

Original Article

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Population differentiation in the Persian Gulf and Gulf of Oman: insights from the ghost shrimp's associated copepods, *Clausidium iranensis* and *Clausidium persiaensis*

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Abstract

Evolution and population genetic structure of marine species across the Persian Gulf and Gulf of Oman are shaped by two complex factors: the geological history and the present pattern of marine currents. Characterizing and comparing the genetic structures of co-existing species, such as host–parasite associations, allow the discrimination of the relative importance of environmental factors and life history traits that influenced gene flow and demographic events. In this study, we compare two associated *Clausidium* copepod species (*C. persiaensis* Sepahvand & Kihara 2017 and *C. iranensis* Sepahvand, Kihara & Boxshall 2019) along the south coast of Iran in two geological settings. We analysed partial nucleotide sequences of the *mtCOI* gene using divergence estimates (FST) and haplotype networks to infer intraspecific population connectivity in the two Gulfs. The results obtained demonstrate the existence of two genetically and geographically distinct clades, corresponding to the Persian Gulf and Gulf of Oman populations. Our results also indicate high diversity, population expansion and high connectivity among populations of *C. persiaensis* and *C. iranensis* in the Persian Gulf and Gulf of Oman.

Introduction

The Persian Gulf and Gulf of Oman, in the north-west of the Indian Ocean, are connected by the Strait of Hormuz. In the Persian Gulf, the thermohaline circulation system and other physical factors (e.g. winter surface isotherms) play a crucial role in shaping the current species distribution (Sheppard *et al.*, 2010). The surface water of the Indian Ocean with lower-salinity enters the Persian Gulf through the northern part of the Hormuz Strait and is deflected along the Iranian coast, forming a basin-wide cyclonic circulation in the southern Persian Gulf (Yao, 2008). Relatively, the Persian Gulf is geologically young, as its basin was completely dried during the Pleistocene glacial periods about 17,000 years ago (Barth & Khan, 2008). Around 12,500 years ago, the Strait of Hormuz opened up, and marine water started to enter the central basin. The present shoreline was established about 6000 years ago (Lambeck, 1996); therefore, the corresponding biota is also young. Consequently, the Persian Gulf has an impoverished fauna and flora, not only because of its young age, but mostly because of its harsh environment (Sheppard *et al.*, 1992).

Studying population genetic structures enhances our knowledge of how populations evolve under evolutionary forces such as gene flow. Small passively dispersed marine organisms can maintain gene flow between populations over long distances (Gómez *et al.*, 2000). On the other hand, many taxa show high levels of genetic differentiation and form cryptic species complexes, even across small spatial scales within the range of their dispersal (e.g. Zeller *et al.*, 2006; Fontaneto *et al.*, 2008; Xiang *et al.*, 2011).

Genetic diversity of holoplanktonic organisms such as copepods has been largely underestimated in the past owing to their high dispersal capacities, large population sizes, wide geographic ranges and high tolerance to variable environmental factors (Goetze, 2003). Pelagic species may become geographically segregated (allopatric speciation) by oceanographic barriers, isolation by distance, selection due to environmental adaptations or recent historical events (Palumbi, 1994; Blanco-Bercial *et al.*, 2011). Historical events, such as glaciation events or bottleneck effects followed by a sudden population expansion may result in establishment of unique haplotypes (Nei *et al.*, 1975; Nuwer *et al.*, 2008). Moreover, ecology and habitat affinity of populations are probably the main drivers for the speciation of the diverse marine copepod fauna apart from environmental barriers such as continental landmasses and large-scale ocean circulation (Goetze, 2005). Assortative mating can lead to sympatric and micro-allopatric speciation (Palumbi, 1994; Doebeli *et al.*, 2000) and genetic variability might occur, even though morphological differences are absent, leading to the formation of cryptic and pseudo-cryptic species complexes (e.g. Goetze, 2003; Goetze & Ohman, 2010; Cornils *et al.*, 2017). Furthermore, evolutionary processes are not only driven by selective pressures, but also influenced by genetic drift, random changes of gene frequencies in populations (Lande, 1976).



