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Population genetics of the fiddler crab *Uca sindensis* (Alcock, 1900) (Crustacea: Brachyura: Ocypodidae) from the Arabian Sea

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Abstract

Background: The fiddler crab *Uca sindensis* (Alcock, 1900) (Crustacea: Brachyura: Ocypodidae) is distributed in the northern coasts of the Arabian Sea (Pakistan, Iran, Iraq, and Kuwait). Its typical habitat is on high intertidal areas with higher salinity, which might restrict its distribution, especially within the Persian Gulf. The purpose of the present phylogeographic study is to understand whether the Strait of Hormuz acts as a barrier to the gene flow of this species.

Results: The genetic analyses of the mitochondrial 16S rRNA, cytochrome oxidase subunit I (COI), and control region (CR) of specimens from various localities showed that there was no genetic differentiation between the populations inside and outside of the Persian Gulf.

Conclusions: We conclude that the narrow Strait of Hormuz does not form a barrier for the larval dispersal in this species. Its restricted distribution in the northern Arabian Sea may instead be associated with its preference for higher salinity sediments present in the coasts of this region.

Keywords: *Uca sindensis*; Phylogeography; Arabian Sea; Persian Gulf; 16S rRNA; COI; Control region

Background

Uca sindensis (Alcock, 1900) (Ocypodidae) is a species of fiddler crab with a relatively restricted distribution in the northern Arabian Sea. Described from Karachi, Pakistan (Alcock 1900), it has since been reported from Iran, Iraq, and Kuwait (Collins et al. 1984; Yamaguchi 1994; Apel and Türkay 1999; Naser et al. 2010; Mokhlesi et al. 2011; Naderloo and Türkay 2012). Its ecology and behavior have been studied in Kuwait (Collins et al. 1984), Iran (Mokhlesi et al. 2011), and Pakistan (Saher and Qureshi 2012).

With regard to the taxonomy of *U. sindensis*, Alcock (1900) originally considered it as a variety of *Uca inversa* (Hoffmann, 1874), a decision followed by Crane (1975). She treated it as a subspecies of *U. inversa* and established a subgenus *Amphiuca* (= *Paraleptuca* Bott, 1973) for the two taxa that also included *Uca chlorophthalmus* (H. Milne Edwards, 1837) and *Uca crassipes* (White,

1847). However, Beinlich and von Hagen (2006) established a new subgenus, *Cranuca*, exclusively for *U. inversa* on the basis of its unusual pleonal structure and form of the dactylar tooth of the major chela. They also transferred the other taxa in Crane's (1975) Indo-West Pacific *Celuca* (= *Austruca* Bott, 1973) to the subgenus *Paraleptuca*, an action later followed by Ng et al. (2008). However, Beinlich and von Hagen's (2006) definition of *Paraleptuca* seems to be paraphyletic (Naderloo et al. 2010). Shih et al. (2013a,b) studied the phylogeny of the Indo-Pacific broad-fronted group and the results support the concept of the subgenera *Austruca* (= Crane's *Celuca* for Indo-West Pacific taxa), *Parathelphuca*, and *Cranuca*, with *U. sindensis* included in *Austruca*. The morphological similarity of *U. sindensis* and *U. inversa* (cf. Alcock 1900; Crane 1975) thus appears to be superficial. In fact, Alcock (1900) had mentioned that *U. sindensis* resembles *Uca annulipes*, and this has been supported genetically (Shih et al. 2013b).

Most phylogenetic and phylogeographic studies of marine crabs use the mitochondrial 16S rRNA and cytochrome oxidase subunit I (COI) genetic markers (e.g.,

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Levinton et al. 1996; Sturmbauer et al. 1996; Shih and Suzuki 2008; Shih et al. 2009, 2010, 2012; Davie et al. 2010; Wong et al. 2010, 2011, 2012). In addition, the mitochondrial control region marker, with highly variable and fast divergence rates (Avise 2000), has also recently been used for phylogeographic studies of crabs, e.g., *Portunus trituberculatus* (Miers, 1876) (Portunidae) (Cho et al. 2009; Guo et al. 2012), *U. crassipes* (Aoki and Wada 2013), *Uca boninensis* (Ocypodidae) (Shih et al. 2013a), *Grapsus grapsus* (Linnaeus, 1758) (Grapsidae) (Ströher et al. 2011), *Episesarma versicolor* (Tweedie, 1940) (Sesarmidae) (Supmee et al. 2012), *Ucides cordatus* (Linnaeus, 1763) (Oliveira-Neto et al. 2007) (Ucididae), *Cardisoma guanhumi* (Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828) (Oliveira-Neto et al. 2008), and *Discoplax celeste* Ng and Davie, 2012 (Gecarcinidae) (Turner et al. 2013).

