Population persistence within an extreme environment: genetic connectivity of the coral reef fish *Lutjanus ehrenbergii* across the Arabian Peninsula

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Abstract

Resolving the pattern of genetic connectivity in the ocean is necessary for fishery management, conservation and in answering key questions in evolutionary ecology. A main theme in terms of connectivity in the ocean is how environmental and oceanographic factors shape population structure. Such questions weave an understanding of genetic and demographic patterns with the importance of environmental gradients and oceanographic processes.

This project is focused on the Arabian Gulf, which has the largest thermal SST range globally, whilst also showing extremes in salinity. This system is connected to the Gulf of Oman, via the Strait of Hormuz, which has comparatively more benign oceanic conditions which are expected for a typical tropical marine system. Researchers postulated that an environmental gradient across the Arabian Peninsula that may act as a potential barrier to survival and larval dispersal of fish communities across this region. I will show how populations of the coral reef associated fish, *Lutjanus ehrenbergii*, are shaped across the Arabian Peninsula, using genetic analysis of mitochondrial DNA to describe patterns of genetic similarity.

The pattern of environmental conditions presented that the Strait of Hormuz contains conditions that are an intermediate between the Arabian Gulf and the Gulf of Oman. Yet, considering the presence of this 'filter' or environmental gradient, this area did not act as a geographic break in population structure across the Arabian Peninsula. Overall no significant genetic differentiation occurred between populations grouped as; the Arabian Gulf, the Strait of Hormuz and the Gulf of Oman. Haplotypes, and defined clade groupings were found spread over the entire Arabian Peninsula which can be interpreted as a pattern of genetic connectivity. However, there were 3 clade groupings composed of few haplotypes which were found in restricted areas, which could signify a degree of restriction of clades. In the analysis between sampling locations, many populations showed no significant departure from 0. However, in the markers control region and COI significant moderate genetic differentiation was revealed in a small number of populations. This genetic differentiation did not fit with a spatial or environmental pattern. This could suggest a pattern of chaotic genetic patchiness in the region. The predominant lack of genetic subdivision can be interpreted as an overall pattern of connectivity in the region which could be due to the initial movement and colonisation of the Arabian Gulf from the Indian Ocean.

Larval dispersal projection gave a preliminary description of the movement of a generic fish larva across the Arabian Peninsula. The results showed a high level of self-recruitment, with

little connectivity. This pattern shows that passive particle movement via oceanographic forces leads to restricted movement of larvae and showed little connectivity between neighbouring regions. A contemporary pattern of restricted movement would be expected to lead to genetic isolation of populations. This provides a good starting point, which can be continued to model how stochastic movement occurs over a longer period of several years, and can be combined with genetic analysis in the future.

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1.1 General Introduction

Genetic diversity is the foundation on which selection and adaptation acts on; and the loss of genetic variation can reduce the capacity for adaptation (Frankham et al. 2004). Understanding the ways genetic diversity is subdivided amongst populations will be important in understanding evolutionary questions, whilst also being useful in the management of populations. In this respect, there are increased conservation efforts to protect genetic biodiversity, as lowered genetic diversity puts populations at risk of extinction (Hedrick, 2011) while also reducing resilience to environmental disturbances. Lastly discriminating genetically distinct populations can be used to define units of population stock and dictate successful management, which is particularly useful in managing fisheries stocks.

1.2 Population Connectivity

Population connectivity describes the level of exchange of individuals, through adult, juvenile and larval movements between populations, and can be broken down into demographic or genetic connectivity (Robert K Cowen & Sponaugle, 2009). Demographic connectivity focuses on the physical movement of individuals though migration and dispersal between populations (Lowe, 2010). In contrast, genetic connectivity is a term used to describe the degree of genetic similarity between populations, which is influenced by demographic connectivity (Mora & Sale, 2002). The distinction between genetic and demographic connectivity is that genetic connectivity is understood as 'movement that results in genetic exchange' (Hedrick, 2011). In addition, whilst measuring demographic connectivity provides insight into contemporary exchange of individuals (Stephen R. Palumbi, 2003; Sale et al., 2010), the degree of genetic connectivity between populations can be a representation of both contemporary and historical exchange (Benzie,1999).