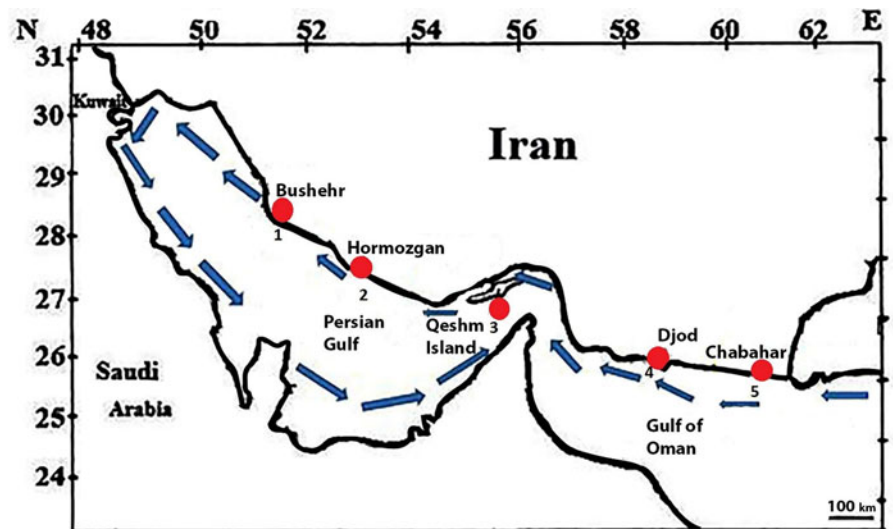


Fig. 1. Map of sampling stations in the Persian Gulf and the Gulf of Oman. The arrows show the circulation of water within the Persian Gulf.

Symbiotic copepods have one or more planktonic phase for dispersal, infection, host switching, mating, and presumably, predator-avoidance (Kearn, 2004; Huys, 2014). Usually, the primarily planktonic naupliar stages play a key role in dispersal. The first copepodid stage is infective, and the subsequent stages, including adults, then typically establish a symbiotic association with a host organism.

Copepods of the genus *Clausidium* Kossmann, 1874 are external associates of burrowing decapod families Callinassidae and Upogebiidae (Kihara & Rocha, 2013). Males of these copepods are often found attached to their larger female partner. The dispersal capacity of adult *Clausidium* individuals is not known, due to the cryptic lifestyle of their hosts. Members of this copepod genus are certainly not proficient swimmers, as they resemble a larval stage compared with free-living marine planktonic copepods. Little is known about the lifestyle, the dispersal capacities and the genetic variability of this parasitic copepod genus. The life cycle is likely similar to species belonging to *Hemicyclops* as this is a common member of the same family (Clausidiidae). Descriptions of some parts of life cycles of *Hemicyclops* have been published but these have mostly focused on the copepodid stages (Itoh & Nishida, 2007), but it is doubtful if naupliar stages have been described. Based on *Hemicyclops* species' life cycle, it would be expected that members of genus *Clausidium* should have six naupliar stages followed by six copepodid stages (the sixth counts as an adult) (Geoff Boxshall, personal communication, June 2018). This is the typical pattern for many families of parasitic or associated copepods. The nauplius stages are generally planktonic and the primary dispersal phase. The first copepodid stage is the infective stage that locates the host, and the remaining copepodid stages are found associated with the host. If the copepod is only loosely associated with the host, copepodid stages of the Clausidiidae may occasionally occur in plankton samples (these were erroneously given the generic name *Saphirella*; Geoff Boxshall, personal communication, June 2018).

Two species of *Clausidium* occur in the study region, *Clausidium persiaensis* in the Persian Gulf and *Clausidium iranensis* in the Gulf of Oman (Sepahvand et al., 2017, 2019). In the present study, we used the mitochondrial marker gene, cytochrome oxidase *c* subunit 1 (COI) to determine the population structure of these two species in order to establish the importance of environmental factors and life history traits on intraspecific diversity of either species. We hypothesize that the populations of both species undergo similar evolutionary forces and that this is reflected in a similar genetic structure.

Materials and methods

Study areas, sampling and sample processing

In total, 130 specimens were collected from bodies of the burrowing shrimps *Callinidea tyta* (*C. persiaensis*) and *Neocallichirus jousseaumei* (*Clausidium iranensis*) from five localities along the coastal region of the Persian Gulf and the Gulf of Oman (Figures 1 and 2, Table 1). Single individuals, from each locality, were preserved in 99.5% ethanol. All specimens were morphologically identified to species level using the original species descriptions and a identification key to *Clausidium* copepod species (Sepahvand et al., 2019).

DNA isolation, PCR and sequencing

From 79 morphologically identified specimens, DNA was extracted using the whole specimen in 40 μ l of Chelex (InstaGene Matrix, Bio-Rad) or 100 μ l DNeasy Tissue Extraction Kit (QIAGEN, Hilden, Germany) following Gollner et al. (2016).

A 658 base pair fragment of the mitochondrial gene COI, was amplified using universal primers LCOI (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCOI (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994). PCR conditions for the above-mentioned primers were described by Gollner et al. (2016). Sequences were manually edited using Bioedit v.7.1.30 (Hall, 1999) and Chromas v2.23 (available at www.techneleysium.com.au). To check for stop codons, COI sequences were translated into amino acids using Mega 6 (Tamura et al., 2013).

Population genetic and demographic analysis

To depict the evolutionary relationships among the mtDNA haplotypes, a haplotype network was constructed using TCS version 1.18 (Clement et al., 2000), and then rearranged and drawn using the tool tcsBU (Múrias dos Santos et al., 2015). The number of mtDNA haplotypes, the levels of haplotype diversity (*h*) and nucleotide diversity (π) were calculated for each population, using DnaSP 5.00 (Librado & Rozas, 2009). The pairwise fixation index (*F_{ST}*) was evaluated in Arlequin 3.5 (Excoffier & Lischer, 2010), with 10,000 permutations to measure the genetic differentiation among the populations.