The Persian Gulf is a shallow semi-enclosed basin with average depth of only 35 m. It has a low-salinity current flowing towards the northwest from the Gulf of Oman and along the coast of Iran, forming a series of eddies around the Central Trough of the Gulf. It also has a high-salinity current flowing towards the southeast, mainly along the coast of Arabia and out through the Strait of Hormuz (Thoppil and Hogan 2010). The narrow (approximate width 50 km) outlet of the Strait of Hormuz has a major influence on the circulation and salinity inside the Gulf, making it quite different from conditions outside (Johns et al. 2003). As such, it may act as a barrier to the gene flow of marine organisms, resulting in different genetic structures inside and outside the Gulf. Examples studied showing this pattern include corals (Eghtesadi-Araghi 2011), barnacles (Tsang et al. 2012), sea cucumber (Claerebout and Al-Rashdi 2011), and reef fishes (Burt et al. 2011). However, the Persian Gulf was completely dried in glacial periods due to its shallow depth, with marine organisms reestablishing themselves in the Gulf after that. This suggests that historic factors are less important in determining geographical distribution of marine organisms (Tsang et al. 2012).

Compared with the Persian Gulf, another semi-enclosed basin, the Red Sea, has a very different geography and geological history, with a prominent sill to constrain the outflow and the formation of land bridge across the Arabian Sea during glaciation events (Johns et al. 2003; Sirocko 2003); resulting in a higher endemism (Tsang et al. 2012; DiBattista et al. 2013).

To understand whether the larval dispersal of *U. sindensis* is blocked by the narrow Strait of Hormuz, we examine the genetic variation of 16S, COI, and control region (CR) from different localities of its range. The possible biogeographic mechanisms for the limited distribution of this species are discussed.

Methods

The specimens of *U. sindensis* have been collected from Pakistan, Iran, and Iraq (Table 1; Figure 1), preserved in 70% to 95% ethanol and deposited in Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL) and Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

Genomic DNA was isolated from the muscle tissue of the legs by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A region of approximately 550 basepairs (bp) of the 5'-end of the 16S gene was selected for amplification with polymerase chain reaction (PCR) using the primers 1471 and 1472 (Crandall and Fitzpatrick 1996). A portion of the COI gene was amplified with PCR using the primers LCO1490, HCO2198 (Folmer et al. 1994), and COH6 (Schubart and Huber 2006). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45°C to 47°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. The primers for a region of approximately 960 bp of CR gene are the recently designed CR-F4 (Shih et al. 2013a) and ILEUCAR3 (Pie et al. 2008), with the annealing temperature of 45°C to 50°C in PCR condition. Sequences were obtained by automated sequencing (Applied Biosystems 3730, Applied Biosystems Inc., Foster City, CA, USA) and were aligned manually, with the aid of ClustalW v 1.4 (Thompson et al. 1994), after verification with the complementary strand. According to Shih et al. (2013b), *U. sindensis* belongs to the monophyletic *Austruca*, so other consubgeneric species from Indian Ocean are used as outgroups, viz. *Uca albimana* (Kossmann, 1877), *U. annulipes* (H. Milne Edwards, 1837), *Uca* aff. *annulipes*, *Uca bengali* Crane, 1975, and *Uca iranica*, Pretzmann, 1971. Sequences of different haplotypes have been deposited in the DNA Data Bank of Japan (DDBJ), with other sequences which were published in earlier papers of author HTS (accession numbers see Table 1).

For a combined analysis of 16S and COI markers, phylogenetic congruence among the two dataset partitions was tested under the maximum parsimony (MP) criterion using the incongruent length difference (ILD) test (Farris et al. 1994) implemented in the PAUP* program v 4.0b10 (Swofford 2003) as the partition homogeneity test. The parameters included 1,000 reiterations of a heuristic search with 100 randomly added sequence replications and tree bisection-reconnection (TBR) branch-swapping, using Steepest Descent and the MULTREES option enabled, and total number of rearrangements for each search was limited to 500,000 to avoid excessive computation time. The topologies of the two datasets were congruent ($p = 0.901$) and as such, the sequences were combined.