Genetic connectivity requires relatively few successful migration events which lead to interbreeding to homogenise genetic variation between populations (Slatkin, 1985). In this respect, rare, long distance dispersal events may be missed by studying demographic connectivity, but can be a major driver of genetic connectivity. There is increasing evidence of demographic connectivity of populations, with migrants exchanging individuals between populations but little genetic connectivity occurring. Such lack of genetic connectivity between populations may result from an ecological or behavioural barrier that prevents breeding (Marshall *et al.* 2010). For example, despite a range of organisms showing high motility and

long distance dispersal between populations, to achieve genetic connectivity the exchange of genes between populations must be followed by successful mating (Nielsen & Slatkin, 2013).

Population genetics aims to describe the pattern of genetic diversity present in a population (Holsinger, 2009). A population is broadly defined as a group of conspecifics that can reproduce, which inhabit a geographic area (Hoelzel,1991) and may also be fragmented into smaller subpopulations that occur discontinuously across a geographic range (Hedrick, 2011). The earliest model, describing how variation in gene frequency within populations is linked to geographical location, was based on the island model by Sewall Wright (Wright,1943). In this model to explain the structure of genetic variation populations are fragmented by geographic isolation but are genetically connected by the movement of migrants between subpopulations (Wright, 1943). The assumption of this theory is that an equal number of migrants move between populations, leading to gene flow between populations and therefore homogenisation of genetic variation (Rousset, 2013). In this model, genetic diversity is seen as a product of genetic drift and selection. This model has been developed into the 'stepping stone' model, which differs to the preceding 'island' model as subpopulations are restricted to migrants moving only between neighbouring subpopulations (Kimura & Weiss, 1964). Within the stepping stone model, as the distance between populations increases so does genetic variation between populations (Kimura &Weiss, 1964). The stepping-stone model is the basis for the Isolation by Distance model, which describes how genetic structure can be a result of the reduction of gene flow as a product of geographic distance (Hardy & Vekemans 1999;Purcell *et al.* 2006). Within the Isolation by Distance model the exchange of genes between populations is dependent upon the distance between populations, or the dispersal of organisms (Hardy & Vekemans, 1999). Physical features of the landscape and geographic distance will restrict movement and breeding between subpopulations (Manel, 2003).

Several expectations in terms of expected genetic variation arise from the way subpopulations exchange migrants, and can lead to high, intermediate and low genetic similarity (Hellberg *et al* 2002). If gene flow is high between subpopulations then genetic variation will be homogenized between groups, leading to a single panmictic population (Nielsen, 2013). Gene flow can be reduced as geographic distance increases leading to increased genetic differentiation across increased geographic distances (Nielsen, 2013). Gene flow between sites may be restricted or prevented, causing subpopulations to become increasingly genetically distinct as a result of mutation, selection and genetic drift, resulting in high genetic divergence

between subpopulations (Hedrick, 2011). Therefore, measuring the levels of genetic variation between subpopulations at different geographic distances can provide an understanding of how genetic diversity is differentiated throughout a geographically distributed population.

Understanding the degree of genetic connectivity between populations can be vital for managing natural populations (Waples, 2006), especially in the conservation of populations and can substantially influence policy on biodiversity protection and management of marine protected areas (Palumbi, 2003). For example, to develop successful marine protected areas the spatial boundaries of the reserve need to be large enough to encapsulate reproducing populations, but small enough to allow populations adjacent or outside the protected area to be successfully seeded (Botsford *et al.* 2009; Planes *et al.* 2009). In addition, understanding the level of genetic isolation of populations may allow us to predict their ability to resist environment disturbances, and therefore determine their vulnerability to extinction (Sgro *et al.* 2011). For example areas of coral reef within the Great Barrier Reef have been found to be genetically isolated, which may make them more vulnerable to warming events and episodes of coral bleaching (Ayre & Hughes, 2004).