To infer the historical demography, separately for each species, Tajima's *D* statistics of neutrality (Tajima, 1989) and the frequency

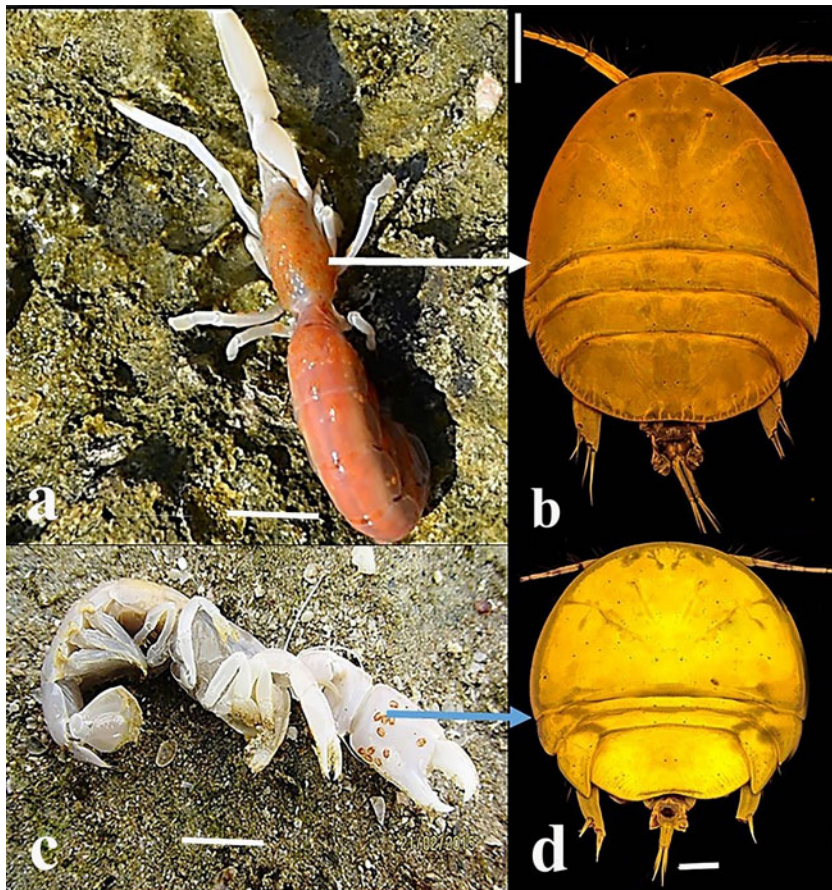


Fig. 2. (A) *Callianidea typea* (female), habitus, dorsal view, and (B) its parasite *Clausidium persiaensis*. Confocal laser scanning microscopy maximum projections, female habitus; (C) *Neocallichirus jousseaumei*. Habitus, lateral view; (D) *Clausidium iranensis*. Confocal laser scanning microscopy maximum projections, Female habitus. Scale bar, A and C 1 cm, B and D 100 μ m.

Table 1. Detail of collection localities for two species of *Clausidium*

Station number	Location	Latitude and longitude	Copepod species	Host species
1	Bushehr	27°50'15"N 51°53'25"E	<i>C. persiaensis</i>	<i>Callianidea typea</i>
2	Hormozgan	26°42'50"N 53°44'00"E	<i>C. persiaensis</i>	<i>C. typea</i>
3	Qeshm Island	27°11'06"N 56°24'11"E	<i>C. persiaensis</i>	<i>C. typea</i>
4	Djod	58°25'51"E 25°26'58"N	<i>C. iranensis</i>	<i>Neocallichirus jousseaumei</i>
5	Chabahar	59°30'28"E 25°21'10"N	<i>C. iranensis</i>	<i>N. jousseaumei</i>

distribution of pairwise differences between mtDNA haplotypes (i.e. mismatch distribution) were employed. A significantly negative deviation from zero can be interpreted as being the result of past population expansion and/or purifying selection, whereas a significantly positive value can result from balancing selection and/or a decrease in population size. Tajima's D values was evaluated using the coalescent algorithm implemented in DnaSP 5.0, in which the observed value is compared to a null distribution generated by 10,000 replicates, given an empirical population sample size and the observed number of segregating sites. To determine whether population has gone through an expansion, the mismatch distribution, with Harpending's raggedness index (Harpending, 1994), was calculated using Arlequin 3.5 (Excoffier & Lischer, 2010) under the sudden expansion model with 1000 bootstrap replicates. If the raggedness index value is insignificant ($P > 0.05$), demographic expansion cannot be rejected (Schneider & Excoffier, 1999).