Table 1 Haplotypes of 16S rRNA, COI, and CR genes

Species	Locality	Sample size	Haplotype of 16S	DDBJ accession number	Haplotype of COI	DDBJ accession number	Haplotype of CR	DDBJ accession number	
<i>U. sindensis</i>	Pakistan: Sandspit, Karachi [1]	1	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR1	LC015065	
		1	Usd-1	AB813652	Usd-C3	LC015061	Usd-CR2	LC015066	
		1	Usd-1	AB813652	Usd-C4	LC015062	Usd-CR3	LC015067	
		1	Usd-2	LC015053	Usd-C1	AB813673	Usd-CR4	LC015068	
		2	Usd-1	AB813652	Usd-C1	AB813673	Usd-CR5, 6	LC015069, LC015070	
		2	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR7, 8	LC015071, LC015072	
		1	Usd-3	LC015054	Usd-C1	AB813673	Usd-CR9	LC015073	
		1	Usd-4	LC015055	Usd-C1	AB813673	-		
	Pakistan: Sonmiani, Balochistan [2]	1	Usd-1	AB813652	Usd-C1	AB813673	Usd-CR10	LC015074	
		1	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR11	LC015075	
		1	Usd-5	LC015056	Usd-C2	LC015060	Usd-CR12	LC015076	
		1	Usd-6	LC015057	Usd-C2	LC015060	Usd-CR13	LC015077	
		1	Usd-1	AB813652	Usd-C3	LC015061	-		
		Iran: Qeshm [3]	1	Usd-1	AB813652	Usd-C1	AB813673	Usd-CR14	LC015078
			1	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR15	LC015079
			2	Usd-1	AB813652	Usd-C1	AB813673	Usd-CR16, 17	LC015080, LC015081
	Iran: Bandar Abbas [4]	1	-		Usd-C2	LC015060	Usd-CR18	LC015082	
		1	Usd-7	LC015058	Usd-C1	AB813673	Usd-CR19	LC015083	
		3	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR20, 21, 23	LC015084, LC015085, LC015087	
		1	Usd-1	AB813652	Usd-C5	LC015063	Usd-CR22	LC015086	
Iraq: Khur Al-Zubair [5]	1	Usd-8	LC015059	Usd-C2	LC015060	Usd-CR24	LC015088		
	1	Usd-1	AB813652	Usd-C2	LC015060	Usd-CR24	LC015088		
Outgroups									
<i>U. bengali</i>	Thailand: Ranong			AB813651		LC015064	-		
<i>U. annulipes</i>	India: Tamil Nadu, Porto Novo			AB471894		AB471907	-		
<i>U. aff. annulipes</i>	Madagascar			AB813648		AB813669	-		
<i>U. iranica</i>	Iran: Hormozgan, Qeshm			AB471897		AB471911	-		
<i>U. albimana</i>	Egypt: Sinai			AB471893		AB471906	-		

Haplotypes of 16S rRNA, COI, and control region (CR) genes for the specimens of *Uca sindensis* from the Arabian Sea and the outgroups. The numbers within brackets after the localities correspond to those in Figure 1.

Maximum likelihood (ML) analysis was conducted in RAxML v 7.2.6 (Stamatakis 2006) for the combined dataset. The model GTR + G (i.e., GTRGAMMA) was used for all subsets with 100 runs and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1,000 bootstrap pseudoreplicates under the model GTRGAMMA. A consensus MP tree was constructed using PAUP* with

2,000 bootstrap replications of a simple heuristic search, TBR branch-swapping, and 100 random addition sequence replications. Gaps in MP tree construction were treated as missing. All characters were equally weighted. To examine the relationships of the combined 16S and COI haplotypes in detail, a gene genealogy was constructed using TCS v 1.20 (Clement et al. 2000), with the treatment of gaps as missing states.

