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Phylogeography of a commercially important reef fish, *Lutjanus ehrenbergii*, from the coastal waters of the Arabian Peninsula

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ABSTRACT

The coastal waters of the Arabian Peninsula include a heterogeneous marine region comprising the Persian/Arabian Gulf and Sea of Oman at its northeastern boundary and the Arabian Sea, Gulf of Aden, and Red Sea at its southern and western boundary. The environment within this region shifts from highly variable coral cover and extreme temperatures within the Persian/Arabian Gulf to sparse coral cover, lower summer temperatures, and nutrient-rich upwelling within the Sea of Oman. Within the Gulf of Aden and Red Sea there is high coral cover and warm, stable conditions. We tested for barriers to pelagic dispersal across this peninsula for the commercially important blackspot snapper *Lutjanus ehrenbergii* using mitochondrial DNA sequences. We found scant evidence for population genetic differences when comparing within northern and southern sections, but instead found strong evidence of genetic differentiation between northern and southern sections, with the Persian/Arabian Gulf and Sea of Oman populations being highly differentiated from the Gulf of Aden and Red Sea populations. Low levels of haplotype sharing between the Persian/Arabian Gulf – Sea of Oman and the Gulf of Aden – Red Sea probably reflect scenarios of historical colonization into these peripheral bodies of water, or the presence of a contemporary ecological barrier preventing further genetic exchange.

KEYWORDS: *Lutjanus ehrenbergii*, blackspot snapper, phylogeography, Arabian Peninsula.

INTRODUCTION

The fields of population genetics and phylogeography provide tools to visualize patterns in species distributions, based on genetic information influenced by historical and contemporary processes, which may not be evident from contemporary species distributions alone (Slatkin 1987, Benzie 1999). Diverse phylogeographical patterns may be present even among species that are closely related and show comparable demography and distributions (Affonso and Galetti 2007, Gaither *et al.* 2010). In contrast, a high degree of genetic similarity has also been found for taxa across substantial geographical ranges (Taylor and Hellberg 2006). Determining species phylogeographical patterns across areas separated by both historical and contemporary barriers related to geology and environment, respectively, may provide a more robust understanding of how the latter influences gene flow, and can help to guide species management efforts.

The coastal waters of the Arabian Peninsula, encapsulating the Persian/Arabian Gulf, Sea of Oman, Arabian Sea, Gulf of Aden, and the Red Sea (Fig. 1), are unique and environmentally variable marine ecosystems. The marine environment of the Persian/Arabian Gulf is characterized by extremes in water temperature and salinity (Riegl 1999, Coles 2003) and low primary productivity (Nezlin *et al.* 2007) due to its high-latitude position, shallow

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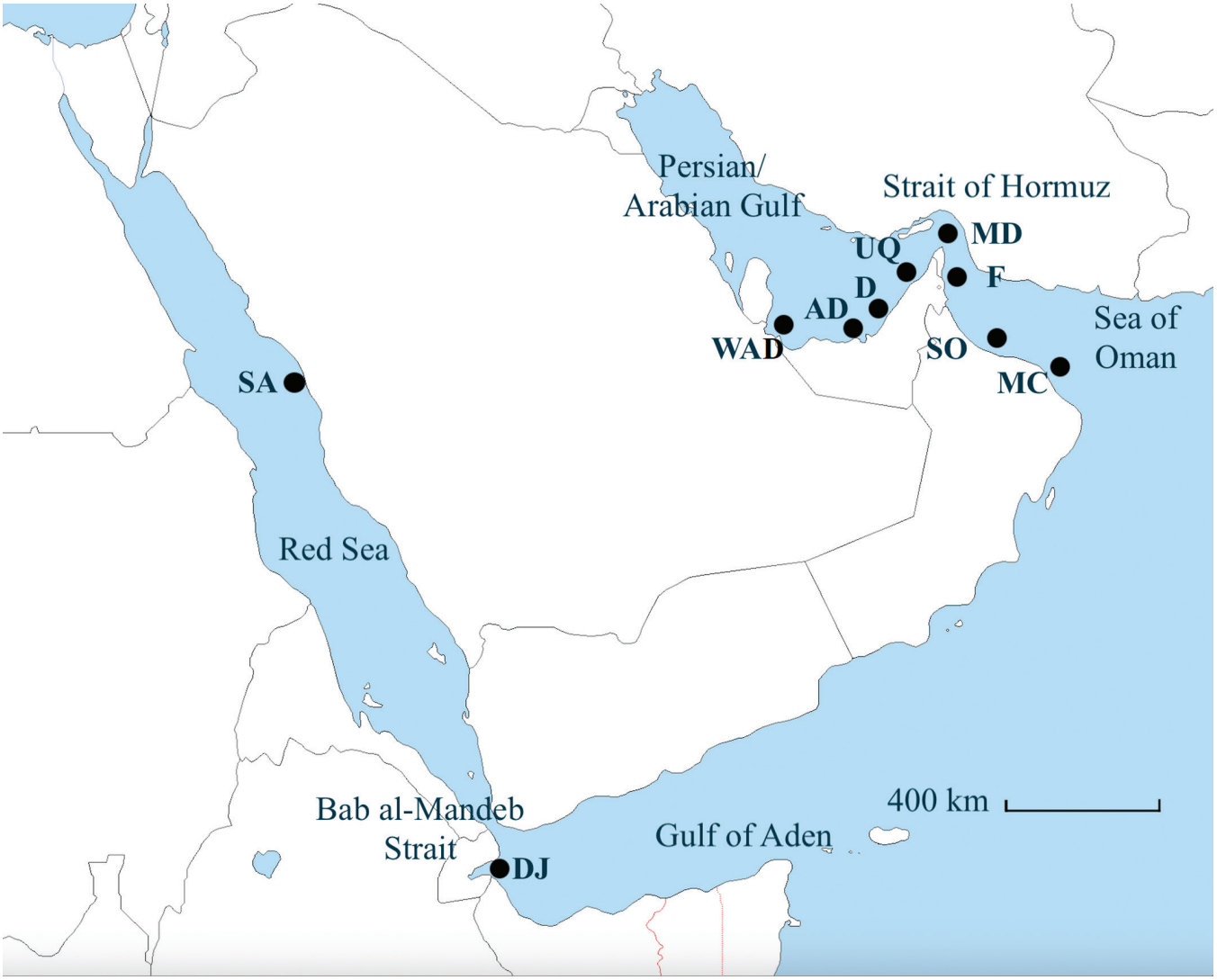

