Coral Reefs - Report

Comparative phylogeography of reef fishes from the Gulf of Aden to the Arabian Sea reveals two cryptic lineages

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Abstract

The Arabian Sea is a heterogeneous region with high coral cover and warm stable conditions at the western end (Djibouti), in contrast to sparse coral cover, cooler temperatures, and upwelling at the eastern end (southern Oman). We tested for barriers to dispersal across this region (including the Gulf of Aden and Gulf of Oman), using mitochondrial DNA (mtDNA) surveys of 11 reef fishes. Study species included seven taxa from six families with broad distributions across the Indo-Pacific and four species restricted to the Arabian Sea (and adjacent areas). Nine out of 11 species showed no significant genetic partitions, indicating connectivity between contrasting environments spread across 2,000 km. One butterflyfish (*Chaetodon melannotus*) and a snapper (*Lutjanus kasmira*) showed phylogenetic divergences of d = 0.008 and 0.048, respectively, possibly indicating cryptic species within these broadly distributed taxa. These genetic partitions at the western periphery of the Indo-Pacific reflect similar partitions recently discovered at the eastern periphery of the Indo-Pacific (the Hawaiian and the Marquesan Archipelagos), indicating that these disjunctive habitats at the ends of the range may serve as evolutionary incubators for coral reef organisms.

Introduction

Phylogeographic analyses provide a unique means to detect historical and ecological processes that may not be apparent from contemporary species distributions (Palumbi 1997; Avise 2000). Such studies can reveal a diversity of outcomes, even among closely related species with similar life histories and geographic ranges (Bird et al. 2007; Gaither et al. 2010; Barber et al. 2011; Carpenter et al. 2011; DiBattista et al. 2012; Fouquet et al. 2012). Conversely, diverse taxa can also show concordant genetic patterns across broad spatial scales (Toonen et al. 2011; Selkoe et al. 2014). Multi-taxon studies across regions characterised by spatially and historically variable environmental conditions (i.e. comparative phylogeography) often generate a better understanding of how historical processes, environmental gradients, and ecological traits affect population structure and genetic diversity.

Comparative phylogeography has been used in many terrestrial and freshwater environments for delimiting regional phylogeographic patterns (Avise 1992; Hewitt 2000; Soltis et al. 2006; Waters et al. 2007; Bowen et al. 2016). However, resource and logistical limitations have restricted multi-taxon studies to only a few coral reef habitats. The Hawaiian Archipelago is a nearly linear habitat array extending 2,500 km with no obvious physical barriers or strong oceanographic discontinuities that might lead to hierarchical genetic structuring. Here, isolation by distance (IBD) was predicted to explain population structure, but multi-species studies across 35 taxa found diverse patterns of genetic structuring including panmixia, chaotic genetic heterogeneity, regional structuring, as well as IBD (Selkoe et al. 2014). Reef taxa in the Coral Triangle (centred on Indonesia, the Philippines, and New Guinea) show a similar lack of congruence in patterns of genetic structure, which may in part be driven by the complex geological history of the region (Barber et al. 2011; Carpenter et al. 2011). These studies show that, like terrestrial and freshwater systems, geological history and species-specific traits may play a role in determining patterns of population structure and genetic diversity in the coral reef environment, although this hypothesis has not been formally tested.

A major difference between marine and terrestrial or freshwater species is that marine species generally have much larger geographic ranges, which often span vast areas devoid of suitable habitat. Most reef-associated species also have a dispersive pelagic larval stage that can potentially connect populations across these uninhabitable areas. Contrary to expectations, the duration of the pelagic larval phase seems to be a poor predictor of population structure or range sizes (Weersing and Toonen 2009; Selkoe and Toonen 2011; Luiz et al. 2013; Riginos et al. 2011, 2014; Gaither et al. 2016). Instead, latitudinal range (as a proxy for temperature tolerance), adult size (Luiz et al. 2012), species abundance (Strona et al. 2012), as well as behavioural factors (e.g. nocturnal activity and a tendency to school) correlate with range size (Luiz et al. 2012, 2013). The importance of these factors may also vary depending on the size of the geographic range. A recent study of coral reef fishes indicates that small range endemics are under a suite of selection pressures that differ from widely distributed taxa, indicating that adaptation to local environmental conditions may also restrict species ranges (Gaither et al. 2015). Consequently, endemics may be expected to show greater genetic structure than widespread species (Tenggardjaja et al. 2016), especially across regions that span strong environmental gradients or have a turbulent geological history.

Here we use a multi-taxon approach to investigate phylogeographic patterns in the distinct reef biota of the greater Arabian Sea, a vastly understudied region with diverse coral communities. The Arabian Sea is at the western margin of the Indo-Pacific and contains a contact zone between the distinct faunas of the Indo-Polynesian and Western Indian Ocean provinces (Briggs and Bowen 2012; DiBattista et al. 2015). The Western Indian Ocean province is bordered in the north by endemic hotspots in the Red Sea and the Arabian Gulf (DiBattista et al. 2016a), and represents one of the most geologically and oceanographically volatile regions of the world's tropical oceans (Cowman and Bellwood 2013; DiBattista et al. 2016a, 2016b).

Currently, the dominant environmental feature of the Arabian Sea region is the Indian Ocean monsoon system. The upwelling induced by the southwest monsoon brings changes in temperature and productivity, especially on the southern coast of Oman (Fein and Stephens 1987), and reversals of monsoon-driven currents prompt strong seasonal variation in temperature and salinity in the Gulf of Aden (Sofianos et al. 2002; Smeed 2004). Subsequently, dramatic changes in reef habitats occur over distances of less than 2,000 km, which are well within the dispersal capacity of most reef fishes (Lessios and Robertson 2006; Keith et al. 2011, 2015). At the western extreme in the Gulf of Aden, the coastal waters of Djibouti have a high and relatively stable temperature regime with notable coral cover (Wilkinson 2008), and at the eastern extreme, the coastline of Oman supports rocky reefs with sparse coral cover and seasonal upwelling driving changes in productivity (Currie et al. 1973; Savidge et al. 1990; Sheppard et al. 1992; Barber et al. 2001; McIlwain et al. 2011). Due to the unique geomorphology of the coastline and seabed (e.g. Hanish Sill in the Strait of Bab al Mandab and Strait of Hormuz constricting the shallow Arabian Gulf), historic changes in sea level have caused significant alterations in habitat availability, oceanographic currents, and environmental conditions (references from DiBattista et al. 2016a, 2016b). These fluctuations have had profound effects on the evolution of marine organisms across the region (DiBattista et al. 2016a, 2016b). Specifically, these forces have generated population genetic structure in some, but not all, species across the boundary of the Red Sea into the Gulf of Aden, indicating that historical conditions may have influenced each species differently (DiBattista et al. 2013; Fernandez-Silva et al. 2015; Ahti et al. 2016; Coleman et al. 2016; Waldrop et al. 2016).