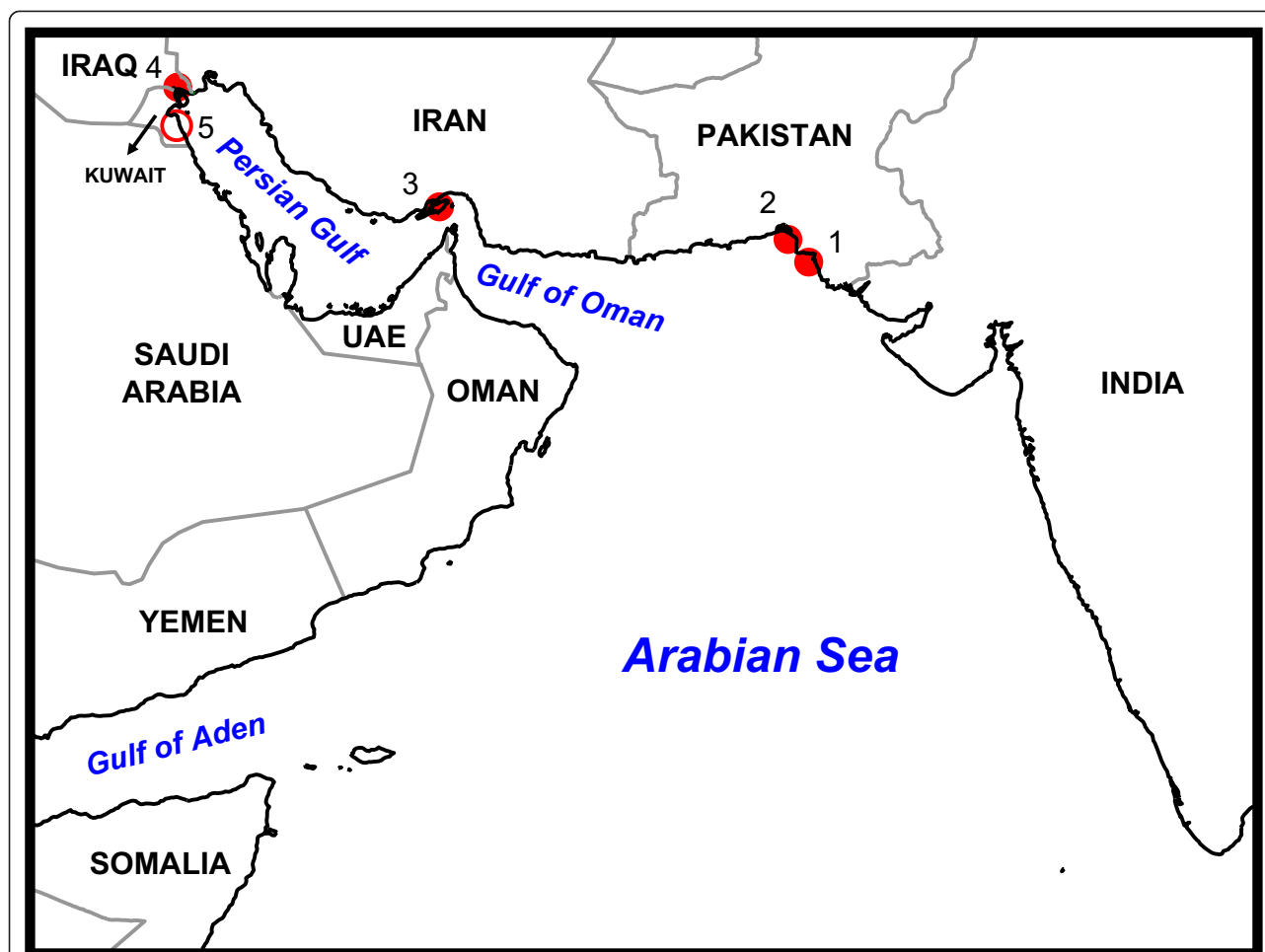


Figure 1 Collection sites. Collection sites (red solid circles; nos. 1 to 4) for specimens of *Uca sindensis* used in this study. Red empty circle (no. 5) means the additional record of Kuwait (Collins et al. 1984).

To understand whether there is genetic differentiation between the populations inside and outside the Persian Gulf, we treated the specimens from Iran and Iraq (nos. 3 and 4; Figure 1) as one population, and another population is composed of specimens from Pakistan (nos. 1 and 2; Figure 1). The nucleotide diversity (π), number of haplotypes (nh), and haplotype diversity (h) for each population were estimated by using the program DnaSP v 5.10.01 (Librado and Rozas 2009). To determine whether patterns of sequence variation was consistent with prediction of the neutral model, Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) tests were calculated by Arlequin v 3.5.1.2 (Excoffier et al. 2005), with 1,000 permutations for the significance assessment of the neutrality test. To determine whether a population expansion is valid, the mismatch distribution, with the Harpending's raggedness index (Hri, Harpending 1994), was computed by Arlequin using the demographic expansion model for pairwise differences with 1,000 bootstrap replicates. If the Hri value is significant ($p < 0.05$), the sudden population expansion

model should be rejected (Schneider and Excoffier 1999). To estimate the degree of differentiation between populations, pairwise F_{ST} between groups was calculated by Arlequin. Sometimes the value of F_{ST} is negative, which was discussed by several authors and we follow the usual treatment to round it to zero (Weir 1996; Roesti et al. 2012; Willing et al. 2012).

Results

A 548-bp segment of the 16S was amplified and aligned; six positions are variable and none are parsimoniously informative. Among the total number of sequences, eight different haplotypes are distinguished (Table 1). The studied segment of 16S sequences is AT rich (68.7%) (T, 36.0%; A, 32.7%; G, 19.9%; and C, 11.4%). For the COI gene, a 658-bp segment was compared, resulting in five different haplotypes (Table 1). The studied segment of the COI sequence is also AT rich (58.4%) (T, 32.2%; A, 27.2%; G, 17.8%; and C, 23.8%). In this gene, five positions are variable and two parsimoniously informative. A 963-bp

segment of CR was compared, and 24 different haplotypes were obtained (Table 1). The segment of CR is AT rich (75.8%) (T, 35.1%; A, 40.7%; G, 10.1%; C, 14.1%), with 75 positions variable and 34 parsimony informative.