Figure 1. Sampling locations for collection of *Lutjanus ehrenbergii* across the Arabian Peninsula (Western Abu Dhabi, WAD; Abu Dhabi, AD; Dubai, D; Umm al Quwain, UQ; Musandam, MD; Fujairah, F; Sohar, SO; Muscat, MC; Djibouti, DJ; Saudi Arabia, SA).

nature, and restricted water exchange with the adjacent Sea of Oman (Vaughan *et al.* 2019). The narrow Strait of Hormuz, connecting the Persian/Arabian Gulf and Sea of Oman, restricts water exchange and serves as a substantial environmental boundary between the two systems, with benign oceanic temperatures and salinity within the Sea of Oman shifting to the more extreme environmental conditions within the Persian/Arabian Gulf (Reynolds 1993, Feary *et al.* 2013). Despite this, there is evidence for genetic panmixia of populations across waters adjacent to the peninsula for narrow-barred Spanish mackerel, *Scomberomorus commerson* (Hoolihan *et al.* 2006), and yellowbar angelfish, *Pomacanthus maculosus* (Torquato *et al.* 2019), as well as genetic population differentiation between the Persian/Arabian Gulf and Sea of Oman for Indo-Pacific sailfish, *Istiphorus platypterus* (Hoolihan *et al.* 2004), yellow hind grouper, *Cephalopholis hemistiktos* (Priest *et al.* 2016), corals and coral symbiotic microalgae (Howells *et al.* 2016, Hume *et al.* 2018), and the sea urchin *Echinometra* sp. EZ (Ketchum *et al.* 2020).

Within the Sea of Oman, low levels of reef habitat are associated with the influx of cold, nutrient-rich waters during the Indian Ocean monsoon, which substantially impacts seasonal temperature and productivity within the region (Kemp and Benzoni 2000, Schott and McCreary 2001; Claereboudt 2019). This upwelling results in a break in environmental conditions between the northern Sea of Oman and the Arabian Sea (situated near Ras al Hadd), creating an ephemeral environmental boundary and a break in genetic population structure in macroalgae (Schils and Wilson 2006), snails (Williams *et al.* 2011), and cuttlefish (Anderson *et al.* 2010).

The Red Sea is a narrow semi-enclosed basin that is connected to the Gulf of Aden/Indian Ocean in the south through the narrow Bab al-Mandab strait. There is a substantial environmental gradient from the Gulf of Aden into the Red Sea based on decreasing water temperature and salinity (Sheppard *et al.* 1992, Carvalho *et al.* 2019) structured predominantly by interannual variability via the influx of cold nutrient-rich waters associated with the winter Indian Ocean monsoon (Dreano *et al.* 2016, Raitsos *et al.* 2017). The combination of environmental extremes, and the physical constraints to water flow across the Bab al-Mandab strait suggest this region is a barrier to connectivity between the Red Sea and the Gulf of Aden (Nanninga *et al.* 2014, DiBattista *et al.* 2017, Raitsos *et al.* 2017).

Historical sea level changes within the Red Sea and Persian/Arabian Gulf, associated predominantly with Pleistocene glacial cycles, impacted the historical availability of habitat, direction or magnitude of oceanographic currents, and abiotic conditions within both regions, which has also had a substantial impact on current levels of biodiversity (Sheppard *et al.* 1992, Riegl and Purkis 2012). The Red Sea formed during the geological separation of Arabia from Africa 5 million years ago, and has experienced intermittent periods of drying and flooding, repeatedly becoming isolated from the wider Indian Ocean throughout the Pleistocene (DiBattista *et al.* 2016, Carvalho *et al.* 2019). In parallel, although geologically younger, the Persian/Arabian Gulf was completely dry during the Pleistocene (Sheppard *et al.* 1992, Reynolds 1993). Global increases in temperature in the Holocene led to the Persian/Arabian Gulf being completely flooded between 14 and 8 kya, with this comparatively short period being when most reef-associated fauna are expected to have re-colonized the Persian/Arabian Gulf (Teller *et al.* 2000, Smith *et al.* 2022).

In the present study we utilize a common reef-associated coastal fish species, the blackspot snapper *Lutjanus ehrenbergii* (F. Lutjanidae [Peters, 1879]), to examine whether patterns of genetic structure are apparent within populations across this geologically and environmentally heterogeneous peninsula. *Lutjanus ehrenbergii* is commonly found on coral reefs and rocky substrata throughout the regions, with a population range that extends to the entire Indo-Pacific (Randall 1995, D'Agostino *et al.* 2021) and is a generalist carnivore, feeding on benthic invertebrates associated with turfing algae (i.e. amphipods, isopods) and small fish (Randall 1995, D'Agostino *et al.* 2020). This work examines populations across several potential barriers to larval dispersal: the Strait of Hormuz dividing the environmentally extreme Persian/Arabian Gulf and oceanic Sea of Oman; the area of substantial upwelling environmentally dividing the northern Sea of Oman from the Arabian Sea (Currie *et al.* 1973); and the Strait of Bab-al-Mandeb dividing the southern Red Sea from the Gulf of Aden (Bower *et al.* 2000). We test the hypothesis that resident populations within each sea or gulf will exhibit low genetic structure, with high genetic structure apparent when comparing populations across seas or gulfs.

METHODS

Replicate tissue samples of *L. ehrenbergii* (dorsal fin and gill tissue) were collected from each of 10 coastal reef sites (Fig. 1; Table 1):

i. Southern Persian/Arabian Gulf [four sites: Western Abu Dhabi (WAD; centred on the city of As-Sila), Central Abu Dhabi (AD; centred on the city of Abu Dhabi), Dubai (D), and Umm al Quwain (UQ)];
ii. Strait of Hormuz [Musandam (MD; centred on the city of Khasab)];
iii. Sea of Oman [three sites: Fujairah (F; centred on the city of Dibba Al Fujairah), Sohar (SO) and Muscat (MC)];
iv. Gulf of Aden [Djibouti (DJ; collectively sampled from Maskali, Obock, and the Bay de Ghoubett)]; and
v. Saudi Arabia (SA; centred on the city of Thuwal).

