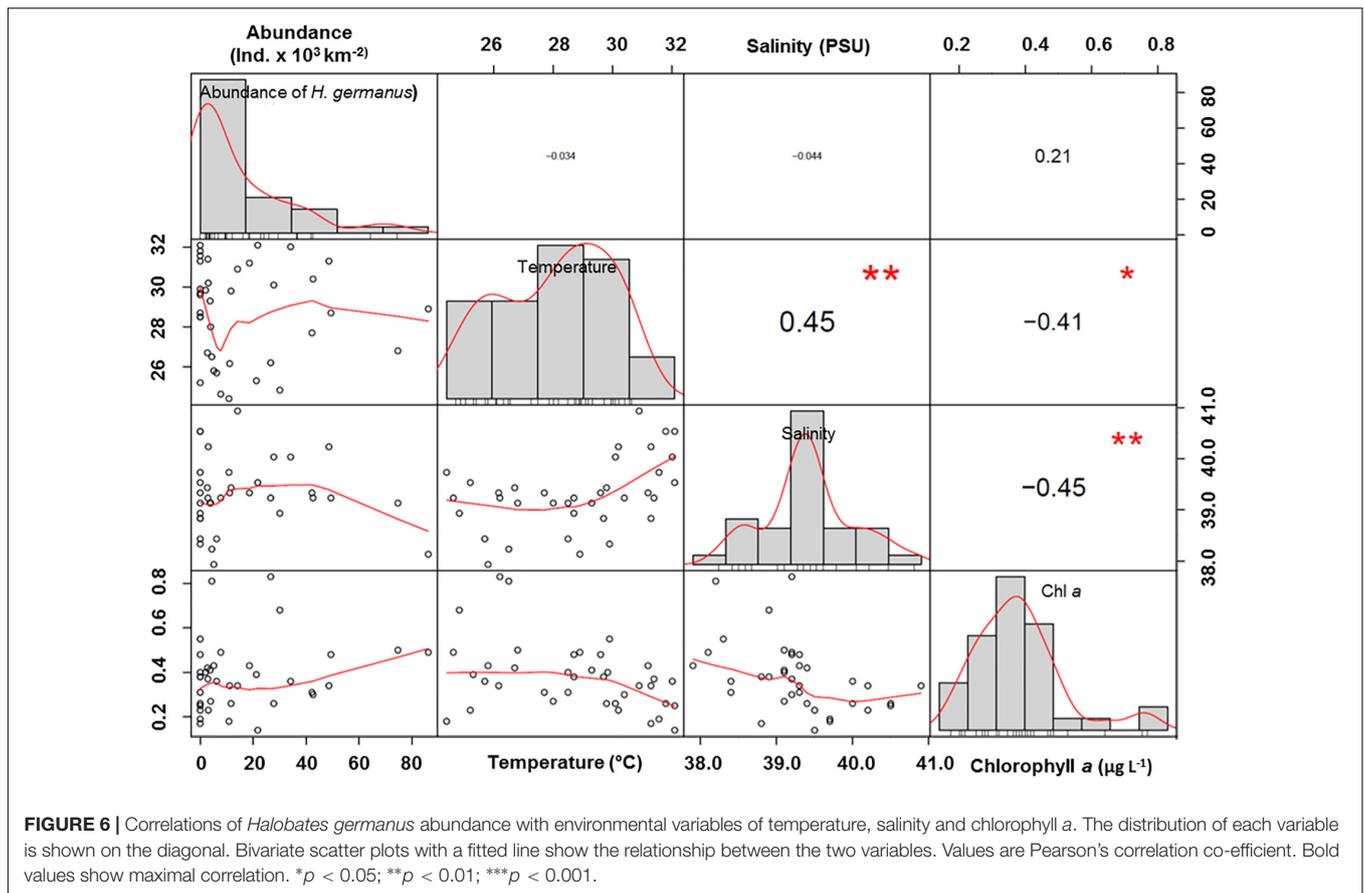
DISCUSSION

Distribution and Abundance

Halobates germanus was the only species found in the samples collected from several locations during this study, extending from the northern tip of the Red Sea to the south. On a global scale, the presence of *H. germanus* is reported in a latitude band extending from the Equator to 40°N in the northern hemisphere (Andersen and Cheng, 2004), except for the Mediterranean Sea (Cheng et al., 2012). Its distribution is restricted to the western and central half of the Pacific Ocean and the Indian Ocean. In the Indian Ocean, its range skirts the land masses and it is commonly found around the islands and island groups of the Indo-Malaysian region (Herring, 1961). *H. germanus* is the only pelagic species found in the Red Sea and the Gulf of Aqaba (Schmidt and Muller, 1973; Cheng and Holdway, 1983; Cheng, 1989). Previously, the presence of *H. germanus* has been documented in the Red Sea and in the adjoining Gulf of Aden (Sagaydachnyy, 1975; Cheng and Holdway, 1983), its distribution extending from near the northern tip of the Red Sea (Schmidt and Muller, 1973) to the southern two-thirds of the sea (Cheng and Holdway, 1983). In addition to *H. germanus*, two other species of *Halobates* associated with mangrove habitats, namely, *H. hayanus* and *H.* melleus, Linnavuori, 1971 (H. *mangrovensis*) have also been reported from the Red Sea (Schmidt and Muller, 1973;

Por et al., 1977; Andersen and Cheng, 2004), but we did not find any of these species in our study. While we sampled different ecological habitats like mangroves, seagrass meadows and coral reefs during our survey, the sampling stations did not cover areas very close to the land, the closest sampling point being 2.45 km away from the land. Given the distribution of these two species being restricted to the shallower, nearshore areas, very close to the land, it is possible that these two species were not caught during our survey. In fact, *Halobates* individuals were caught only in locations beyond 6.07 km away from the land during our survey.

Halobates germanus is characterized among the five oceanic *Halobates* species for a tendency to stay closer to the coasts than other oceanic species (Cheng, 1989). Preference for areas close to islands or margin of continents suggests a stronger affinity of *H. germanus* for coastal environments (Ikawa et al., 2008, 2012). Polhemus (1990) reported the occurrence of this