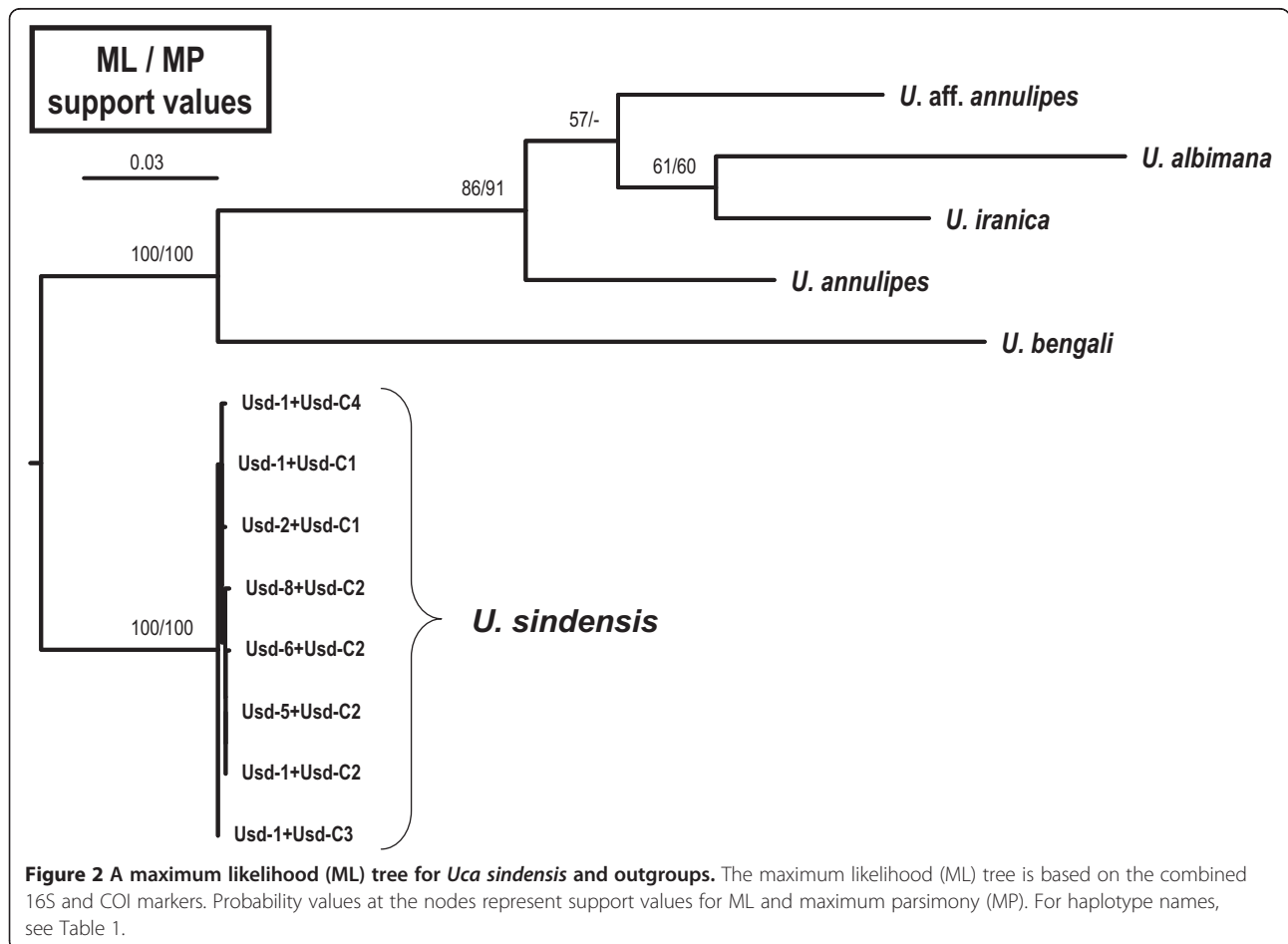
The genealogic tree of the combined 16S and COI (Figure 2) shows that there is no subdivision of *U. sindensis* specimens from various localities. The haplotype network of the combined dataset (Figure 3) shows the haplotype 'Usd-1 + Usd-C1' to be central, relative to all other haplotypes. As such, it is here regarded as the ancestral haplotype (cf. Clement et al. 2000). It is also clear that a lot of individuals, inside and outside the Gulf, share the same haplotypes. Although some haplotypes seem to exclusively appear in each locality, their difference from the common ones is only 1 or 2 bp.

The molecular diversity indices for 16S, COI, and CR are shown in Table 2. For the 16S of all populations, the nucleotide diversity per site (π) = 0.076 and the haplotype diversity (h) = 0.380; for COI, π = 0.13 and h = 0.63; and for CR, π = 1.35 and h = 0.996. The divergence of COI is about five times that of 16S and CR is about 3.5 times that of COI.

The pairwise F_{ST} value between populations is -0.0309 (and has rounded to zero) which implies that the gene flow between them is very high. As a result, the two populations are combined into a single population. Tajima's D is -1.7519 ($p = 0.02$) and Fu's F_S value is -27.9037 ($p < 0.001$). The significant negative values of the neutrality tests may imply that the population has experienced a recent expansion (Tajima 1989; Fu 1997). The Hri value is 0.08172 ($p = 0.29$), which is not significant and also implies that the population might experience sudden population expansion. In addition, the mismatch distribution is smooth and unimodal (Figure 4), with the simulated sum of squared deviation (SSD) being 0.00555 ($p = 0.44$), which also supports the recent population expansion.

Discussion

The results of the present study suggest that the Strait of Hormuz is not a barrier to gene flow between the populations of *U. sindensis* inside and outside the Gulf, at least on the basis of the low nucleotide diversities of 16S (0.08%), COI (0.13%), and CR (1.35%) (Table 2),