Here we employ a multi-taxon approach to determine if there are concordant patterns of genetic structure across this environmentally heterogeneous region. Our sampling design crosses two previously described barriers to dispersal: the upwelling region off Oman (see Priest et al. 2016), and the Strait of Bab al Mandab, which separates the Red Sea from the adjacent Gulf of Aden (DiBattista et al. 2016a, 2016b). We focus on 11 reef fishes from six families, with four range-restricted and seven widespread taxa, and test the hypothesis that endemic species are more likely to exhibit genetic structure than widespread species in a region where environmental conditions vary strongly across space and time..

Materials and methods

Sample collections

We collected tissue samples (fin clip or gill filaments) from 11 reef fish species at sites in the greater Arabian Sea region while scuba diving or snorkelling between 2012 and 2015 (Fig. 1, Table 1). Geographic coordinates and sample sizes are provided in Table 2. Cases of low (or nil) samples for a species from a particular site reflect rarity or complete absence in those locations, presumably owing to the heterogeneous nature of habitat in this region. Tissues were preserved in a saturated salt-DMSO solution or 96% ethanol, and subsequently stored at -20 ˚C. Select fish specimens were vouchered at the California Academy of Sciences (CAS; ESM Table S1).

Mitochondrial DNA sequencing

Total genomic DNA was extracted using the "HotSHOT" protocol of Meeker et al. (2007). Fragments of the mitochondrial cytochrome *c* oxidase subunit I gene (*COI*) were amplified using the primers FishF2 and FishR2 (Ward et al. 2005). Polymerase chain reaction (PCR) mixes contained 7.5 μl of BioMix Red (Bioline Ltd., London, UK), 0.26 μM of each primer and 5 to 50 ng template DNA in 15 μl total volume. PCR conditions included an initial denaturing step at 95 ˚C for 3 min, 35 cycles of amplification (30 s of denaturing at 94 ˚C, 60 s of annealing at 50 ˚C, and 60 s of extension at 72 ˚C), with a final extension at 72 ˚C for 10 min. PCR products were visualised on 2% agarose gels and purified by incubating with exonuclease I and FastAP™ Thermosensitive Alkaline Phosphatase (ExoFAP; USB, Cleveland, OH, USA) at 37 °C for 60 min, followed by 85 °C for 15 min. DNA was sequenced in the forward direction (and reverse direction for questionable haplotypes, $N = 5$) with fluorescently labelled dye terminators following manufacturer's protocols (BigDye; Applied Biosystems Inc., Foster City, CA, USA) using an ABI 3130XL Genetic Analyzer (Applied Biosystems). The sequences were aligned, edited and trimmed to a uniform length using GENEIOUS PRO 5.6.7 (Drummond et al. 2009). Individual mtDNA sequences are deposited in GenBank (accession numbers: XX-XX); mtDNA sequences for *Chaetodon melapterus* were available from a related study in the region (DiBattista et al. 2015).

ARLEQUIN 3.5.1.2 (Excoffier et al. 2005) was used to calculate haplotype (*h*) and nucleotide diversity (π), as well as to test for population structure. jModelTest 1.0.1 (Posada 2008) was used to select the best nucleotide substitution model using the Akaike information criterion (*AIC*). Genetic differentiation among sampling sites was first estimated with analysis of molecular variance (AMOVA) based on pairwise comparisons of sample groups; deviations from null distributions were tested with non-parametric permutation procedures (N = 99,999). Pairwise Φ_{ST} statistics were also calculated in ARLEQUIN, significance tested by permutation (N = 99,999) and P-values adjusted according to the modified false discovery rate (FDR) method (Narum 2006). For Φ_{ST} calculations, samples were pooled as follows given their close proximity (< 65 km), lack of genetic differentiation (data not shown) and low individual sample size: 1) Bay de Ghoubett, Moucha/Maskali, and Obock in Djibouti, 2) Mirbat and Salalah in Oman and 3) Barr Al Hickman and Masirah Island in Oman.

Evolutionary relationships among haplotypes were evaluated using median joining spanning networks (Bandelt et al. 1999) in PopART 1.7 (http://popart.otago.ac.nz). In two cases (*Chaetodon melannotus* and *Lutjanus kasmira*; see Fig. 2), sequences from outside the Arabian Sea (see DiBattista et al. 2013) were included to highlight the presence of cryptic species within this region, which was not the case for other surveyed species. Deviations from neutrality were assessed with Fu's F_S (Fu 1997) for each species using ARLEQUIN; significance was tested with 99,999 permutations.

Results

COI sequences from 11 species of reef fish sampled across the Gulf of Aden to Arabian Sea included 2 to 42 haplotypes. Haplotype (*h*) and nucleotide (π) diversity ranged from 0.037 to 0.879 and 0.00006 to 0.02933 (Table 1), respectively, with significantly higher nucleotide diversity values in widespread versus range-restricted fishes (two sample t-test, t = 2.09, df = 40, P = 0.043) but no discernable geographical trends across the Arabian Sea (One-way ANOVA, F = 0.75, df = 6, P = 0.61; see Fig. 3). Higher nucleotide diversity values in widespread versus range-restricted fishes remained significant after excluding *L. kasmira* (two sample t-test, t = 2.08, df = 38, P = 0.044), an apparent outlier in the data set. This disparity in genetic diversity also does not appear to be driven by a sampling bias towards widespread versus range-restricted fish given a lower average sample size in the former (ESM Fig. S1). With two exceptions (*C. melannotus* and *L. kasmira*), the most common haplotype within a species was shared across sampling locations (Fig. 4). Analyses of molecular variance revealed significant population structure only for these two widespread species, *C. melannotus* (Φ_{ST} = 0.813, P < 0.001) and *L. kasmira* (Φ_{ST} = 0.838, P < 0.001), differentiated at Oman to Socotra and Djibouti to Somalia, respectively (also see ESM Table S2). These partitions are matched by divergences seen in the median joining spanning networks that include outgroup sequences (i.e. central Red Sea, Seychelles, and Maldives; see Fig. 2), invoking the possibility of cryptic species. The Red Sea to Djibouti lineage of *C. melannotus* is distinguished from a widespread Indian Ocean lineage (Socotra to Maldives) by five fixed substitutions (d = 0.008). The divergence is much larger for *L. kasmira*, 22 fixed substitutions (d = 0.048), distinguishing a Red Sea/Djibouti/Somalia to Seychelles lineage and a Socotra to Oman lineage, with both lineages observed in Djibouti.