Samples were collected from local fish markets or speared while snorkelling or on SCUBA (n = 20 per site). Care was taken when collecting market samples to obtain only locally caught specimens. To ensure that fish were local when collecting from fish markets, the research team would arrive early at fish markets as

Table 1. Sampling sites, collection methods, and number of *Lutjanus ehrenbergii* specimens successfully sequenced for *COI* and CR at each site.

Region	Site	Map reference	Latitude, longitude	Fishing method	No. of specimens sequenced
Persian/Arabian Gulf	Western Abu Dhabi (Sila)	WAD	24°04′07.9″N, 51°47′50.6″E	EAD research vessel	11
	Abu Dhabi	AD	24°31′32.47″N, 54°21′35.93″E	Local fishers	10
	Dubai	D	25°17′33.27″N, 55°19′20.61″E	Local fishers	10
	Umm Al Quwain	UQ	25°32′52.22″N, 55°33′38.60″E	Local fishers	8
Musandam	Khasab	MD	26°12′00.4″N, 56°14′43.0″E	Local fishers	10
Oman Sea	Fujairah	F	25°07′24.41″N, 56°21′29.78″E	Local fishers	10
	Sohar	SO	24°22′42.69″N, 56°44′24.70″E	Local fishers	9
	Muscat	MC	23°41′19.99″N, 58°10′44.17″E	Local fishers	10
Gulf of Aden	Djibouti	DJ	11°57.527″N, 43°18.812″E	SCUBA	8
Red Sea	Saudi Arabia	SA	27°54′35.6″N, 35°03′55.5″E	SCUBA	10

boats were coming in and spent time discussing with fishermen where the specimens were caught. Although there is a possibility that fish could have been transported between markets, this is unlikely over large distances. Fish were photographed at sites, to ensure that identification was correct; *Lutjanus fulviflamma* has similar morphological features to *Lutjanus ehrenbergii*, but the additional black coloration around the eye differentiates the two species. Any ambiguous samples were discarded. Tissue samples following collection were immediately placed in 100% ethanol and stored at −20°C.

DNA extraction was performed for 12 individuals from each site using either DNeasy Blood and Tissue kits (Qiagen) or a modified protocol of the CTAB extraction method (Goodacre and Wade 2001). DNA extraction aliquots were nanodropped to quantify DNA concentration and subsequently stored at −20°C. Two mitochondrial DNA (mtDNA) gene fragments were amplified for each specimen: cytochrome *c* oxidase I (*COI*; 638 bp) using primers FishF2 and FishRR (Ivanova *et al.* 2007) and control region (CR; 336 bp) using universal primers Cr-e and Cr-a (Lee *et al.* 1995). Each PCR consisted of a total volume of 25 µL, including 1× buffer, 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.2 µM of each primer, 1 U Taq polymerase, 1 µL of DNA template and DNA-free water. Thermocycling conditions were set for both *COI* and CR with a 2-min initial denaturation at 95°C, a 30-s denaturation at 94°C, annealing for 36 s at 56°C, extension for 1 min at 72°C for 35 cycles, and a final extension for 10 min at 72°C. A 'no-template' control (all other reagents included but excluding DNA) was included in every PCR run to control for contamination. PCR products were visualized on a 1.5% agarose gel stained with ethidium bromide. Successful amplification of the target region was verified with a DNA ladder to determine product size. Amplified PCR products were sequenced by Macrogen Inc. using an ABI3730XL DNA analyser. Primers were removed from sequences using Trev (Bonfield *et al.* 2002) and contigs were assembled and manually edited for misreads in Gap4 (Bonfield *et al.* 1995). The sequences were manually aligned using the Genetic Data Environment (GDE) (Smith *et al.* 1994). All analyses were undertaken using (i) each marker separately, then (ii) concatenated sequences for both markers.

The evolutionary relationships among the *L. ehrenbergii* sequences were determined by building maximum likelihood trees in PhyML v.3.2.4 (Guindon *et al.* 2009). Multiple hits were accounted for by using a GTR+Γ model of sequence evolution, and bootstrap analysis (1000 replicates) was undertaken to determine support for branches in the trees. Trees were initially constructed with reference sequences from GenBank of *L. ehrenbergi*, *L. fulviflamma*, *Lutjanus campechanus*, and *Perca fluviatilis* to confirm our morphological identifications, with trees rooted using Percidae as the outgroup. Tree topology alongside a high bootstrap support value (~70%) was used to define clades and subclades, as well as groups of haplotypes sharing a common ancestry. Defined clades and subclades were spatially mapped onto collection sites to determine the extent of geographical isolation between clades. Median-joining networks were produced using Network v.5 (Bandelt *et al.* 1999). Haplotype data files were generated in DnaSP; invariable site options were removed (Librado and Rozas 2009).

Divergence times were estimated using BEAST v.1.10.4, using molecular clock calibrations for *COI* and the CR derived from the literature and used in previous studies of the Lutjanidae (Gold *et al.* 2011, 2015, da Silva *et al.* 2020). For *COI*, a calibration of 1.2% divergence/Mya was used as estimated by Bermingham *et al.* (1997) from 19 marine fish species based on the rise of the Isthmus of Panama ~3.8 Mya. For the CR, a calibration of 4% divergence/Mya was used based on six germinate species of snook (*Centropomus*; Donaldson and Wilson 1999). For the concatenated dataset, the data were partitioned by loci, with different substitution models and rates applied to each locus. A strict clock Bayesian approach with the GTR+Γ substitution model was used, in addition to a constant size prior approach and a random starting tree. A maximum clade credibility tree was visualized and annotated with mean node ages for 10 000 burn-in states in FigTree v.1.4.4.

Genetic variation (within each genetic marker) at each sampling site was determined by examining the haplotype diversity, nucleotide diversity, and mean pairwise nucleotide difference among haplotypes (Arlequin v.3.5; Excoffier and Lischer 2010). In addition, the number of haplotypes and variable sites within each sampling site were provided. The spatial subdivisions of haplotypes were then determined by mapping the number of unique or 'private' haplotypes across sites.

Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) were used for assessing population growth; 10 000 permutations allowed for statistical significance to be calculated using Arlequin v.3.5 (Excoffier and Lischer 2010). Differentiation in sequences between populations was measured by calculating pairwise F_{ST} (Arlequin 3.5; Excoffier and Lischer 2010).

RESULTS

Table 1 shows the number of *L. ehrenbergii* specimens sequenced for both *COI* and CR at each site. The inclusion of our *L. ehrenbergii COI* sequences within a molecular phylogeny incorporating Lutjanid reference sequences from GenBank confirms the identity of all collected samples as *L. ehrenbergii* (Supporting Information, Fig. S1).