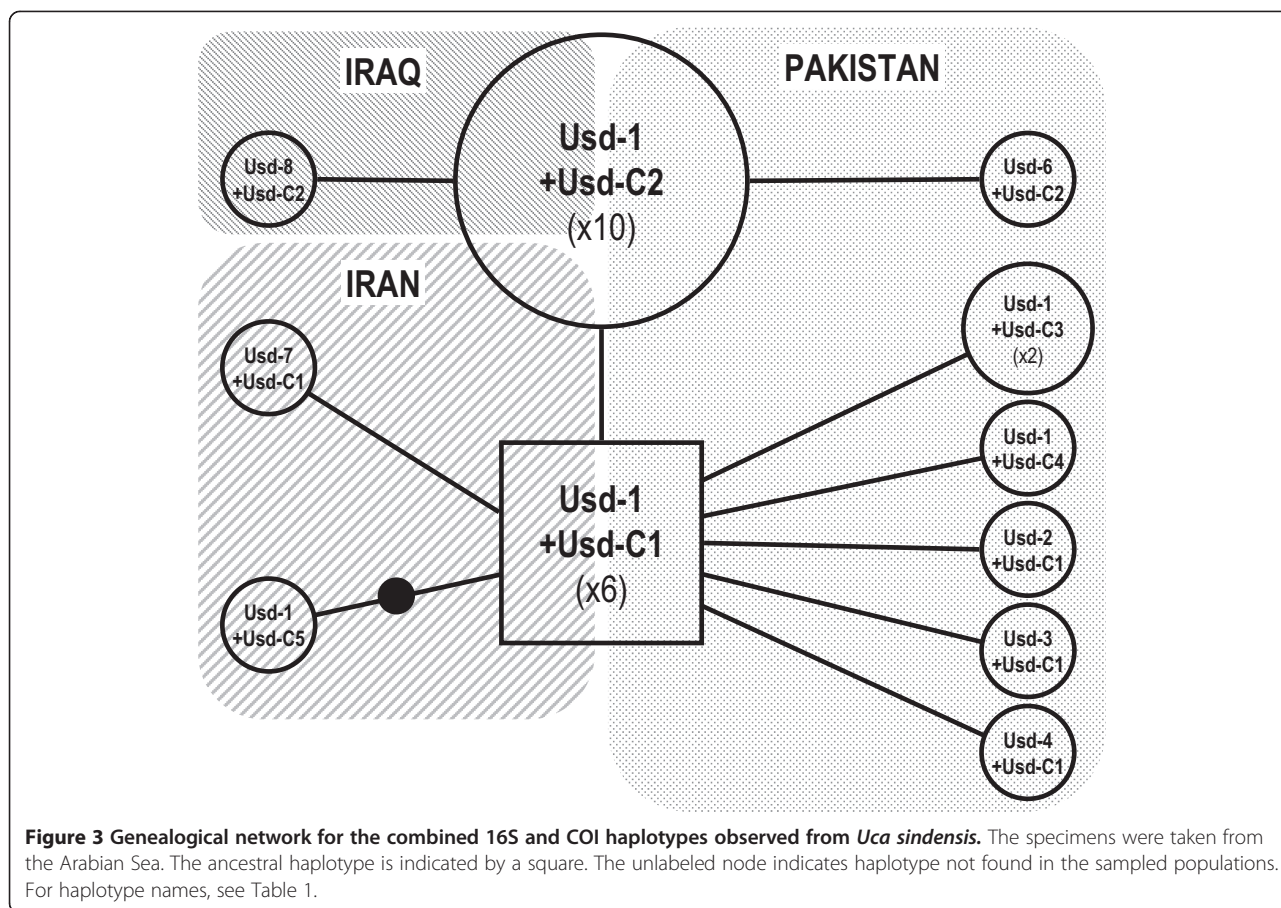


Table 2 The measures of 16S, COI, and CR

	<i>n</i>	<i>nh</i>	π (%)	<i>h</i>
16S				
Inside the Gulf	11	3	0.067	0.345
Outside the Gulf	13	4	0.084	0.423
Total	24	6	0.076	0.380
COI				
Inside the Gulf	11	3	0.138	0.618
Outside the Gulf	13	4	0.129	0.679
Total	24	5	0.130	0.630
CR				
Inside the Gulf	11	10	1.406	0.982
Outside the Gulf	13	13	1.290	1
Total	24	23	1.351	0.996

The measures of 16S, COI, and control region (CR) diversity for specimens of *Uca sindensis* from the Arabian Sea. Inside the Gulf includes Iraq and Iran; outside the Gulf includes only Pakistan. *n*, number of sampled individuals; *nh*, number of recovered haplotypes; π , nucleotide diversity; *h*, haplotype diversity.

genealogic tree (Figure 2), haplotype network (Figure 3), and the estimate of gene flow (F_{ST}).

Low genetic variability of COI has been reported in other *Uca* species, which is usually attributed to the high levels of larval dispersal, e.g., *U. annulipes* (= *U. aff. annulipes*, see Shih et al. 2013b) from East Africa (0.04%, Silva et al. 2010), *U. crassipes* from eastern Indian Ocean to Central Pacific Ocean (0.02%, Shih et al. 2012), and *Uca maracoani* from Brazilian coast (0.291%, Wieman et al. 2014). However, some *Uca* species and other intertidal crabs are known to show relatively high genetic variability, e.g., *Uca pugnax* (Smith, 1870) from the Atlantic coast of USA (0.61%, Sanford et al. 2006), *Uca splendida* (Stimpson, 1858) from Vietnam and East Asia (0.82%, Shih et al. 2012), and *Neohelice granulata* (Dana, 1851) (Varunidae) from Brazil (0.706%, Ituarte et al. 2012), which may be explained by past historical barriers to their larval dispersal that may have affected their behavior, physiology, etc. (McEdward 1995; Brodie et al. 2007; Anger et al. 2008; López-Duarte et al. 2011; discussed below).