Table 2. Genetic diversity indices for *C. iranensis*

	N	S	H_n	H_d	Π
Djod	6	3	4	0.86	0.00182
Chabahar	19	8	8	0.75	0.00165
Total	25	10	10	0.76	0.00167

N, number of individuals sampled; S, number of segregating sites; H_n , number of haplotypes; H_d , haplotype diversity; π , nucleotide diversity.

Results

A COI fragment of 658 bp length of 74 specimens was sequenced, including 49 and 25 sequences belong to *C. persiaensis* and *C. iranensis* respectively. For *C. iranensis*, 10 segregating sites, substantial haplotype diversity (0.76), low nucleotide diversity (0.0016) and only one parsimony informative site were identified (Table 2). The haplotype network consists of 10 haplotypes

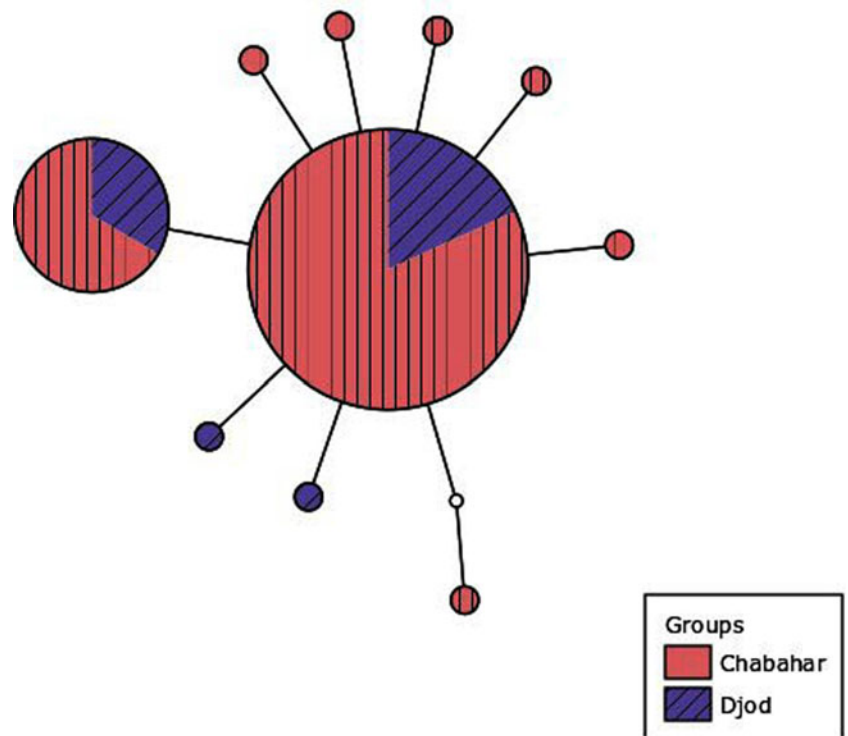


Fig. 3. COI haplotype network of *Clausidium iranensis*. Coloured circles represent individual haplotypes and the sizes of the circles are proportional to the frequency of the haplotypes. Each point mutation is symbolized by a mark on the lines connecting haplotypes.

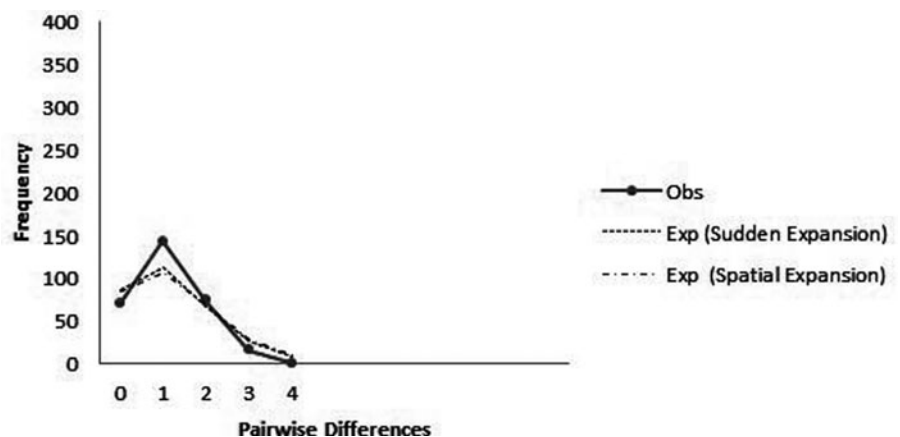


Fig. 4. Mismatch distributions for the COI locus for *C. iranensis*.