Despite the strong genetic differences *within* both *C. melannotus* and *L. kasmira*, no morphological or meristic differences were observed in preliminary examinations by L.A.R (also see ESM Table S1). Tests for *COI* neutrality revealed negative and significant Fu's F_S values in 7 of the 11 species (Fu's Fs = -27.39 to 4.29; Table 1).

Discussion

The study region, from the Gulf of Aden to the north-eastern coast of Oman, is characterised by environmental gradients and defined by historical barriers to gene flow (for review see DiBattista et al. 2016a, 2016b). To the west, the Strait of Bab al Mandab separates the endemism hotspot of the Red Sea from the adjacent Gulf of Aden. To the east, the coastline of Oman supports rocky reefs with sparse coral cover and is characterised by monsoonal upwelling that drives seasonal changes in productivity (McIlwain et al. 2011; DiBattista et al. 2016b). Mean sea temperatures on the Omani coast are significantly lower than the adjacent Gulf of Aden during the monsoon. The Yemeni island of Socotra, although influenced by the monsoon on its southern coast, supports carbonate reefs with notable live coral cover and a more stable annual sea temperature pattern on its northern coast (Kemp 1998, 2000). These environmental and geological factors are likely reflected in the genetic signatures of fish that inhabit these coral reefs.

Our mtDNA datasets reveal cryptic evolutionary divergences within two widespread reef fishes. In the butterflyfish *C. melannotus*, the mtDNA partition distinguished samples from the Red Sea and Djibouti by 0.8% at the *COI* barcoding gene compared to the widespread Indian Ocean lineage. In the snapper *L. kasmira*, a highly divergent lineage is apparent in the eastern Gulf of Aden and Oman (4.8% divergence from the widespread lineage). This lineage was not detected in a previous range-wide survey of *L. kasmira* (Gaither et al. 2010), in which sampling in the Western Indian Ocean was limited to the Seychelles and South Africa. The Red Sea/Djibouti/Somalia lineage detected here is the same as the widespread lineage reported in Gaither et al. (2010). In the same study, Gaither and colleagues reported population genetic homogeneity across 12,000 km of the Pacific and Indian Oceans, therefore the genetic partition observed in the Arabian Sea is not due to limited dispersal ability. Interestingly, Gaither et al. (2010) described a cryptic evolutionary lineage on the eastern extreme of the range in the Marquesas Islands. This symmetry of divergent lineages at the eastern (Marquesas) and western (Socotra/Oman) ends of the range, and vast connectivity in between, adds to the accumulating evidence that peripheral habitats, especially those with unique environmental conditions, can serve as evolutionary incubators (Budd and Pandolfi 2010; Bowen et al. 2013; Hodge et al. 2014; Gaither et al. 2015).

The isolation of two lineages in the Arabian Sea is not surprising given the region's tumultuous paleo-climactic history and current heterogeneity in environmental conditions (DiBattista et al. 2016a, 2016b). Both Randall (1998) and Allen (2008) have noted that endemic hotspots for tropical marine organisms are located in peripheral areas of the Indo-Pacific. The Arabian Sea is bordered by two such hotspots (Red Sea and Arabian Gulf), which contain many species that have diverged from widespread sister taxa (Cowman and Bellwood 2011, 2013; Hodge and Bellwood 2016). This peripheral endemism has likely been augmented by historical sea level fluctuations and unique environmental conditions that may have isolated populations of widespread species (DiBattista et al. 2016a, 2016b), including *C. melannotus* and *L. kasmira*. The divergence of these cryptic lineages is estimated at 0.4 Ma and 2.4 Ma, respectively, which date to the Pleistocene Epoch and thus the period of modern glacial cycles with frequent sea level fluctuations. In addition to historical isolation, the Arabian Sea is characterised by heterogeneous environmental conditions, also likely to have been a chronic condition during most of the Pleistocene (DiBattista et al. 2015). Thus, the genetic structure of *C. melannotus* and *L. kasmira* across the Arabian Sea may be explained by a combination of isolation and local adaptation, a hypothesis which warrants further investigation.

Congruence across species is seldom the case in comparative phylogeography studies of reef organisms (Lessios and Robertson 2006; Toonen et al. 2011; Selkoe et al. 2014). In the Coral Triangle, population genetic breaks and phylogenetic partitions appear in a variety of regions, with little discernible concordance (Barber et al. 2011; Carpenter et al. 2011; Sorenson et al. 2014). Similar discordance was observed in the Hawaiian Islands, and analyses of various traits revealed that dispersal ability, taxonomy (fish versus invertebrates), and habitat specificity were significant predictor variables, although almost 90% of the variance remains unexplained (Selkoe et al. 2014). Closer to the Arabian Sea, DiBattista et al. (2013) showed genetic structure across the Strait of Bab al Mandab for some but not all species of reef fishes. For those species that did show structure, the depth of divergences showed no discernable concordance with each other or with glacial climate cycles. Although multi-taxon studies and comparative phylogeographic studies of reef organisms are few, some generalisations are emerging (Bowen et al. 2016). Those generalisations reinforced by this study include: 1) the geographic factors that define population structure in terrestrial and freshwater systems may not be as important in coral reef ecosystems, 2) habitats at the periphery of the Indo-Pacific have higher endemism than previously expected, and 3) peripheral reef habitats like those contained in the Arabian Sea may host cryptic evolutionary lineages, and thus genetic novelty, for even some of the most widely distributed species.

The most interesting finding of this study is that only two of the 11 species (*C. melannotus* and *L. kasmira*) had significant genetic structure and micro-evolutionary partitions across the Arabian Sea. Determining why this is the case will help elucidate the factors generating novel biodiversity in marine organisms. The two species that had genetic structure are widely distributed across the Indo-Pacific; however, five of the other nine species surveyed are also widespread and show no structure. A comparison of various biological and ecological traits thought to be associated with dispersal and colonisation success (Brown et al. 1996; Gaston 2003; Luiz et al. 2012, 2013) such as geographic range size, body size, spawning mode, pelagic larval duration (PLD), diet, dietary specialisation, depth range, habitat use, schooling behaviour, and nocturnal activity did not reveal any obvious differences between species that did or did not display genetic structure (Table 3). Although *C. melannotus* is somewhat unique because its diet includes soft coral (Cole and Pratchett 2013), other specialist butterflyfishes (e.g. *C. melapterus* and *C. trifascialis*) did not show genetic structure. Furthermore, the only other species showing genetic structure (*L. kasmira*) is a generalist carnivore, like many other coral reef mesopredators (Hiatt and Strasburg 1960, Froese and Pauly 2016), including *C. argus* from this study, which itself did not show genetic structure. Contrasting patterns of genetic structure have also been reported in other closely-related, ecologically-similar, and widely-distributed reef fishes (e.g. Gaither et al. 2010) for reasons that remain unresolved.