Strong similarities in genetic variation were apparent between mitochondrial markers across the different *L. ehrenbergii* populations. For *COI*, haplotype diversity ranged from 0.5111 to 0.910, while nucleotide diversity ranged from 0.001 to 0.006 (Table 2). In comparison, CR haplotype diversity ranged from 0.840 to 1.0, while nucleotide diversity ranged from 0.013 to 0.025 (Table 2). For *COI*, 25 variable sites and a total of 19 haplotypes from 96 samples were identified. In comparison, for CR a total of 50 variable sites and 51 haplotypes from 96 samples were identified.

The concatenated (*COI*–CR) phylogenetic tree (Fig 2A) showed a division of the *L. ehrenbergii* sequences into two main clades (supported in 99% of bootstrap replicates), which when mapped by site location presents a major division between sites in the Red Sea and Gulf of Aden (Clade 1) compared with those in the Persian/Arabian Gulf and Sea of Oman (Clade 2) (Fig. 2B). Within each clade there was relatively little geographical structure in subclades across sites (Fig. 2B). Similar phylogenies were inferred for each gene individually (Supporting Information, Figs S2, S3). Divergence time estimation analyses

Table 2. Estimates of DNA sequence diversity for (i) cytochrome *c* oxidase I (*COI*) and (ii) control region (CR) markers in *Lutjanus ehrenbergii* per collection site across the Arabian Peninsula.

Marker	Location	Haplotypes	Variable sites	Haplotype diversity (*h*)	Nucleotide diversity (%)	Mean pairwise nucleotide difference (%)
COI	WAD	5	4	0.78 (0.10)	0.001 (0.001)	1.02 (0.74)
	AD	5	11	0.82 (0.10)	0.005 (0.003)	3.62 (2.00)
	D	7	11	0.91 (0.07)	0.003 (0.002)	2.53 (1.48)
	UQ	5	11	0.86 (0.11)	0.01 (0.004)	4.28 (2.37)
	MD	5	10	0.82 (0.09)	0.003 (0.002)	2.42 (1.43)
	F	5	5	0.80 (0.10)	0.002 (0.001)	1.33 (0.90)
	SO	5	4	0.86 (0.09)	0.002 (0.001)	1.22 (0.85)
	MC	6	5	0.91 (0.06)	0.002 (0.001)	1.64 (1.05)
	DJ	5	6	0.86 (0.11)	0.004 (0.003)	2.93 (1.71)
	SA	3	5	0.51 (0.16)	0.002 (0.002)	1.62 (1.04)
CR	WAD	10	20	0.98 (0.05)	0.017 (0.01)	5.60 (2.91)
	AD	10	26	1.00 (0.04)	0.02 (0.01)	8.64 (4.36)
	D	9	24	0.98 (0.05)	0.02 (0.01)	6.93 (3.56)
	UQ	6	20	0.93 (0.08)	0.02 (0.01)	7.53 (3.94)
	MD	7	24	0.91 (0.08)	0.02 (0.01)	7.04 (3.61)
	F	9	17	0.98 (0.05)	0.01 (0.01)	4.58 (2.45)
	SO	9	21	1.00 (0.05)	1.00 (0.05)	6.50 (3.39)
	MC	6	16	0.84 (0.10)	0.02 (0.01)	5.55 (2.91)
	DJ	8	17	1.00 (0.06)	0.02 (0.01)	6.89 (3.63)
	SA	9	16	0.98 (0.05)	0.02 (0.01)	5.98 (3.11)

Number of haplotypes, number of variable sites, haplotype diversity (±SE), nucleotide diversity (%) (±SE), and mean pairwise nucleotide difference (%) (±SE) are provided. Location: Western Abu Dhabi (WAD); Abu Dhabi (AD); Dubai (D); Umm al Quwain (UQ); Musandam (MD); Fujairah (F); Sohar (SO); Muscat (MC); Djibouti (DJ); Saudi Arabia (SA).

showed that the division between Clade 1 (Red Sea – Gulf of Aden) and Clade 2 (Persian/Arabian Gulf – Sea of Oman) was ~2 Mya [95% highest posterior density (HPD) 3.52–1.38 Mya) based on the concatenated *COI* and CR dataset (Fig. 3), 1.38 Mya (95% HPD 0.74–2.15 Mya) for *COI* (Fig. S4), and 2.26 Mya (95% HPD 1.38–3.52 Mya) for CR (Fig. S5).

Within clades, there were a number of subclades identified (all subclades form a monophyletic group in the tree supported in ≥ 70% bootstrap replicates). Within Clade 1, Subclade 1A contained a majority of haplotypes (66%) from the Red Sea and Gulf of Aden but there were also a number of haplotypes (33%) from Abu Dhabi, Umm al Quwain, Dubai, and Musandam. In comparison, Subclade 1B contained haplotypes restricted solely to the Red Sea and Gulf of Aden. There were also an additional three haplotypes from the Red Sea and Gulf of Aden in Clade 1 that were not assigned to subclades. Within Clade 2, eight subclades were identified, consisting solely of haplotypes from sites throughout the southern Persian/Arabian Gulf, Strait of Hormuz, and Sea of Oman. Subclade 2A contained haplotypes from Abu Dhabi, Fujairah, and Muscat. Subclade 2B held haplotypes from Western Abu Dhabi, Dubai, Sohar, and Muscat. Subclade 2C contained haplotypes from Western Abu Dhabi, Abu Dhabi, Fujairah, and Sohar. Subclade 2D held haplotypes from all eight sites across the Persian/Arabian Gulf, Strait of Hormuz, and Sea of Oman. Subclade 2E contained haplotypes from the sites of Western Abu Dhabi, Abu Dhabi, Musandam, Fujairah, and Sohar. Subclade 2F contained haplotypes from Dubai, Fujairah, and Muscat. Subclade 2G contained haplotypes from Western Abu Dhabi, Abu Dhabi, Dubai, Umm al Quwain, Musandam, and Muscat. Subclade 2H held haplotypes from all eight sites across the Persian/Arabian Gulf, Strait of Hormuz, and Sea of Oman.