(accession number pending), of which eight are rare haplotypes with a single individual and two major haplotypes sharing the remaining 17 individuals. All orphan haplotypes, two from Djod and six from Chabahar populations, were separated only by one mutation step from the main haplotype, giving a star-shaped topology (Figure 3). There is a significant genetic differentiation between the two populations belonging to the Gulf of Oman, Djod and Chabahar ($\Phi_{st} = 0.51$, $P < 0.05$). The population's demography of *C. iranensis* supports a recent expansion model due to significant negative value of the neutrality test (Tajima's $D = -1.93$; $P < 0.05$). The skewed unimodal shape of mismatch distribution and insignificant value of the raggedness index ($r = 0.15$, $P < 0.01$), in line with results from neutrality test and network topology, reflects a scenario of recent population expansion (Figure 4, Table 3).

For *C. persiaensis* the data set included 24 parsimony informative sites, 44 segregating sites, substantial haplotype diversity (0.96) and nucleotide diversity (0.0078) (Table 4). The haplotype network includes 29 haplotypes, with one main haplotype

Table 3. Mismatch distribution and significance values (P) of Harpending's raggedness index (HRI) and sums of squared deviation (SSD) for *C. iranensis* and *C. persiaensis*

Groups	SSD (P)	HRI (P)
Gulf of Oman	0.01 (0.05)	0.15 (0.05)
Persian Gulf	0.007 (0.05)	0.009 (0.9)

Table 4. Genetic diversity index of populations of *C. persiaensis*

	N	S	H_n	H_d	Π
Hormozgan	32	34	27	0.95	0.0085
Qeshm	13	3	9	0.94	0.0053
Bushehr	4	7	4	1	0.0065
Total	49	44	29	0.96	0.0078

N , number of individuals sampled; S , number of segregating sites; H_n , number of haplotypes; H_d , haplotype diversity; π , nucleotide diversity.

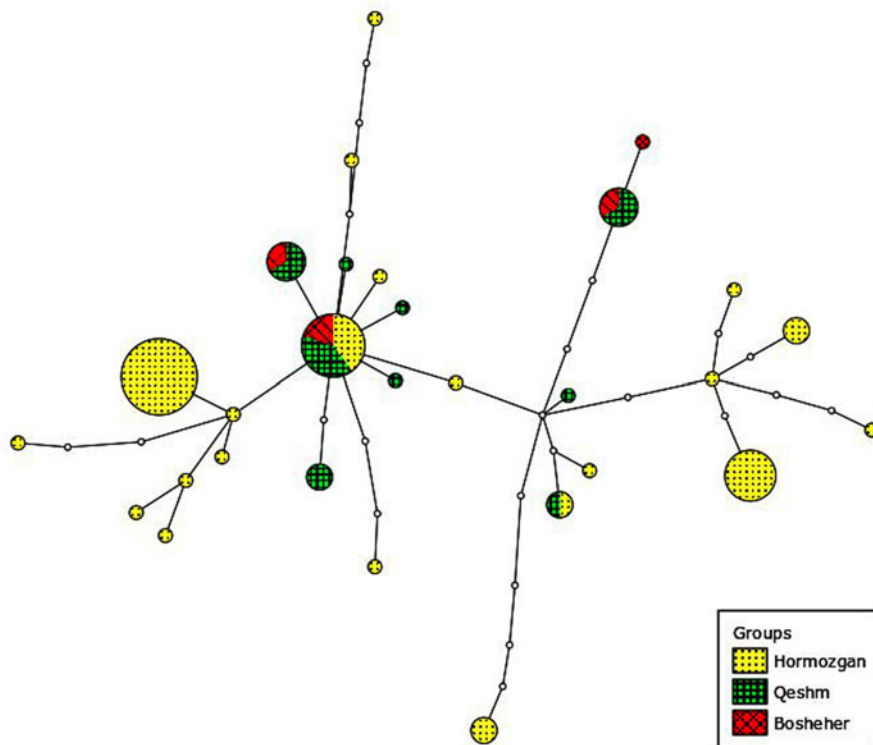


Fig. 5. Median-joining haplotype network for COI sequences from *C. persiaensis* taxa. Coloured circles represent individual haplotypes and the sizes of the circles are proportional to the frequency of the haplotypes. Each point mutation is symbolized by a mark on the lines connecting haplotypes.

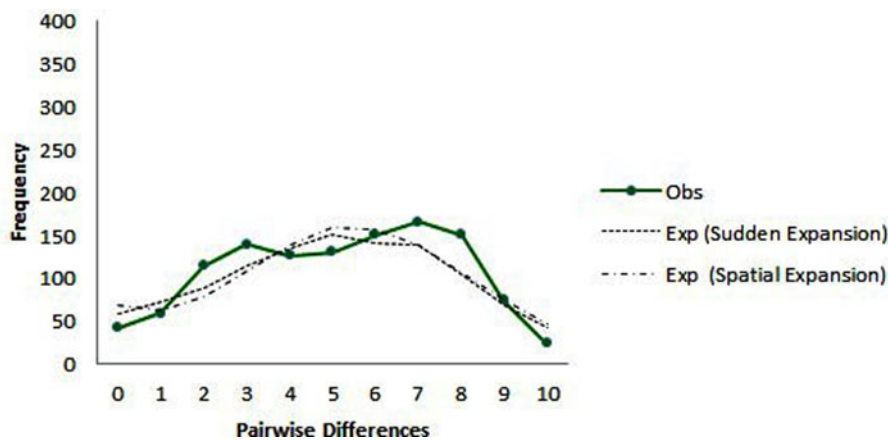


Fig. 6. Mismatch distributions for the COI locus for *C. persiaensis*.