Among the two cryptic evolutionary lineages revealed here, one lies primarily inside the Red Sea to the western Gulf of Aden and the other is distributed from the eastern Gulf of Aden to

Oman. Recent genetic surveys have found several more of these biodiversity gems hidden in Red Sea populations of widely-distributed species (DiBattista et al. 2013; Fernandez-Silva et al. 2015, 2016; Coleman et al. 2016; Priest et al. 2016). These findings at the western periphery of the Indo-Pacific are remarkably concordant with surveys at the eastern periphery, which revealed cryptic evolutionary lineages at the Marquesas and Hawai'i (Gaither et al. 2010, 2011, 2015; DiBattista et al. 2011; Szabo et al. 2014; Bowen 2016). Together these data sets invoke a general finding that reef habitats in peripheral seas are important evolutionary incubators. As peripheral habitats lie at the geographic limits of a taxon's distribution, exposure to divergent environmental and habitat conditions are expected. Under such circumstances, strong and novel selection pressures are likely to contribute to genetic diversification (Gaither et al. 2011; Suzuki et al. 2016); the critical emerging issue is why this may involve only a proportion of the taxa present. The development of phylogeographic hypotheses based on taxon-specific traits (as per Papadopoulou and Knowles 2016) are therefore required to illuminate the diversification of evolutionary lineages in peripheral environments.

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Table 1 Number of sample sites, fragment length and nucleotide substitution model (see Posada, 2008) for mitochondrial DNA cytochrome *c* oxidase subunit I (*COI*), Fu's F_S statistic, molecular diversity indices and differentiation metrics (i.e. AMOVA) for range-restricted and widespread reef fish sampled in the Arabian Sea region. All negative Φ_{ST} values were adjusted to zero. Average values are $\pm$ one standard deviation.

species	sites	fragment size (bp)	model	N^b	H_N	Fu's F_S	haplotype diversity ($h \pm SD$)	nucleotide diversity ($\pi \pm SD$)	Φ_{ST} (p-value)	evidence for barriers?
range-restricted										
Chaetodon dialeucos (Oman butterflyfish)	5	647	HKY	50	6	-2.81	0.505 ± 0.064	0.00089 ± 0.00081	0 (0.468)	No
Chaetondon melapterus (Arabian butterflyfish)	10	590	HKY	198	17	**-6.95**[a]	0.723 ± 0.020	0.00261 ± 0.00174	0.008 (0.244)	No
Chaetodon nigropunctatus (black-spotted butterflyfish)	2	625	K80	54	2	-1.70	0.037 ± 0.035	0.00006 ± 0.00018	0.018 (0.404)	No
Chaetodon pictus (horseshoe butterflyfish)	10	582	TIM2	178	19	**-24.71**	0.404 ± 0.047	0.00089 ± 0.00083	0 (0.951)	No
widespread										
Abudefduf vaigiensis (Indo-Pacific sergeant)	9	576	K80	193	45	**-27.39**	0.879 ± 0.013	0.00341 ± 0.00215	0.013 (0.05)	No
Cephalopholis argus (peacock hind)	6	528	HKY	63	7	**-8.22**	0.211 ± 0.069	0.00042 ± 0.00056	0 (0.769)	No
Chaetodon melannotus (blackback butterflyfish)	4	619	K80	29	3	4.292	0.507 ± 0.079	0.00359 ± 0.00227	0.813 (< 0.001)	Yes (isolation at Socotra)
Chaetodon trifascialis (chevron butterflyfish)	8	577	TrN	117	12	**-5.74**	0.722 ± 0.028	0.00181 ± 0.00134	0.007 (0.333)	No

Ctenochaetus striatus (striated surgeonfish)	5	519	TrN	97	14	**-9.76**	0.624 ± 0.054	0.00183 ± 0.00140	0.011 (0.204)	No
Halichoeres hortulanus (checkerboard wrasse)	6	551	HKY	95	19	**-16.06**	0.611 ± 0.056	0.00211 ± 0.00152	0 (0.435)	No
Lutjanus kasmira (bluestripe snapper)	7	483	GTR	145	32	1.15	0.718 ± 0.034	0.02933 ± 0.01464	0.838 (< 0.001)	Yes (isolation at Djibouti & Somalia)

[a]Numbers in bold are significant, $P < 0.02$ (Fu, 1997).

[b]Abbreviations are as follows: N, sample size; H_N, number of haplotypes.

Table 2 Sample size and location for reef fish sampled in the Arabian Sea.

sampling site	location	*A. vaigiensis*	*Ce. argus*	*Ch. dialeucos*	*Ch. melannotus*	*Ch. melapterus*	*Ch. nigropunctatus*	*Ch. pictus*	*Ch. trifascialis*	*Ct. striatus*	*H. hortulanus*	*L. kasmira*
Moucha/Maskali, Djibouti	N 11.759° E 43.217°	20	20	–	1	20	–	21	20	19	20	25
Obock, Djibouti	N 11.967° E 43.333°	21	21	–	15	29	–	28	20	19	21	15
Bay de Ghoubett, Djibouti	N 11.533° E 42.667°	23	1	–	3	20	–	19	23	20	20	24
Berbera, Somalia	N 10.400° E 44.783°	16	13	–	–	16	–	20	14	15	12	21
Socotra, Yemen	N 12.617° E 54.350°	23	–	–	10	25	–	23	21	–	20	38
Salalah, Oman	N 16.912° E 53.960°	20	–	–	–	–	–	6	–	–	–	–
Mirbat, Oman	N 16.959° E 54.757°	–	1	7	–	12	–	16	7	–	–	–
Al Hallaniyats, Oman	N 17.483° E 55.983°	23	8	14	–	13	–	18	4	24	2	–
Schwaymeeyah, Oman	N 17.895° E 55.710°	–	–	2	–	–	–	–	–	–	–	–
Barr Al Hickman, Oman	N 20.383° E 58.217°	–	–	6	–	3	–	–	–	–	–	–
Masirah Island, Oman	N 20.165° E 58.634°	25	–	21	–	26	22	22	8	–	–	2
Muscat, Oman	N 23.525° E 58.740°	21	–	–	–	35	32	5	–	–	–	20

Table 3 Biological and ecological traits associated with dispersal and colonisation abilities for the eleven study species. These include: geographic range size (extent of occurrence km^2), body size (total length or TL) (Froese and Pauly 2016), spawning mode (Froese and Pauly 2016), pelagic larval duration (PLD) (Brothers and Thresher 1985; Victor 1986; Leis 1989; Thresher et al. 1989; Soeparno et al. 2012; Trip et al. 2014; J.P. Hobbs unpub. data) diet and dietary specialisation (Hiatt and Strasburg 1960; Bellwood and Pratchett 2013; Cole and Pratchett 2013; Froese and Pauly 2016), depth range (Froese and Pauly 2016), habitat use (Froese and Pauly 2016), schooling behavior, and nocturnal activity (Allen et al. 1998; Kuiter 2002; Yabutu and Berumen 2013).