The main geographical split in clade groupings was similar in the median-joining network (Supporting Information, Fig. S6), with the main split between the Clade 1 grouping predominantly structured by Saudi Arabia and Djibouti populations, and Clade 2 groupings associated solely with the Persian/Arabian Gulf, Strait of Hormuz, and Sea of Oman populations.

There was a high frequency of private haplotypes (46% of total haplotypes) in all localities within the concatenated dataset (Fig. 4). In addition, there was a high level of haplotype sharing separately within Persian/Arabian Gulf and Red Sea sites, despite little sharing across the peninsula (Fig. 4).

There was evidence of an excess of low-frequency polymorphisms relative to expectation across the majority of Persian/Arabian Gulf sites, whereas there were low levels of both low- and high-frequency polymorphisms within the Red Sea populations (Table 3). There was evidence of recent site-specific population expansion throughout northeastern Arabian locations (Persian/Arabian Gulf – Sea of Oman), depending on the marker examined (Table 3). Both markers had largely negative Tajima's D values, but these were not statistically significant. Fu's Fs showed negative and statistically significant values for Western Abu Dhabi, Abu Dhabi, Fujairah (CR), and Sohar (*COI* and CR) (Table 3).

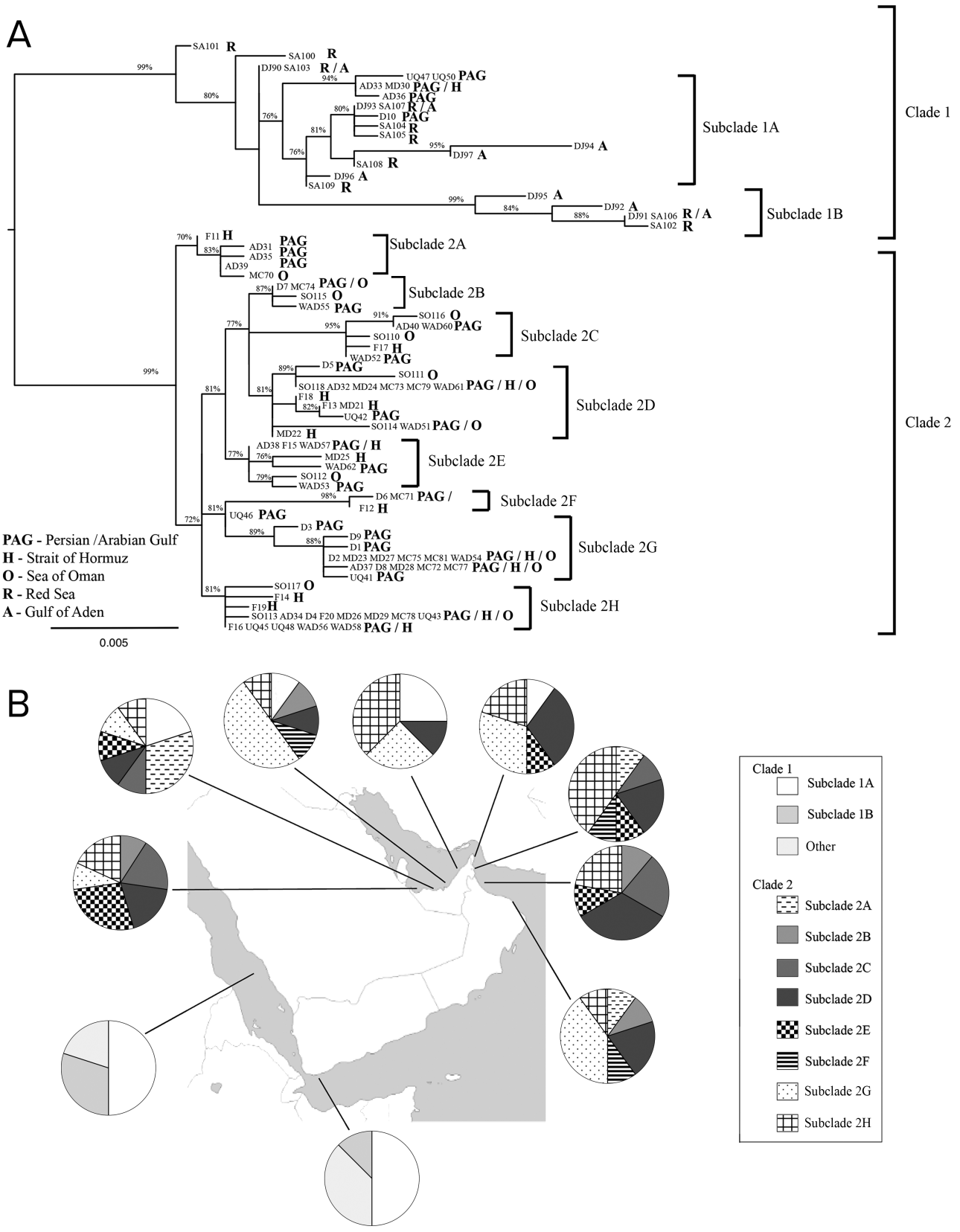

Figure 2. A, maximum likelihood (ML) tree of *Lutjanus ehrenbergii* populations based on concatenated sequences of the cytochrome *c* oxidase I (*COI*) and control region (CR) markers (904 bp). Bootstrap support values are indicated on the branches and the scale bar corresponds to 0.5 changes per 100 nucleotide positions. The tree was rooted based on the topology of a tree built using reference outgroups from GenBank (see Supporting Information, Fig. S1). Distinct clades and subclades are labelled on the tree. B, map of the Arabian Peninsula showing the distribution of *L. ehrenbergii* clades and subclades.