species nearly one kilometer or more offshore, either over the fore reef or on the deeper offshore waters of the Aldabra and Cosmoledo atolls in the western Indian Ocean. During the 2 year circumnavigational cruise of "Operation Drake," individuals of *H. germanus* were caught at several stations in the Gulf of Aden and the Red Sea with population densities up to 24 individuals per standard 30-min tow. No specimen was however, caught in the open stretch of the Indian Ocean (Cheng and Holdway, 1983). Difference in food preferences has been suggested to be a possible explanation for

FIGURE 6 | Correlations of *Halobates germanus* abundance with environmental variables of temperature, salinity and chlorophyll *a*. The distribution of each variable is shown on the diagonal. Bivariate scatter plots with a fitted line show the relationship between the two variables. Values are Pearson's correlation co-efficient. Bold values show maximal correlation. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

FIGURE 7 | Temperature preference of *Halobates germanus* at the fixed station in the central Red Sea during 2016–2018. Gaussian curve is adjusted to total *H. germanus* abundances versus temperature (°C). The optimum temperature estimated is as 28.2°C.

open waters of the CRS (extending 151.3 km) from the coast, the further distance from the shore possible in this narrow sea.

In terms of density (abundance of individuals per square kilometer), the values in this study are comparable to abundances of *H. germanus* reported in the Pacific Ocean (11,688) (Furuki et al., 2016), Western Pacific Ocean (4,100), East China Sea (12,000) (Ikawa et al., 2004), Banda Sea (15,000) (Cheng et al., 1990), and in the Red Sea (22,500) (Cheng and Holdway, 1983). The average number of individuals caught per tow during this study was 4.3 ± 1.6 (5.1 ± 1.7 considering only the positive tows). These values are much lower than previously reported a mean of 27.3 individuals per tow in the Red Sea (Cheng and Holdway, 1983). Also in the Indian Ocean and Java Sea, similarly higher values with catches of 25.6 and 46.2 individuals of *H. germanus* have been reported. The highest number of individuals per tow (220) during this study was higher than previously reported catch of 78 and 141 individuals per tow in the Red Sea and the Java sea, respectively (Cheng and Holdway, 1983), but lower than the catch of 584 individuals caught in a single tow in the Banda sea (Cheng et al., 1990).