Commercial enterprises, such as fisheries, took on molecular approaches early to define stock units (Ward, 1994; Ayre & Hughes 2004). Fisheries management can utilise population genetics to characterise units of fishing stocks by their genetic structure (Carvalho & Hauser, 1995). Within fisheries, a stock can be characterised as genetically distinct populations, continuous populations or panmitic populations (Laikre, Palm, & Ryman, 2005). Overfishing threatens genetic diversity by greatly reducing population size (Mora, 2015). The population size that fisheries consider healthy or collapsed can be misleading, as overfishing can reduce genetic diversity and reduce the genetically effective population size. The New Zealand snapper, *Pagrus auratus*, showed reduced genetic diversity population size despite a population of ~3 million individuals (Hauser, Adcock, Smith, Ramiréz, & Carvalho, 2002). The significance of this work is that exploitation through fishing reduces genetic diversity which can be overlooked by that solely considering abundance.

1.3 The marine environment and patterns of connectivity

The ocean environment was considered to be an open system, with marine populations being predominantly connected across large distances, due to the medium of water allowing unrestricted movement of both adults and larvae (R. K. Cowen, 2000; Cowman & Bellwood,

2013). This posed an issue to evolutionary biologists, who suggested that evolutionary process requiring spatial isolation, such as allopatric speciation, would be reduced or non-existent (Rocha, Robertson, Roman, & Bowen, 2005). The effect of unrestricted movement on the genetic structure of marine populations would prevent complete population subdivision (Mora & Sale, 2002). The assertion that movement of adults and larvae were unhindered across the ocean lead to a view of 'open' marine populations with high genetic connectivity (Cowen, 2000). However, the ocean environment is heterogeneous, summarised by the statement that 'the ocean is not one mass, but can be thought of as being divided or stratified by temperature and salinity gradients' (Palumbi, 1994). Barriers to movement of adults and larvae are often invisible in the ocean, and may be temporary or weak (Briggs & Bowen, 2013). Therefore, it is difficult to determine marine barriers whilst terrestrial barriers, such as mountain ranges and bodies of water, are easier to determine.

The historical assumption of open marine populations was additionally supported by the high dispersive capacity of marine species larval stage (Cowen *et al.* 2000). Unrestricted larval dispersal would potentially allow movement over large distances between populations (Cowen *et al.* 2000). However larvae are not merely passive particles but can instead exhibit differing levels of self-recruitment, whereby larvae return to their natal reef (Jones *et al.* 1999; Jones *et al.* 2005). Control of potential recruitment to specific habitat is associated with differing levels of larval swimming behaviour and directed movement (Stobutzki & Bellwood, 1997), environmental sensing using sound (Tolimieri, Jeffs, & Montgomery, 2000), and olfactory cues (Atema, Kingsford, & Gerlach, 2002). Self-recruitment can be associated with exceptionally fine spatial scales, for example Jones et al (2005) showed that Panda clownfish (*Amphipirion polymnus*) larvae returned to a 2 hectare natal site, despite this site being surrounded by open oceanic water (G. P. Jones, Planes, & Thorrold, 2005). The presence of invisible barriers and self-recruitment suggested that marine populations would not be completely open, with the work of molecular analysis providing strong evidence that genetic structure could occur at small scales, and therefore barriers to movement and gene flow in the ocean are substantial enough to cause isolation of subpopulations (Mora & Sale, 2002).

1.4 Processes driving genetic structure in the ocean

The question of whether population structure would be present in the ocean has since shifted towards the question of how populations can be isolated in the ocean (Cowen, 2000). The mechanisms that have shaped the pattern of genetic variation are difficult to disentangle, but

attempts can be made to distinguish the processes that can impede or enhance gene flow. Landscape ecology can be utilised to characterise potential physical barriers that could prevent movement or dispersal and subsequently impede gene flow (Manel, Schwartz, Luikart, & Taberlet, 2003). However, landscape ecology has predominantly been focused on terrestrial environments in which physical barriers such as mountains and habitat discontinuities are more obvious than those in the ocean. In the ocean, physical barriers can be invisible, yet the emerging field of seascape genetic is providing a method of characterising 'seascape' features using modelling of oceanographic environments and circulation patterns (White *et al.* 2010; Liggins *et al*. 2013). The results from seascape genetics can provide a predictive framework under which patterns of population structure can be compared (Riginos, 2013). The key factors influencing the genetic structure of marine populations are biogeographical barriers, ocean currents, oceanic expanses and larval dispersal (Rocha et al., 2005).