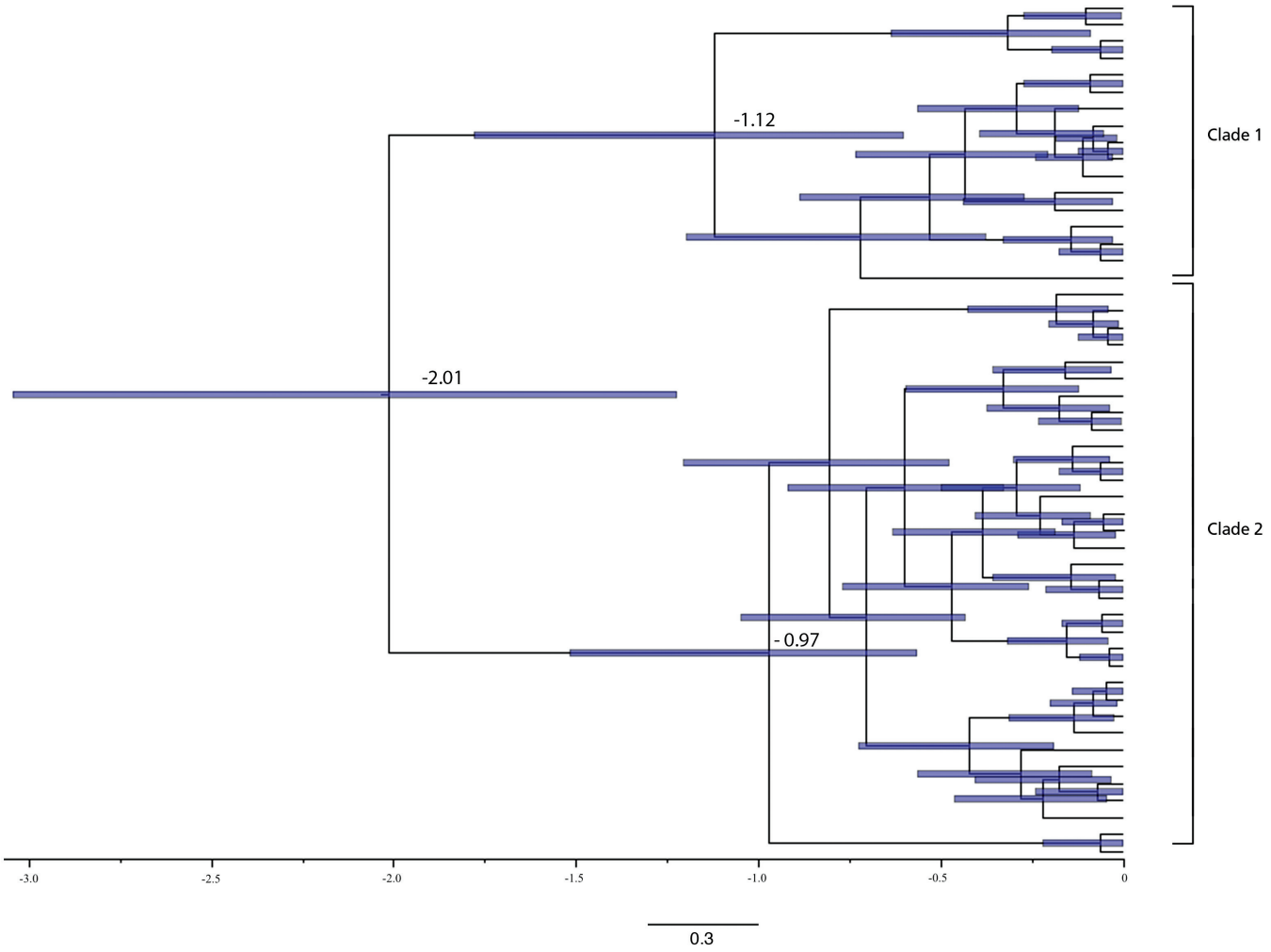

Figure 3. Molecular clock calibrated phylogenetic tree of *Lutjanus ehrenbergii* based on concatenated sequences of cytochrome *c* oxidase I (*COI*) and the control region (CR). For calibration, rates of 1.2% and 4% per million years are used for *COI* and CR respectively. The scale bar corresponds to 0.3 million years.

Pairwise F_{ST} values were highest when comparing the Red Sea to other Arabian Peninsula populations, which was concordant with tree, network, and haplotype sharing figures showing that the Red Sea populations are highly differentiated from other Arabian Peninsula populations (Table 4). There was little to no genetic differentiation within the majority of northeastern Arabian Peninsula populations, although Western Abu Dhabi and Sohar populations showed relatively high differentiation compared to most other populations. Little genetic differentiation within each of the Red Sea populations and Gulf of Aden populations was apparent (Table 4).

DISCUSSION

The genetic structure of *L. ehrenbergii* populations resident within the Persian/Arabian Gulf and Sea of Oman and separately within the Red Sea and Gulf of Aden are concordant with a pattern of high genetic similarity within each region. Pairwise F_{ST} values were low among sites within each region, indicating limited population differentiation across sampled populations. The presence of genetic homogeneity between populations within regions suggests that sufficient gene flow between populations has occurred to counteract historical and/or contemporary genetic divergence.

Low genetic similarity between populations from the Persian/Arabian Gulf – Sea of Oman and those of the Gulf of Aden – Red Sea highlight the low levels of connectivity between *L. ehrenbergii* populations between the two major regions of this study (Anderson *et al.* 2010, Williams *et al.* 2011). Low connectivity may be partly due to the lack of substantial coral reef habitat throughout the southern Sea of Oman, reducing potential step-wise connections between adult populations. However, this region demarcates one of the sharpest biotic transition zones known in marine biogeography (Schils and Wilson 2006), which may be partly due to the substantial seasonal upwelling during the Indian Ocean southwest monsoon (June to September), which brings an influx of cold, nutrient-rich waters onto the coastline (Longhurst 2010). Such upwelling reduces coastal water temperatures, while also increasing productivity (Kemp and Benzoni 2000, Schott and McCreary 2001), with a substantial turnover in marine diversity noted across this area (Schils and Wilson 2006). In fact, the southern Sea of Oman at