including 13 individuals sharing by all populations. Twenty-five haplotypes represent private haplotypes (Figure 5), of which four haplotypes include more than one specimen. The haplotype network indicates close linkage among haplotypes as the Hormozgan population was shared among the samples collected from Qeshm and Bushehr and its private haplotypes are partially close to other two populations (Figure 5).

F-statistics showed insignificant genetic differentiation between Hormozgan and Bushehr ($\Phi_{st} = -0.09$, $P < 0.05$) and between Bushehr and Qeshm ($\Phi_{st} = -0.00032$, $P < 0.05$), otherwise it was significant between Hormozgan and Qeshm ($\Phi_{st} = 0.067$, $P < 0.05$). AMOVA test, shows no detection of any genetic structure among populations; $F_{ST} = 0.07$. Tajima's *D* values were -1.67 ($P < 0.05$), indicating a recent event of population expansion (Figure 6, Table 3). The skewed bimodal shape of mismatch distribution and significant value of the raggedness index ($P = 0.009$), in contrast to results from the neutrality test, cannot demonstrate a scenario of recent population expansion (Figure 6, Table 3). Therefore, it can be excluded that populations are constant.

Discussion

This study is the first to assess the population structure of copepods associated with ghost shrimp between the Persian Gulf and Gulf of Oman. The two *Clausidium* species were studied alive in close association with their ghost shrimps (Sepahvand *et al.*, 2017, 2019). To our knowledge, there is no information on the genetics, behaviour and ecology of *Clausidium* copepods, because of the cryptic lifestyle of their hosts. Our analyses were based on a comparatively large number of specimens (total $N = 130$) of two different *Clausidium* species, from locations spanning across more than 2000 km of coastline. Contrary to previous findings of significant population genetic structure across the region in different taxa (e.g. Afkhami *et al.*, 2016; Ghanbarifardi *et al.*, 2018), the smaller values of Φ_{st} observed in the present study may derive from greater gene flow between subpopulations of *Clausidium* copepods, in particular in *C. persiaensis*. The real distribution and connectivity of intertidal animals in the region and closely related areas (i.e. West Indian Ocean) are determined by

oceanographic regime, environmental conditions and historical events (Tsang *et al.*, 2012; Afkhami *et al.*, 2016; Rahimi *et al.*, 2016; Ghanbarifardi *et al.*, 2018).

Our study suggests that each species of *Clausidium* copepod shows a pattern of generally high haplotype diversity and high connectivity, regardless of their host species. *Clausidium persiaensis* shows no spatial genetic differentiation, while *C. iranensis*, even though populations are in proximity, slight spatial genetic differentiation was observed. A plausible scenario for such a haplotype diversity of *Clausidium* copepods is likely to be the difference in occupancy levels observed between the two copepod species as a consequence of the behaviour or physiology of their hosts, since their attachment mechanisms are the same (Sepahvand *et al.*, 2020). The hosts are different in burrowing patterns, grooming and nutrition behaviours (Griffis & Suchanek, 1991; Sepahvand *et al.*, 2014) and these parameters may influence the number of copepods occupying each host and consequently the haplotype diversity. Sepahvand *et al.* (2020), claimed that, although the number of *Clausidium* copepods increases with the host size, the two host species vary in the degree of symbiont invasion, with large *C. typa* (host for *C. persiaensis*) hosting ~7 times as many symbionts as the similarly sized *N. jousseaumei* (host for *C. iranensis*). Factors such as host gender and host species also affect the density of copepods (Corsetti & Strasser, 2003).

Dispersal capacity and oceanographic barriers may play a central role for genetic differentiation in copepods (Goetze & Ohman, 2010; Norton & Goetze, 2013). Hence, population genetic structure of *Clausidium* copepods could be driven by the oceanography and biological traits along the southern coast of Iran, since the pattern of genetic connectivity corresponds to the ocean current in the Persian Gulf and Gulf of Oman. It is likely that there are different magnitudes of gene flow taking into account the dissimilar dispersal abilities of the two species. Whereas both adult burrowing shrimps and *Clausidium* copepods are able to move, their movement is limited compared with free-living species.