In addition to the wide range of the number of individuals caught per tow (0–220), a significant difference was observed in abundance values both at the fixed station and the cruise stations. While these variations could be primarily due to geographical and environmental factors, they could also be due to the occasional patchy occurrence of *Halobates* in the sea. Individuals

the prevalence of *H. germanus* in coastal water unlike the other oceanic *Halobates* species (Sagaydachnyy, 1975). However, based on our samples, we document the presence of *H. germanus* in the

of *Halobates* are known to form aggregations called *flotillas*, where they gather in high densities of 500 m^{-2} to avoid predation (Treherne and Foster, 1980, 1982). Also, *Halobates* can sense the approaching nets and are able to escape the nets by skating away (Cheng and Enright, 1973). We, therefore, consider our estimates of abundance, as well as other estimates reported, to be conservative due to possible net avoidance behavior by *Halobates*.

Life Cycle and Population Structure

During this study, we report the occurrence of adults, nymphs of all five instar stages of *H. germanus*, eggs as well as exuviae across the extensively surveyed area of the Red Sea. Oceanic *Halobates* species are independent of land throughout their entire life-cycle, and display specialized reproductive strategies like mating and egg-laying at the sea surface. They seem to reproduce all year around (Spence and Andersen, 1994; Andersen and Cheng, 2004) and the entire life-cycle from egg to adult may take 2–3 months (Herring, 1961; Cheng, 1985). The long oviposition period, rather low growth rates and long life spans could have been selected due to their extremely harsh and unpredictable environment of the ocean surface, where strong winds and storms occur too frequently to allow them to form a stable localized aggregation and to complete even one generation. This adaptive life cycle strategies would give them better chances to find conspecifics, food and suitable habitats to regroup and reproduce even after they are dispersed over long distances (Ikawa et al., 2012).

The nymphs resemble adults in general external morphology but are smaller. The first-instar nymphs measure only about 1 mm in body length, and go through five molts before reaching the adult stage. While there is no information available on the diet of the early nymphal stages, adults and older nymphs are predators, preying upon small zooplankton trapped on the sea surface (Cheng, 1985). Their mouthparts are of piercing and sucking type, an adaptation for preying by penetrating and then sucking the fluids out of the prey. Cannibalism is also not uncommon and usually involves adults feeding on small sized nymphs (Spence and Andersen, 1994). The occurrence of cannibalism seems to be dependent on the availability of alternate food source (Andersen and Cheng, 2004). Moreover, the oceanic species also have a food reserve in the form of neutral triglyceride lipids (Lee and Cheng, 1974), which may allow it to withstand much longer periods of starvation. Higher abundance and dominance of nymphs, especially the early 1st and 2nd instars during this study, indicates their prevalence throughout the year across the surveyed area. Moreover, the presence of eggs and exuviae in the samples during all the seasons also suggests a year round reproductive and growth of this species.

In general, the sex ratio was highly female-biased during this study. Relatively higher proportion of females than males, resulting in female-biased sex ratios, have also been reported for *H. micans* (Miyamoto and Senta, 1960; Cheng, 1971; Dias and Lopes, 2009). Cheng (1971) suggests that such predominance of females in the population may be due to their prolonged longevity, permitting them to lay their full complement of eggs. An extended lifespan would also increase the chance of finding

a suitable flotsam, which is generally scarce in open ocean, for oviposition until some days after egg maturation and mating, a life-cycle strategy important for the reproductive success of the species. Conversely, the predominance of females can also be beneficial for proliferation of the species as each male can mate with several females (Dias and Lopes, 2009).

Relationship of *H. germanus* Occurrence With Environmental Parameters

The distribution and abundance of *Halobates* across the ocean surface are known to be influenced by several environmental factors like temperature (e.g., Ikawa et al., 2004; Harada et al., 2018), salinity, wind (Ikawa et al., 2007), precipitation (Harada et al., 2016), oxygen and chlorophyll (Harada et al., 2014).