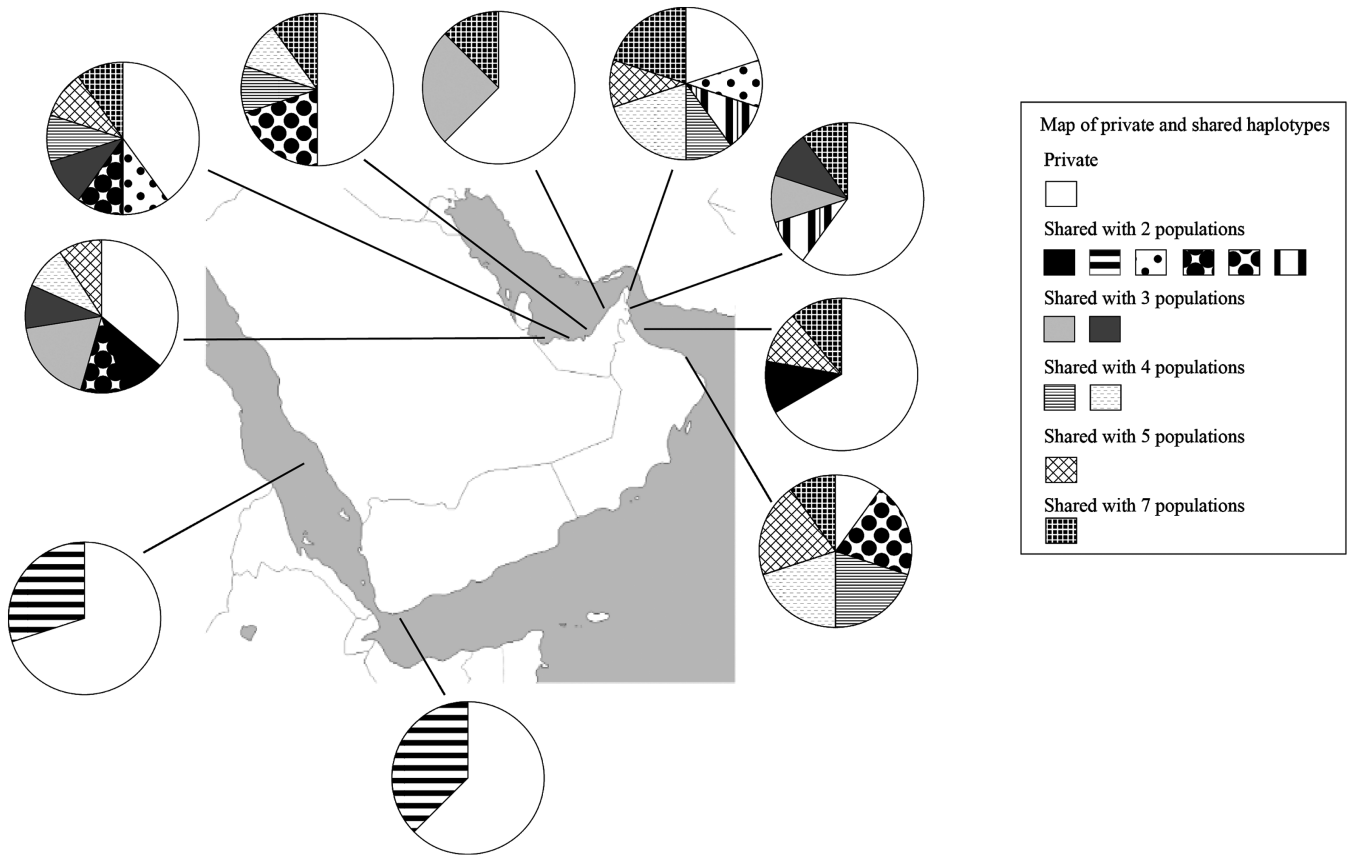

Figure 4. The distribution of shared and private haplotypes of *Lutjanus ehrenbergii* populations for concatenated cytochrome *c* oxidase I (*COI*) and control region (CR) sequences.

Table 3. Estimates of neutrality tests for *Lutjanus ehrenbergii*.

	COI		CR	
Location	**Tajima's D**	**Fu's Fs**	**Tajima's D**	**Fu's Fs**
Western Abu Dhabi	−0.93	−2.02*	−0.81	−4.09*
Abu Dhabi	−0.31	0.76	−0.28	−3.92*
Dubai	−1.56	−2.54*	−0.87	−2.58
Umm al Quwain	0.05	0.46	−0.12	0.35
Musandam	−1.39	−0.17	−0.81	0.07
Fujairah	−0.98	−1.55	−1.11	−3.89**
Sohar	−0.69	−1.99*	−0.78	−4.01**
Muscat	−0.28	−2.36*	−0.08	0.64
Djibouti	1.24	−0.33	0.26	−3.03*
Saudi Arabia	−0.33	1.48	0.26	−3.02*

Tajima's D and Fu's Fs for cytochrome *c* oxidase I (*COI*) and control region markers. *P* values are denoted with asterisks to designate significance at *0.05, **0.01.

Ras al Hadd has been previously shown as an environmental boundary, associated with the presence of the Ras Al Hadd jet—a strong current moving offshore during the monsoon that acts as a physical barrier for larval transport along the coastline (Burt *et al.* 2011). Within this region a break in the genetic population structure in macroalgae, snails, crown of thorns starfish, and the yellowfin hind have been identified (Schils and Wilson 2006, Williams *et al.* 2011, Vogler *et al.* 2012, Priest *et al.* 2016). We can predict then that dispersal of larvae of a number of coral reef fish species may be reduced or substantially impacted by such changes in environmental conditions on this coastline.

Interestingly, populations that shared haplotypes were found across the most distant sites sampled (Western Abu Dhabi and Saudi Arabia), separated by over 4000 km. Such a high level of genetic exchange may be associated with uneven larval contribution between sites from natal populations (Hedgecock 1994, Marshall *et al.* 2010). In marine systems the presence of non-geographically related pockets of genetic connectivity (i.e.

Table 4. Pairwise genetic differentiation (F_{ST}) between populations of *Lutjanus ehrenbergii* for cytochrome *c* oxidase I (*COI*) and control region (CR) markers calculated using ARLEQUIN.

		WAD	AD	D	UQ	MD	F	SO	MC	DJ
COI	AD	0.06								
	D	0.03	0							
	UQ	0.11	−0.10	0.01						
	MD	0	−0.05	−0.09	0					
	F	−0.01	0.03	0.08	0.08	0.03				
	SO	−0.08	0.04	0.06	0.09	0.02	−0.03			
	MC	0.04	0.07	0.01	0.08	−0.05	0.08	0.08		
	DJ	0.80	0.60	0.69	0.55***	0.69	0.78	0.78***	0.77	
	SA	0.82	0.60***	0.70	0.55	0.71***	0.81	0.81	0.79	0.12
CR	AD	0.05								
	D	0.13**	0.05							
	UQ	0.08	−0.06	0.003						
	MD	0.01	−0.02	−0.04	−0.04					
	F	−0.03	0.02	0.12*	0.03	0.001				
	SO	−0.05	0.08	0.20**	0.12*	0.08*	0.02			
	MC	0.05	0.03	−0.05	0.03	−0.07	0.03	0.12*		
	DJ	0.59	0.38***	0.47 ***	0.41***	0.50	0.60	0.59	0.57	
	SA	0.59	0.40***	0.47	0.42***	0.50	0.60	0.59	0.57	−0.058