The genetic variability of *U. sindensis*, with a nucleotide diversity of 1.35% of CR, is 3.5 times that of the COI (Table 2). This CR divergence is relatively low

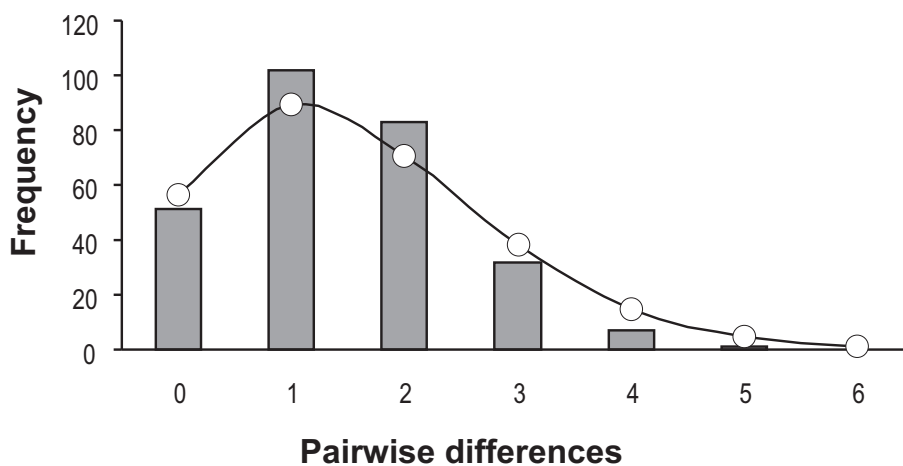


Figure 4 Mismatch distribution for the populations of *Uca sindensis* from the Arabian Sea. The observed pairwise differences are shown in bars, and the expected values under the sudden expansion model are in solid line.

compared with most crab species with wide distributions like *Portunus trituberculatus* (2.72%, Cho et al. 2009; 2.05%, Guo et al. 2012), *Cardisoma guanhumi* (3.0%, Oliveira-Neto et al. 2008; 3.1%, Pie et al. 2008), and *Ucides cordatus* (3.5%, Oliveira-Neto et al. 2007; 4.4%, Pie et al. 2008). Even a species with a restricted distribution like *U. boninensis* (known only from the Ogasawara (= Bonin) Islands, Japan) has a high nucleotide diversity (3.18%, Shih et al. 2013a). The pattern is not always easy to decipher; some species with a low diversity like *D. celeste* (1.0%, Turner et al. 2013), has a small range and is endemic to Christmas Island in the Indian Ocean, while *E. versicolor* (0.7%, Supmee et al. 2012) (studied along the Andaman Sea Coast of Thailand) has a wide Southeast Asian distribution. The highly variable CR marker may therefore provide another line of evidence to better understand the genetic structure and molecular diversity at the population and species level.

The neutrality tests and mismatch distribution (Figure 4) suggest that *U. sindensis* has undergone a recent expansion from a single source, with the most common haplotype 'Usd-1 + Usd-C1' likely to be the ancestral one (Figure 3) (Clement et al. 2000; Avise 2009). Rarer haplotypes, with only 1 or 2 bp difference from the most common haplotype (Figure 3), may have been derived relatively recently through separate mutations (Avise 2009).

Uca sindensis is restricted to the northern Arabian Sea (Pakistan, Alcock 1900) and the northern and north-western coasts of the Persian Gulf (Kuwait, Collins et al. 1984; Iran, Apel and Türkay 1999; Iraq, Naser et al. 2010). An analysis of the fiddler crab fauna in this region may help understand the factors affecting the distribution of *U. sindensis*. In Pakistan, *U. sindensis*, *Uca urvillei*, *U. annulipes*, and *U. iranica* have been reported

(Alcock 1900; Crane 1975; Saher and Qureshi 2012; Saher et al. 2014); Iran has *U. sindensis*, *U. iranica*, and *U. inversa* (Pretzmann 1971; Apel and Türkay 1999; Shih et al. 2009; Naderloo and Türkay 2012), while Kuwait has *U. sindensis* and *U. iranica* (Collins et al. 1984; Apel and Türkay 1999). Interestingly, no *Uca* species has been reported from the southern coasts of the Persian Gulf, and Apel and Türkay (1999) speculated that this may be due to the very high salinity of the area. An exception is the sea in United Arab Emirates (UAE) which has relatively lower salinity, and here, five species are present: *U. iranica*, *U. albimana*, *U. inversa*, *Uca hesperiae*, and *Uca tetragonon* (Apel and Türkay 1999; see below). It is interesting that *U. albimana*, *U. inversa*, *U. hesperiae*, and *U. tetragonon* also occur in the western part of the Indian Ocean (i.e., in the Red Sea and along East Africa) and are believed to be widespread because their larvae are dispersed by currents along the African coast (Apel and Türkay 1999). Only *U. iranica* has a comparatively restricted range.