species	Range[a] size (x 10^6 km^2)	Body size (TL in cm)	Spawning mode	PLD (mean days)	Diet	Dietary specialisation	Depth range (m)	Habitat use	Schooling behaviour	Nocturnal activity
Chaetodon dialeucos (Oman butterflyfish)	0.13	18	Broadcast	n/a	Omnivore (benthic invertebrates)	Generalist	5-25	Rocky and coral reefs	Pairs	No
Chaetondon melapterus (Arabian butterflyfish)	0.28	13	Broadcast	33.8	Corallivore	Moderate specialist	1-16	Coral reefs	Pairs	No
Chaetodon nigropunctatus (black-spotted butterflyfish)	0.11	14	Broadcast	n/a	Omnivore (benthic including coral)	Generalist	1-18	Rocky and coral reefs	Pairs	No
Chaetodon pictus (horseshoe butterflyfish)	0.24	20	Broadcast	39	Omnivore (benthic)	Generalist	1-20	Rocky reefs	Pairs	No
Abudefduf vaigiensis (Indo-Pacific sergeant)	50.2	20	Benthic	21.7	Omnivore (plankton and benthic)	Generalist	1-15	Rocky and coral reefs	Schools	No
Cephalopholis argus (peacock hind)	49.89	60	Broadcast	22.8	Carnivore (fish and benthic invertebrates)	Generalist	1-40	Coral reefs	Harems	Yes
Chaetodon melannotus (blackback butterflyfish)	49.02	18	Broadcast	n/a	Omnivore (benthic and soft corals)	Moderate specialist	1-20	Rocky and coral reefs	Solitary	No
Chaetodon trifascialis (chevron butterflyfish)	51.86	18	Broadcast	35.9	Corallivore	Extreme specialist	1-30	Coral reefs	Solitary	No
Ctenochaetus striatus (striated surgeonfish)	52.50	26	Broadcast	47 to 69	Detritivore	Generalist	1-34	Rocky and coral reefs	Schools	No

Halichoeres hortulanus (checkerboard wrasse)	50.75	27	Broadcast	32.5	Omnivore (benthic invertebrates)	Generalist	1-30	Coral reefs	Harems	No
Lutjanus kasmira (bluestripe snapper)	50.23	40	Broadcast	23.5	Carnivore (fishes and invertebrates)	Generalist	1-265	Coral Reefs	Schools	Yes

[a]Range size estimates were obtained through measurement of the area (km^2) occupied by each species using IMAGE TOOL (as per Choat et al. 2012).

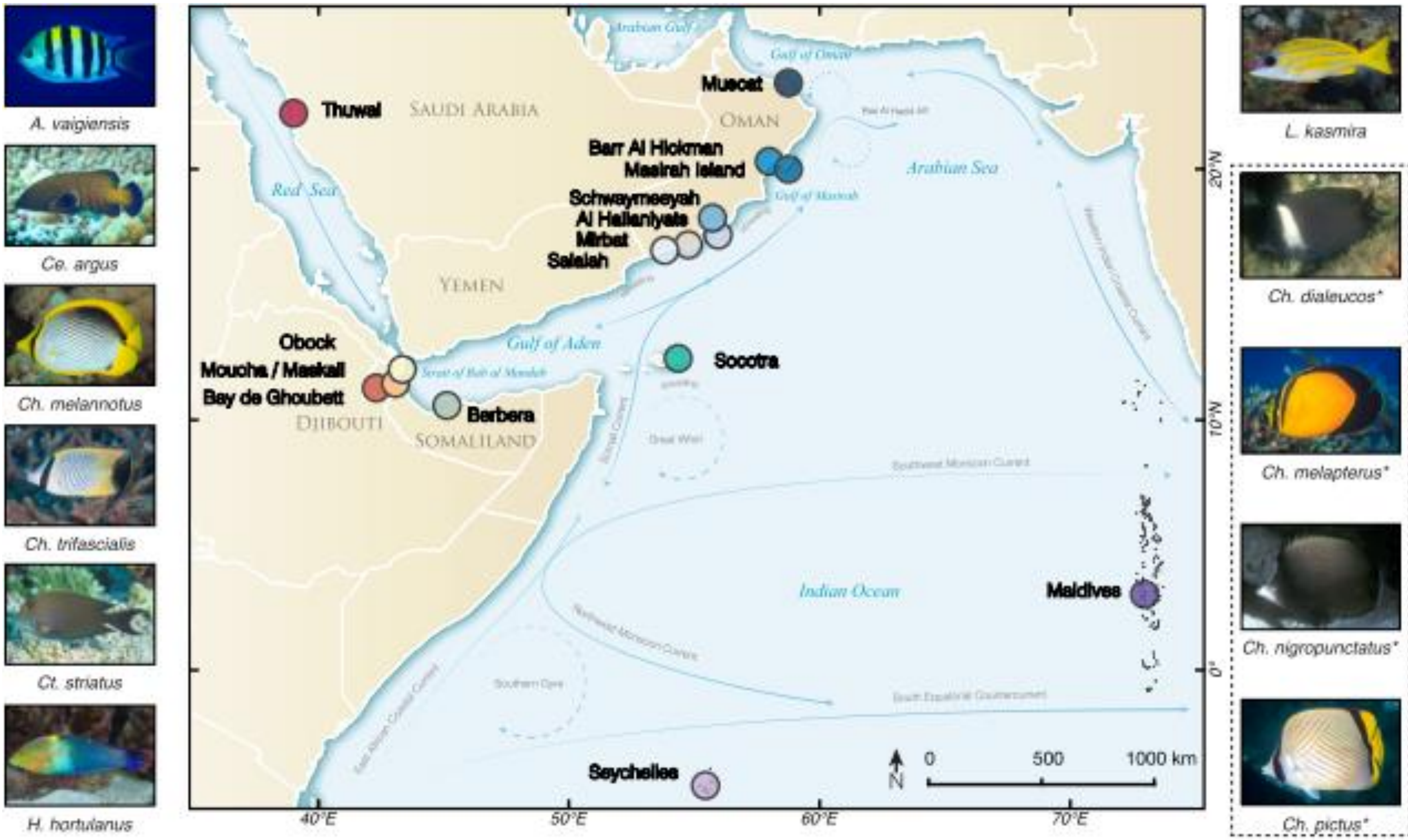
Figures

Fig. 1 Map indicating collection sites for all reef fish considered in this study, with range-restricted species denoted by asterisks. Colours used for collection location are identical to those in Fig. 2. Note the reversing circulation of the Somali Current (from northward to southward), the Southwest Monsoon Current (from westward to the eastward Northwest Monsoon Current), the Western Indian Coastal Current (from eastward to westward), and the current flowing into the Red Sea from the Gulf of Aden (versus out of the Red Sea and into the Gulf of Aden) during the northeast monsoon season (December to March). Site-specific samples sizes are provided in Table 2 (photo credit: T.H.S-T. and J.E. Randall). Samples from Thuwal, Maldives, and the Seychelles were included for only two species demonstrating cryptic lineages within Red Sea to Arabian Sea samples (*Chaetodon melannotus* and *Lutjanus kasmira*)