Higher abundances of the oceanic species *H. micans* in Indian Ocean were found to be associated with high chlorophyll and low oxygen concentrations, suggesting that the fundamental phytoplankton biomass and the resulting higher zooplankton food availability can affects the population density of *Halobates* (Harada et al., 2014). On the contrary, abundance of *H. germanus* were found to be higher under oligotrophic conditions, associated with the lowest chlorophyll (Cheng et al., 1990). The population of *H. germanus* in this study also did not show any correlation with chlorophyll or oxygen, thereby suggesting its dependence on alternative food source and its carnivorous feeding habit (Cheng, 1985). The Red Sea, despite its prevailing oligotrophic conditions, supports a diverse and abundant zooplankton and neuston community (Echelman and Fishelson, 1990; Pearman and Irigoien, 2015; Al-Aidaroos et al., 2016), which is ample prey for *Halobates* (Cheng, 1974, 1985). We, therefore, speculate that *H. germanus*, as a specialized predator (Cheng, 1974), is well adapted to the food conditions of the Red Sea.

Surface temperature has been reported as the most prevailing factor controlling the distribution and abundance of *Halobates* species (Cheng and Shulenberger, 1976; Cheng, 1985; Nakajo et al., 2013). Experimental work also validates the narrow temperature tolerance that varies between different oceanic species and the critical effect of small variations in the environmental temperature on the physiology of *Halobates* (Harada et al., 2011, 2013). In general, a temperature range of 24–30°C had been estimated as optimum for oceanic sea skaters (Cheng and Shulenberger, 1976). Harada et al. (2018) reported the distribution of *H. sericeus* across a wide temperature range of 22–30°C and a critical lower temperature for inhabitation at 21°C, which reflect in its distribution over a wider range of latitudes compared to other oceanic species (Andersen and Cheng, 2004). On the contrary, *H. germanus* is found across a narrow temperature range of around 27–30°C, and a lower temperature limit of temperature for inhabitation around 28°C (Harada et al., 2014). In our study, however, *H. germanus* was found within a much wider temperature of 24.8–32.1°C, and an optimum temperature of 28.2°C. The presence of *H. germanus* over a wide thermal range (7°C) suggests an adaptation of this species to severe seasonal temperature fluctuation as well as its capability to adapt to higher ambient temperatures, a feature common to

organisms inhabiting warmer temperature regimes (Schoepf et al., 2015) and, particularly, the Red Sea (Krueger et al., 2017; Osman et al., 2018). The occurrence of _H. germanus_ at temperatures of 32.1°C in the present study is more than the "moderate high" temperature of 31°C which is "maximum" high ambient temperature for tropical oceanic sea skaters, and, very close to 32.5°C, a temperature previously associated with lower survival and lower tolerance for this species in the Pacific Ocean (Furuki et al., 2018). The local population therefore seems to demonstrate a much efficient temperature adaptation system compared to the population of _H. germanus_ in the Pacific Ocean.

CONCLUSION

This study is the first comprehensive account of occurrence and distribution of _Halobates_ in the Saudi Arabian coast of the Red Sea, conducted over a large spatiotemporal scale. The Red Sea features a gradients of temperature, salinity and nutrients (Edwards, 1987), which reflects in the gradual increase in primary production and nutrient concentrations from the north to south and toward the coasts (Raitsos et al., 2013), which would result in a highly dynamic changes both temporally and spatially on the distribution of _Halobates_. However, we found a prevalence of _H. germanus_ in all its life stages across the latitudinal extend of the Saudi Arabian Red Sea in diverse ecological habitats. The distribution although variable and patchy, was not controlled by a single environmental factor, although an apparent optimal temperature of 28.2°C was observed. _H. germanus_ in the Red Sea appears to be adapted to resist higher temperatures than populations elsewhere, which needs be confirmed experimentally. This is particularly interesting in the

ongoing (Chaidez et al., 2017) and predicted warming of the Red Sea, and the subtropical and tropical ocean.

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