P values are denoted with asterisks to designate significance at *0.05, **0.01, and ***0.001. Locations: Western Abu Dhabi (WAD); Abu Dhabi (AD); Dubai (D); Umm al Quwain (UQ); Musandam (MD); Fujairah (F); Sohar (SO); Muscat (MC); Djibouti (DJ); Saudi Arabia (SA).

chaotic genetic patchiness; Larson and Julian 1999) has previously been noted. Such patchiness may be associated with specific differences in patterns of larval settlement between sites (Selkoe *et al.* 2006). Termed sweepstake recruitment (Hellberg 2009), this theory argues that although marine organisms produce a large quantity of offspring, high mortality predominantly leads to only a few individuals contributing to the majority of the larval cohort surviving to adulthood (Hedgecock 1994). For example, in the kelp bass, *Paralabrax clathratus*, up to 95% of a population were found to be related within a population bounded by < 200 km (Selkoe *et al.* 2006), whereas within conspecific snapper species *Lutjanus kasmira* and *L. fulvus*, some degree of genetic differentiation at a few sites across the Indo-Pacific was also detected (Gaither *et al.* 2010).

Patterns of genetic similarity between *L. ehrenbergii* populations within the Persian/Arabian Gulf and Sea of Oman in the present study may potentially be the result of contemporary larval connectivity. Larval fishes can show exceptionally long periods of pelagic larval dispersal (PLD), potentially lasting weeks to months (Caley *et al.* 1996, Kinlan *et al.* 2005). Within such timelines, larvae may travel hundreds to thousands of kilometres from their natal reefs (Feary *et al.* 2014), maintaining genetic homogenization of distant populations in the absence of dispersal barriers. Importantly, the PLD for Lutjanids has been shown to range from 21 to nearly 40 days (average PLD 30.1 ± 1.86 days) (Alzate *et al* 2019), potentially providing enough time for larvae dispersing within reefs on either side of the Arabian Peninsula to be entrained within inward- or outward-flowing waters, enhancing the likelihood of dispersal throughout the region. Large population sizes and high fecundity could be another factor in the observed pattern of connectivity.

However, genetic similarity between sampled populations of *L. ehrenbergii* may also reflect historical emigration from Indian Ocean populations. The division between the Persian/Arabian Gulf – Sea of Oman and the Red Sea – Gulf of Aden was dated to ~2 Mya (95% HPD 3.52–1.38 Mya). During the Pleistocene, global sea levels fell up to 120 m below current levels (Rohling *et al.* 1998), and these historical sea level fluctuations are predicted to have shaped endemism characteristic of the Red Sea (DiBattista *et al.* 2017). The historical patterns of water movements and isolation of the Red Sea are presumed to represent the genetic structure of the Red Sea to a greater degree than contemporary environmental patterns (DiBattista *et al.* 2020). The impact of historical sea level changes in the Red Sea and Arabian Sea contributed to the divergence of butterflyfish lineages dated to between 4 and 1 Mya (DiBattista *et al.* 2018). Marine communities within the Persian/Arabian Gulf consist entirely of species that colonized the region from the Indian Ocean between 6000 and 9000 years ago, near the end of the last Glacial Period (Riegl and Purkis 2012, Smith *et al.* 2022). Immediately prior to this sea water infilling, the Persian/Arabian Gulf was an area of substantial terrestrial settlement and agricultural development (Teller *et al.* 2000). This relatively recent colonization of the Persian/Arabian Gulf poses the question of whether enough time has passed to potentially allow populations to differentiate genetically. For example, sharing of haplotypes between the Persian/Arabian Gulf and Sea of Oman with the Gulf of Aden and Red Sea may be indicative of ancestral movement between marine regions that have not had enough time to differentiate (DiBattista *et al.* 2015). Despite this, recent work has shown evidence for cryptic speciation within the conspecific *L. kasmira* in the eastern Gulf of Aden and Sea of Oman (Dibattista *et al.* 2017). Such genetic partitioning of *L. kasmira* is unlikely due to limited dispersal

ability (Gaither *et al.* 2010), potentially highlighting the importance that peripheral habitats may serve as regions of speciation, especially those with unique environmental conditions such as the Persian/Arabian Gulf and Red Sea (Bowen *et al.* 2013).

Genetic connectivity across the Arabian Peninsula through to the Red Sea has been noted in the sea urchin *Diadema setosum*, with a clade identified containing individuals from the northern Red Sea, through to Muscat and within the Persian/Arabian Gulf (Bronstein *et al.* 2017), while recent work by Ketchum *et al.* (2020) has shown considerable admixture between populations of *Echinometra* sp. EZ between the Persian/Arabian Gulf and Sea of Oman. Such results may be considered a reflection of the historical colonization of the Persian/Arabian Gulf, supported by contemporary larval dispersal. Moreover, recent cladistic work has shown that Persian/Arabian Gulf populations of the Pharoah cuttlefish, *Sephia pharaonic*, have genetically admixed with individuals from the southern Sea of Oman, Gulf of Aden, and Red Sea (Anderson *et al.* 2010). Our work supports such results, with little genetic differentiation between populations of *L. ehrenbergii* throughout the northern regions of the Arabian Peninsula (Persian/Arabian Gulf and Sea of Oman) or throughout the southern regions (Red Sea and Gulf of Aden). However, we found strong evidence of genetic differentiation between northeastern and southwestern sections of the Arabian Peninsula, with the Persian/Arabian Gulf and Sea of Oman populations highly differentiated from Gulf of Aden and Red Sea populations. Such low levels of haplotype sharing across the region may thus reflect historical colonization or contemporary ecological barriers to exchange.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Marylka H. Griffiths (conceptualisation, resources, formal analysis, investigation, methodology, writing—original draft, writing—review & editing), Christopher M. Wade (conceptualisation, supervision, project administration, writing—original draft, writing—review & editing), Daniele D'Agostino (conceptualisation, resources, writing—review & editing), Michael L. Berumen (resources, writing—review & editing), John A. Burt (writing—review & editing), Joseph D. Di'Battista (resources, writing—review & editing) and David A. Feary (conceptualisation, supervision, project administration, writing—original draft, writing—review & editing).

DATA AVAILABILITY

COI and CR sequences generated in this study are available in GenBank under accession numbers OR643719–OR643815 and OR596223–OR596318.

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