In summary, it seems that ecological, morphological, life-history differences of the host and *Clausidium* copepods as well as abiotic (historical events, ocean current) parameters construct the population structure of the copepods. However, based on Sepahvand *et al.* (2020), host specificity and microhabitat selection of *Clausidium* copepods as the most important parameters of population size may have the most effective role on haplotype diversity of this group of copepods. Future studies should focus on getting a better understanding of the genetic population structure of *C. iranensis* and *C. persiaensis* as well as connectivity among populations and detailed analysis of life cycle strategies of their hosts.

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References

- Afkhami M, Schubart CD and Naderloo R (2016) Morphometric differentiation among populations of *Leptodius exaratus* (H. Milne Edwards, 1834) (Brachyura, Xanthidae) from the Persian Gulf and the Gulf of Oman. *Crustaceana* **89**, 259–271.
- Barth HJ and Khan NY (2008) Biogeophysical setting of the Gulf. In Abuzinada AH, Barth HJ, Krupp F, Böer B and Al Abdessalaam TZ (eds), *Protecting the Gulf's Marine Ecosystems from Pollution*. Basel: Birkhäuser, pp. 101–115.
- Blanco-Bercial L, Álvarez-Marqués F and Bucklin A (2011) Comparative phylogeography and connectivity of sibling species of the marine copepod *Causocalanus* (Calanoida). *Journal of Experimental Marine Biology and Ecology* **404**, 108–115.
- Clement M, Posada D and Crandall K (2000) A computer program to estimate gene genealogies. *Molecular Ecology* **9**, 1657–1659.
- Cornils A, Wend-Heckmann B and Held C (2017) Global phylogeography of *Oithona similis* sl (Crustacea, Copepoda, Oithonidae): a cosmopolitan plankton species or a complex of cryptic lineages? *Molecular Phylogenetics and Evolution* **107**, 473–485.
- Corsetti JL and Strasser KM (2003) Host selection of the symbiotic copepod *Clausidium dissimile* in two sympatric populations of ghost shrimp. *Marine Ecology Progress Series* **256**, 151–159.
- Doebeli M, Dieckmann U and Macdonald GJ (2000) Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *American Naturalist* **21**, 77–101.
- Excoffier L and Lischer HE (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* **10**, 564–567.
- Folmer O, Black M, Hoeh W, Lutz R and Vrijenhoek R (1994) DNA Primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 29–49.
- Fontaneto D, Boschetti C and Ricci C (2008) Cryptic diversification in ancient asexuals: evidence from the bdelloid rotifer *Philodina flaviceps*. *Journal of Evolutionary Biology* **21**, 580–587.
- Ghanbarifardi M, Aliabadian M and Esmaceli H. R. (2018) Phylogeography of Walton's mudskipper, *Periophthalmus waltoni* Koumans, 1941 (Perciformes: Gobiidae), from the Persian Gulf and Gulf of Oman. *Zoology in the Middle East* **64**, 207–218.
- Goetze E (2003) Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae. *Proceedings of The Royal Society of London B* **270**, 2321–2331.
- Goetze E (2005) Global population genetic structure and biogeography of the oceanic copepods *Eucalanus hyalinus* and *E. spinifer*. *Evolution* **59**, 2378–2398.
- Goetze E and Ohman MD (2010) Integrated molecular and morphological biogeography of the calanoid copepod family Eucalanidae. *Deep Sea Research Part II: Topical Studies in Oceanography* **57**, 2110–2129.
- Gollner S, Stuckas H, Kihara TC, Laurent S, Kodami S and Martinez Arbizu P (2016) Mitochondrial DNA analyses indicate high diversity, expansive population growth and high genetic connectivity of vent copepods (Dirivultidae) across different oceans. *PLoS ONE* **11**, e0163776.
- Gómez A, Carvalho GR and Lunt DH (2000) Phylogeography and regional endemism of a passively dispersing zooplankton: mitochondrial DNA variation in rotifer resting egg banks. *Proceedings of The Royal Society of London B* **267**, 2189–2197.
- Griffis R and Suchanek TH (1991) A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea). *Marine Ecology Progress Series* **79**, 171–183.
- Hall TA (1998) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**, 95–98.
- Harpending RC (1994) Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human Biology* **66**, 591–600.
- Huys R (2014) Copepoda. In Martin JW, Olesen J and Høeg JT (eds), *Atlas of Crustacean Larvae*. Baltimore, MD: John Hopkins University Press, pp. 144–163.
- Itoh H and Nishida S (2007) Life history of the copepod *Hemicyclops gomsoensis* (Poecilostomatoida, Clausidiidae) associated with decapod burrows in the Tama-River estuary, central Japan. *Plankton Benthos Research* **2**, 134–146.
- Kearn GC (2004) *Leeches, Lice and Lampreys: A Natural History of Skin and Gill Parasites of Fishes*. Dordrecht: Springer.
- Kihara TC and Rocha CEF (2013) First record of *Clausidium* (Copepoda, Clausidiidae) from Brazil: a new species associated with ghost shrimps *Neocallichirus grandimana* (Gibbes, 1850) (Decapoda, Callinassidae). *Zookeys* **335**, 47–67.
- Kossmann R (1874) Ueber *Clausidium testudo*, einen neuen Copepoden, nebst Bemerkungen über das System der halbparasitischen Copepoden. *Verhandlungen der Physikalischen Gesellschaft zu Würzburg* **7**, 280–294.
- Lambeck K (1996) Shoreline reconstructions for the Persian Gulf since the last glacial maximum. *Earth and Planetary Science Letters* **142**, 43–57.