The importance of salinity as a limiting factor for both larvae and adults of *Uca* species has previously been emphasized (Crane 1975; Hedgecock 1986; Anger 2003; Spivak and Cuesta 2009; Hopkins and Thurman 2010; López-Duarte et al. 2011; Thurman et al. 2013). Salinity has also been proposed as a major factor controlling the crab distribution in the Persian Gulf, especially for *Uca* species by Apel and Türkay (1999). They hypothesized that areas in the Persian Gulf without *Uca* are because of the very high salinities present (>40‰), with the crabs preferring habitats with salinities <39‰. It is likely that the distribution of *U. sindensis*, from Pakistan to the northwestern Persian Gulf, is also influenced by salinity.

Although *U. sindensis* is sometimes sympatric with *U. iranica*, its preferred habitat is in higher intertidal areas

or even in sheltered shores far from the sea (Crane 1975; Collins et al. 1984; Mokhlesi et al. 2011). These are generally habitats with higher salinities than open waters. Within the Persian Gulf and the Gulf of Oman, *U. sindensis* (and other *Uca* spp.) occur in the coast of Iran, Iraq, and Kuwait, areas that have salinities of between 36‰ to 37‰ at least in summer (Apel and Türkay 1999; Johns et al. 2003; Naderloo and Türkay 2012). In the habitats in Pakistan (Sandspit and Korangi, Karachi), the salinity was always above 36.0‰ (Saher 2008). From the Gulf of Oman to Pakistan, the salinity is relatively lower (36.5‰ to 36‰) (Chodankar et al. 2005), but still high enough for *U. sindensis* to survive. Once we reach the western Indian subcontinent, the salinities become even lower (34‰ to 36‰) (Subrahmanyam et al. 2011), and interestingly, there are no records of *U. sindensis* here. From the known range at least, the preferred salinity for *U. sindensis* appears to be between 36‰ to 39‰, and according to Thurman et al. (2013), it should be classified as a hypersaline species since this value exceed 35‰. Other hypersaline species are *Uca burgersi* Holthuis, 1967, *Uca panacea* Novak and Salmon, 1974, *Uca rapax* (Smith, 1870), and *Uca subcylindrica* (Stimpson, 1859) from America (Thurman 2002; Thurman et al. 2013), *U. inversa* (Hoffmann, 1874) from the Indian Ocean (Spaargaren 1977), and *Uca formosensis* Rathbun, 1921 from Taiwan (Shih et al. 1999, 2005; Shih 2008).

López-Duarte et al. (2011) found that the larvae of estuarine *Uca* species have a rhythmic vertical swimming behavior following hatching an action that promotes seaward transport (and dispersal) due to the physiological stresses to low salinities in estuaries. Coastal species with euhaline habitats, on the other hand, exhibit only weakly rhythmic or arrhythmic behavior. The habitats and the adjacent coastal areas of *U. sindensis* are highly saline (see above) which is presumably suitable for the larval development, there is no need to move too far, and as such, the larvae only have weak or no vertical migration behavior (López-Duarte et al. 2011). Surface currents therefore have a greater influence, with larvae transported primarily by advection from adult habitats (Queiroga and Blanton 2005; López-Duarte et al. 2011). As such, populations may become localized due to the direction of surface currents and the hypersaline habits of the species; explaining the low genetic differentiation observed between localities. This habitat salinity hypothesis could explain the low genetic variability of *U. sindensis* in this study as well as that of other coastal and oceanic species like *U. crassipes* (Shih et al. 2012). This is in contrast to the high genetic variability present in estuarine *U. splendida* (Shih et al. 2012), *U. pugnax* (Sanford et al. 2006; López-Duarte et al. 2011), and *N. granulata* (Ituarte et al. 2012). The current understanding is that the distribution of many marine organisms in

the hypersaline Red Sea have been influenced by salinity (e.g., the barnacles, Tsang et al. 2012; reef fishes, DiBattista et al. 2013). This evidence suggests that salinity plays an important role in the distribution of intertidal and shallow subtidal organisms which face extreme environment stresses frequently.

Further studies on the larval development and behavior, as well as the salinity and temperature tolerance for larvae and adults, of *U. sindensis* will be important to better understand how these aspects affect their distribution.

Conclusions

Based on the low nucleotide diversities of mitochondrial 16S, COI, and control region (CR), genealogic tree, haplotype network and the estimate of gene flow, which suggest high levels of larval dispersal, we conclude there was no genetic differentiation between the populations of *Uca sindensis* inside and outside of the Persian Gulf; and the narrow Strait of Hormuz does not form a barrier for the larval dispersal in this species. Its restricted distribution in the northern Arabian Sea may instead be associated with its preference for sediments with higher salinity (36‰–39‰) present in the coasts of this region and *U. sindensis* is best classified as a hypersaline species. The neutrality tests and mismatch distribution also suggest that this species has undergone a recent expansion from a single source, with some rarer haplotypes the result of relatively recent but separate mutations.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

HTS conceived this study, performed the molecular genetic analysis, and drafted the manuscript. NUS and EK collected and processed the samples and drafted the manuscript. PKLN participated in the discussion and drafted the manuscript. YCL carried out the molecular work and helped draft the manuscript. MYL conceived this study and carried out the molecular work. All authors read and approved the final manuscript.

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