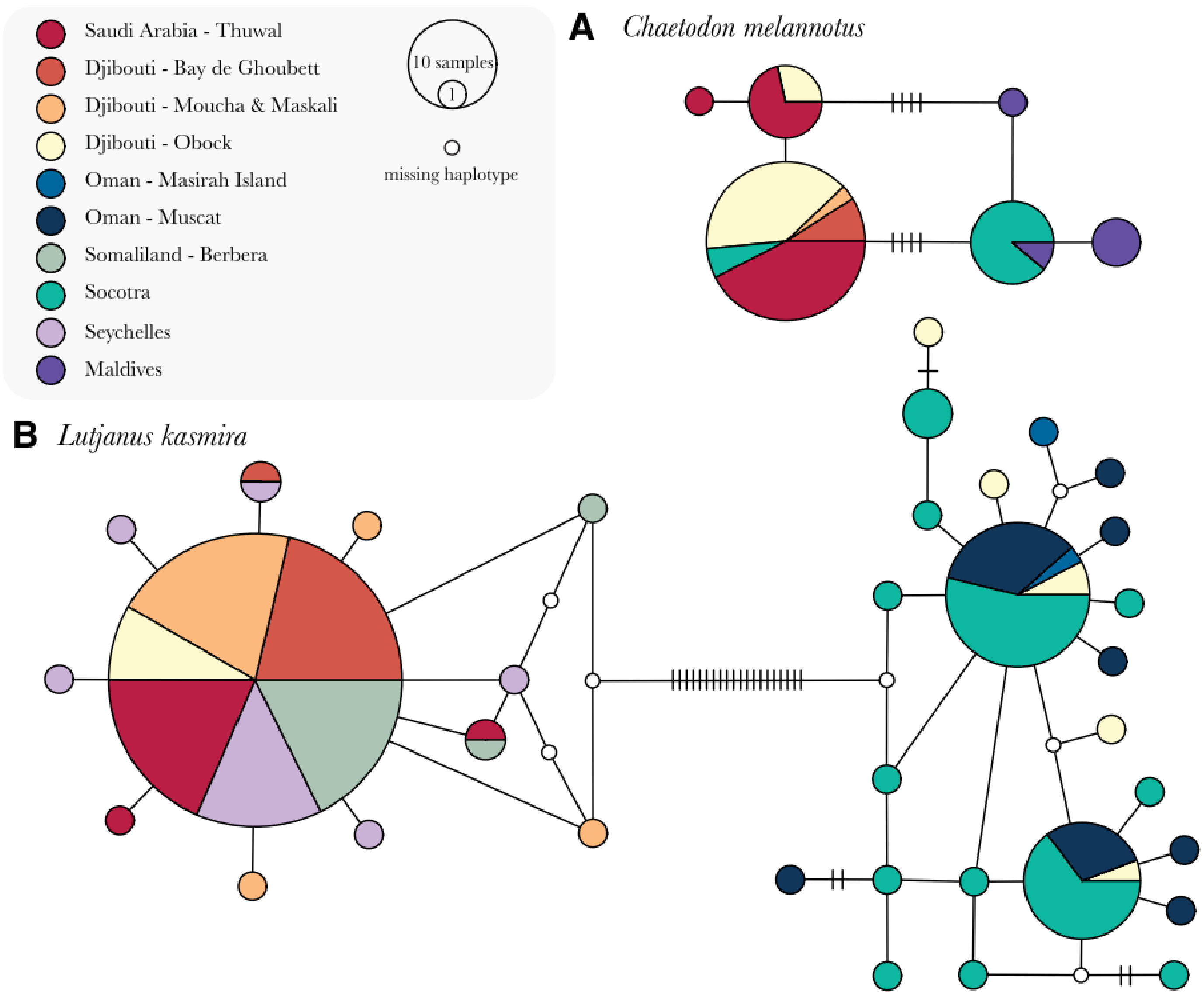
Fig. 2 Median-joining networks showing relationships among mitochondrial DNA cytochrome *c* oxidase subunit I (*COI*) haplotypes for reef fish sampled in the Arabian Sea where cryptic evolutionary lineages were identified. *COI* fragment length and site-specific samples sizes are provided in Table 1 and Table 2, respectively. Outgroup populations are: *Chaetodon melannotus*, Thuwal, Kingdom of Saudi Arabia, $N = 20$ and Maldives, $N = 5$; *Lutjanus kasmira*, Thuwal, Kingdom of Saudi Arabia, $N = 22$ and Seychelles, $N = 20$. Each circle represents a unique haplotype and its size is proportional to its total frequency (i.e. number of samples) as per the provided legend. Thin branches and black cross-bars represent a single nucleotide change, small open circles represent missing haplotypes and colours denote collection location as indicated by the embedded key

Fig. 3 Haplotype (a) and nucleotide diversity (b) for 11 species of reef fish sampled from sites in the Gulf of Aden (Djibouti) to sites in the Arabian Sea (Muscat, Oman). Species and sample sizes are denoted by circle colours and sizes, respectively, as outlined in the provided key.