- Lande R** (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–335.
- Librado P and Rozas J** (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics (Oxford, England)* **25**, 1451–1452.
- Múrias dos Santos A, Cabezas MP, Tavares AI, Xavier R and Branco M** (2015) tcsBU: a tool to extend TCS network layout and visualization. *Bioinformatics (Oxford, England)* **32**, 627–628.
- Nei M, Maruyama T and Chakraborty R** (1975) The bottleneck effect and genetic variability in populations. *Evolution* **29**, 1–10.
- Norton EL and Goetze E** (2013) Equatorial dispersal barriers and limited population connectivity among oceans in a planktonic copepod. *Limnology and Oceanography* **58**, 1581–1596.
- Nuwer ML, Frost BW and Armbrust EV** (2008) Population structure of the planktonic copepod *Calanus pacificus* in the North Pacific Ocean. *Marine Biology* **156**, 107–115.
- Palumbi SR** (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**, 547–572.
- Rahimi P, Rezvani Gilkoliaie S, Ghavam Mostafavi P, Jamili S and Rahnema M** (2016) Population genetic structure of the white sardine, *Sardinella albella*, in the Persian Gulf and Sea of Oman by analysis of mitochondrial control region. *Iranian Journal of Fisheries Sciences* **15**, 995–1008.
- Schneider S and Excoffier L** (1999) Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. *Genetics* **152**, 1079–1089.
- Sepahvand V, Sari A, Tudge C and Bolouki M** (2014) A study of burrow morphology in representative axiidean and gebiidean mud shrimps, from the Persian Gulf and Gulf of Oman, Iran. *Nauplius* **22**, 137–144.
- Sepahvand V, Rastegar-Pouyani N, Kihara TC and Momtazi F** (2017) A new species of *Clausidium* Kossmann, 1874 (Crustacea, Copepoda, Cyclopoida, Clausidiidae) associated with ghost shrimps from Iran. *Nauplius* **25**, 1–16.
- Sepahvand V, Kihara TC and Boxshall GA** (2019) A new species of *Clausidium* Kossmann, 1874 (Copepoda: Cyclopoida) associated with ghost shrimps from the Persian Gulf, including female-male interlocking mechanisms and remarks on host specificity. *Systematic Parasitology* **96**, 171–189.
- Sepahvand V, Brown BL and Gholamifard A** (2020) Host specificity and microhabitat preference of symbiotic copepods (Cyclopoida: Clausidiidae) associated with ghost shrimps (Decapoda: Callichiridae, Callianideidae). *Ecology and Evolution* **10**, 10709–10718.
- Sheppard CA and Andrew P and Roberts C** (1992) *Marine Ecology of the Arabian Region: Patterns and Processes in Extreme Tropical Environment*. San Diego, CA: Academic Press.
- Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J, Benzoni F, Dutrieux E, Nicholas KD, Durvasula SRV, Jones DA, Loughland R, Medio D, Nithyanandan M, Pillingm GM, Polikarpov I, Price ARG, Purkis S, Riegl Bd, Saburova M, Samimi-Namin K, Taylor O, Wilson S and Zainal K** (2010) The Gulf: a young sea in decline. *Marine Pollution Bulletin* **60**, 13–38.
- Tajima F** (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**, 585–595.
- Tamura K, Stecher G, Peterson D, Filipski A and Kumar S** (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* **30**, 2725–2729.
- Tsang LM, Achituv Y, Chu KH and Chan BKK** (2012) Zoogeography of intertidal communities in the West Indian Ocean as determined by ocean circulation systems: patterns from the *Tetraclita* barnacles. *PLoS ONE* **7**, e45120.
- Xiang XL, Xi YL, Wen XL, Zhang G, Wang JX and Hu K** (2011) Genetic differentiation and phylogeographical structure of the *Brachionus calyciflorus* complex in eastern China. *Molecular Ecology* **20**, 3027–3044.
- Yao F** (2008) *Water Mass Formation and Circulation in the Persian Gulf and Water Exchange with the Indian Ocean* (Open Access Dissertations), paper 183. Available online at http://scholarlyrepository.miami.edu/cgi/viewcontent.cgi?article=1182&context=oa_dissertations.
- Zeller M, Reusch TBH and Lampert W** (2006) A comparative population genetic study on calanoid freshwater copepods: investigation of isolation-by-distance in two Eudiaptomus species with a different potential for dispersal. *Limnology and Oceanography* **51**, 117–124.