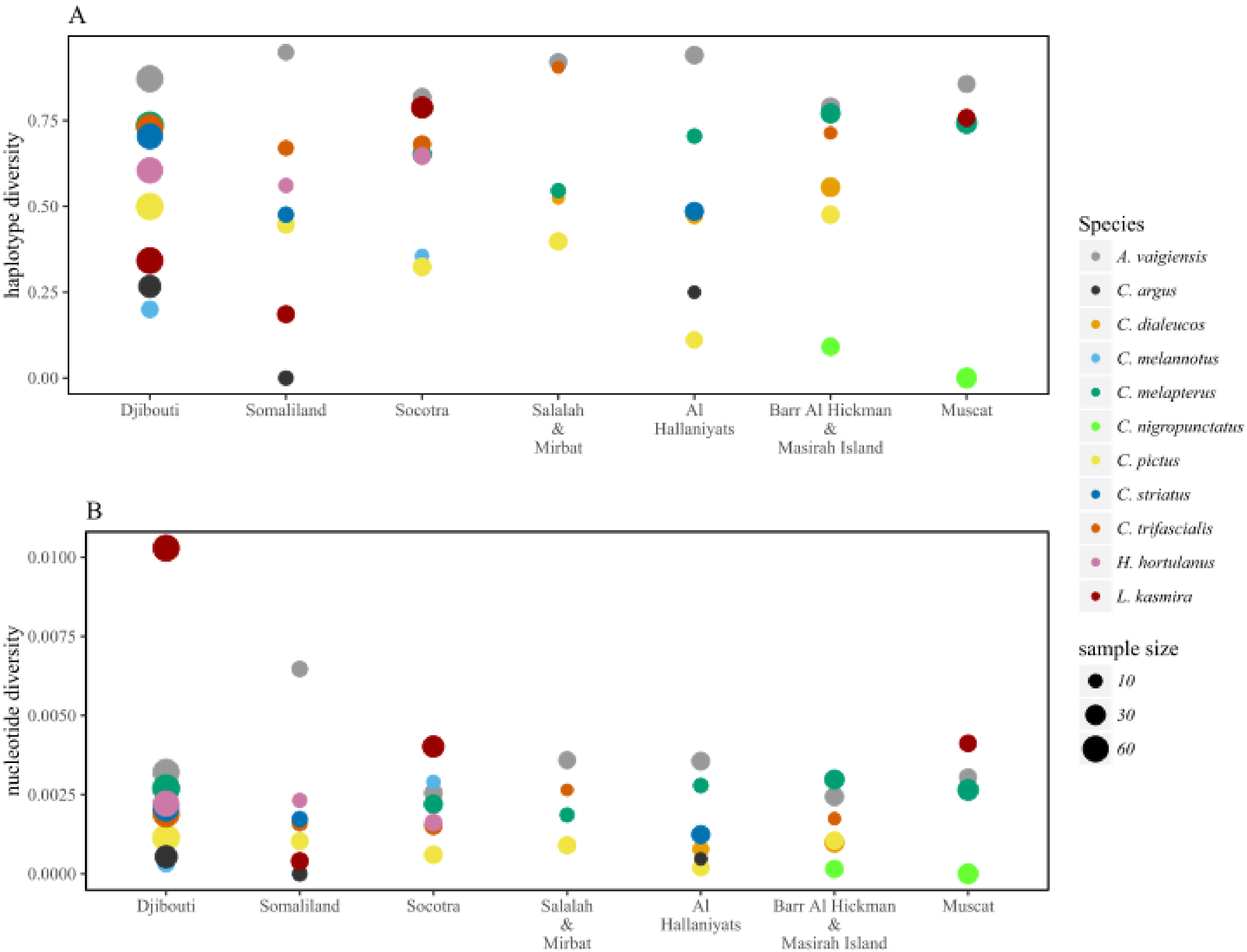
Fig. 4 Median-joining networks showing relationships among mitochondrial DNA cytochrome *c* oxidase subunit I (*COI*) haplotypes for all remaining widespread and range-restricted reef fish sampled in the Arabian Sea region, with range-restricted species denoted by asterisks. *COI* fragment length and site-specific samples sizes are provided in Table 1 and Table 2, respectively. Each circle represents a unique haplotype and its size is proportional to its total frequency as per the included legend. Thin branches and black cross-bars represent a single nucleotide change, small open circles represent missing haplotypes and colours denote collection location as indicated by the embedded key.

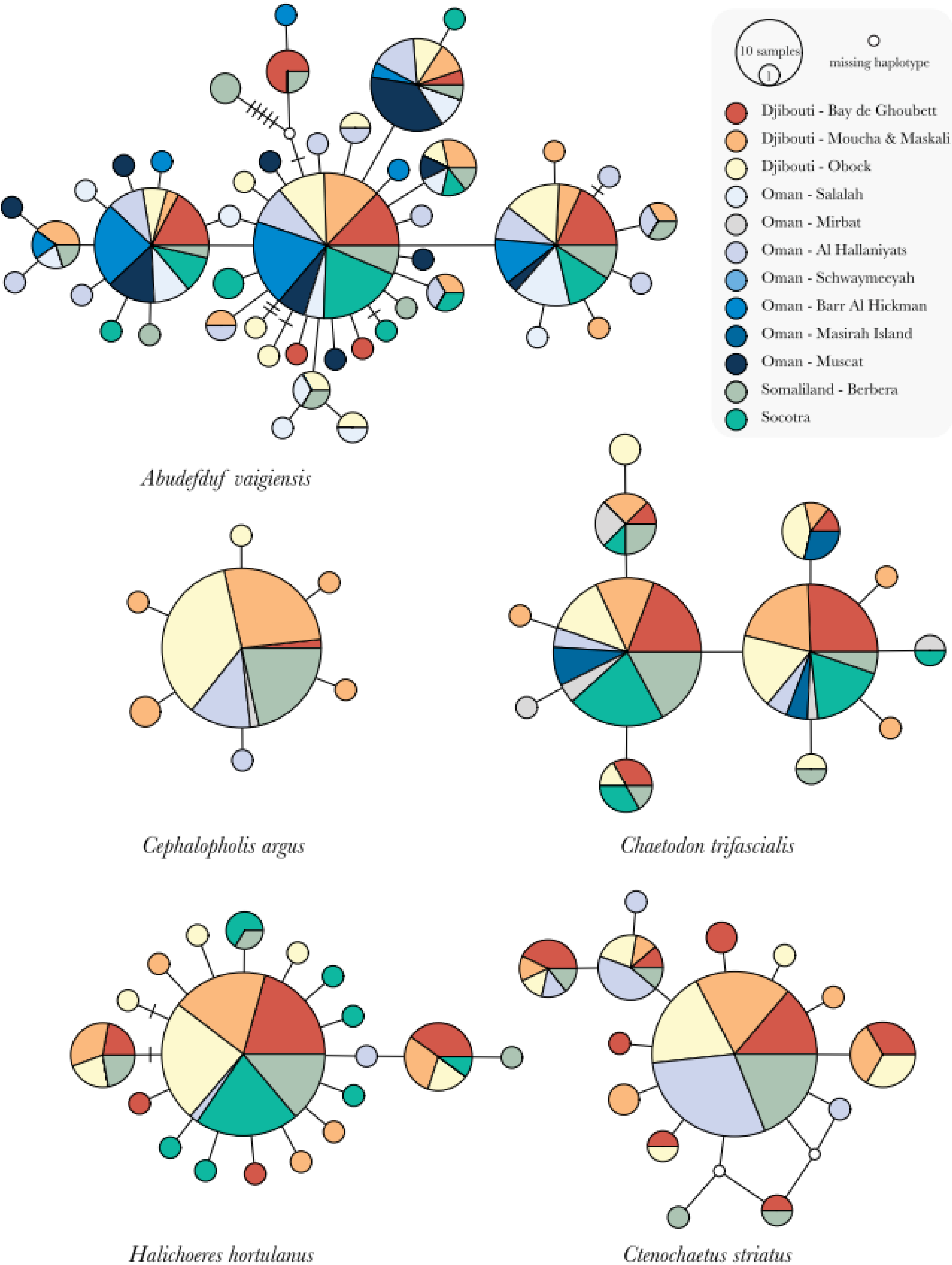


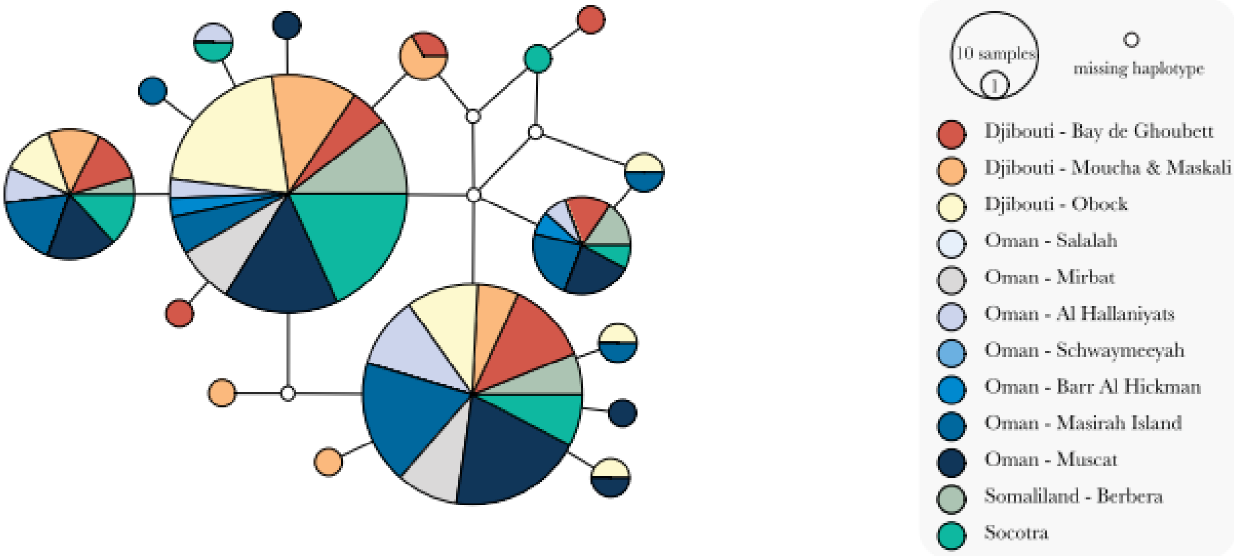
A. vaigiensis
Ce. argus
Ch. melannotus
Ch. trifascialis
Ct. striatus
H. hortulanus
Arabian Gulf
Gulf of Oman
Muscat
Thuwal
SAUDI ARABIA
OMAN
Barr Al Hickman
Masirah Island
Arabian Sea
Red Sea
Gulf of Masirah
Schwaymeeyah
Al Hallaniyats
Mirbat
Salalah
YEMEN
Obock
Moucha / Maskali
Bay de Ghoubett
Gulf of Aden
Socotra
Barbera
DJIBOUTI
SOMALILAND
Indian Ocean
Maldives
Seychelles
N
0
500
1000 km
40°E
50°E
60°E
70°E
20°N
10°N
0°
L. kasmira
Ch. dialeucos*
Ch. melapterus*
Ch. nigropunctatus*
Ch. pictus*


Saudi Arabia - Thuwal
Djibouti - Bay de Ghoubett
Djibouti - Moucha & Maskali
Djibouti - Obock
Oman - Masirah Island
Oman - Muscat
Somaliland - Berbera
Socotra
Seychelles
Maldives
10 samples
1
missing haplotype
A *Chaetodon melannotus*
B *Lutjanus kasmira*

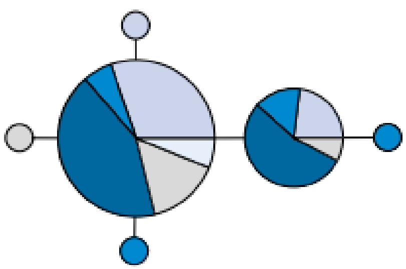
33


A
haplotype diversity
0.00
0.25
0.50
0.75
Djibouti
Somaliland
Socotra
Salalah & Mirbat
Al Hallaniyats
Barr Al Hickman & Masirah Island
Muscat
B
nucleotide diversity
0.0000
0.0025
0.0050
0.0075
0.0100
Djibouti
Somaliland
Socotra
Salalah & Mirbat
Al Hallaniyats
Barr Al Hickman & Masirah Island
Muscat
Species
A. vaigiensis
C. argus
C. dialeucos
C. melannotus
C. melapterus
C. nigropunctatus
C. pictus
C. striatus
C. trifascialis
H. hortulanus
L. kasmira
sample size
10
30
60

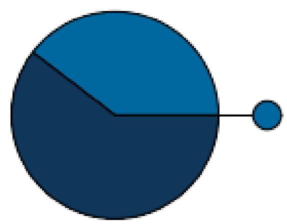

10 samples
1
missing haplotype
Djibouti - Bay de Ghoubett
Djibouti - Moucha & Maskali
Djibouti - Obock
Oman - Salalah
Oman - Mirbat
Oman - Al Hallaniyats
Oman - Schwaymeeyah
Oman - Barr Al Hickman
Oman - Masirah Island
Oman - Muscat
Somaliland - Berbera
Socotra
Abudefduf vaigiensis
Cephalopholis argus
Chaetodon trifascialis
Halichoeres hortulanus
Ctenochaetus striatus



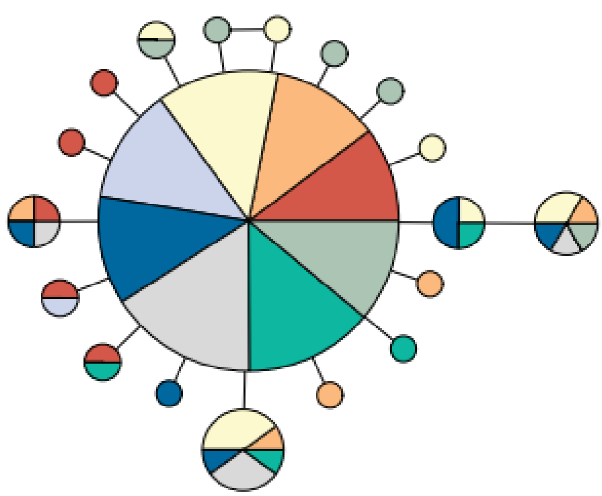
*Chaetodon melapterus**



*Chaetodon dialeucos**



*Chaetodon nigropunctatus**



*Chaetodon pictus**