Environmental gradients can act as barriers to gene flow between populations, as environmental gradients often limit an organism's geographic range in which to survive (Wharton, 2002). Environmental barriers can be gradients or abrupt transitions in abiotic conditions, in the ocean the factors of temperature and oxygen availability are particularly important in acting as boundaries by imposing physiological constraint (Pörtner & Knust, 2007). For example, temperature can act as a physiological restraint to survival of marine species due to its effect on cellular function and reduction on the stability of membranes and proteins (Tomanek, 2008; Helmuth, 2009). Marine species can show variability in phenotypic responses to differing environmental conditions, or can upregulate a normal response, such as the overexpression of heat shock proteins to survive in novel environment (D'Amico, Collins, Marx, Feller, & Gerday, 2006; Garbuz et al., 2008). If organisms have dispersed away from the natal environment the organism must undergo settlement and survival in the non-natal conditions (Selkoe, 2011). The organism may not be locally adapted to the environment, hindering survivorship or reducing of reproductive success (Riginos, 2013). Therefore, environmental conditions may impose a barrier, by constraining survival and reproduction (Harding, 2004). As the larval stage allows organisms to leave their natal environment and enter new environments there is a reduced likelihood that organisms will settle in favourable habitat type with appropriate environmental conditions (Palumbi, 1994). The reducution in fitness in a novel environment is known as the phenotype-environment mismatch (Marshall, Monro, Bode, Keough, & Swearer, 2010). In this case different life stages show not just morphological changes but alterations in performance under different conditions (Aguirre,

Blows, & Marshall, 2014). Environmental barriers that isolate subpopulations can lead to a reduction in gene flow which is isolation by environment. The genetic structure of *Amphipricon bicintus*, an anemone fish, in the Red Sea was partially explained by the environmental gradient of temperature, chlorophyll *a* and salinity (Nanninga, Saenz-Agudelo, Manica, & Berumen, 2014). The pattern was also due to geographic distance, which correlated to the gradients in environmental conditions.

Ocean currents and circulation patterns influence population structure by directing the movement of individuals. Currents act as barriers to marine organisms by influencing the direction of movement of fish and larvae (James, 2002). Circulation patterns are complex to model as they include many variables, such as ocean topography, water stratification, and wind patterns. Another challenge to modelling circulation patterns is to incorporate their dynamic nature such as including temporal variability such as seasonal changes (Schunter et al., 2011). The field of seascape genetics incorporates oceanographic modelling with genetic data to test how oceanographic features influence genetic structure (Schunter et al., 2011). For example, using modelled circulation patterns the presence of potential genetic breaks were predicted and matched to the observed amount of genetic variation in several marine species such false clown anemonefish (Timm, Planes, & Kochzius, 2012), groupers (Priest, 2015) and coral (Galindo, Olson, & Palumbi, 2006). Additionally genetic structure may not be explained by current oceanographic barriers instead it may reflect historical changes in sea level or circulation coined 'ghost of dispersal past' (Benzie, 1999). The pattern of genetic structure in the False Clown Anemonefish *Amphiprion ocellaris* in the Indo-Malay Archipelago showed a pattern of structure reflecting historic oceanic circulation patterns (Timm et al., 2012).

Coral reef fish have a bipartite life cycle consisting of a pelagic phase as larvae and a benthic stage as adults (Green et al., 2014; Warner, 1997). Larval dispersal is often the stage at which individuals of marine species are exchanged between populations, as during this time movement over large distances is possible. Unsurprisingly larvae have undergone extensive study once identified as potential drivers for genetic similarity between populations. The techniques to assess larval movement include directly measuring larval movement through tagging the larvae (Cowen & Sponaugle 2009). Alternatively reproducing females can be chemically tagged which then pass on the on chemical signatures to their offspring (Robert K Cowen & Sponaugle, 2009). The association between larval movement and genetic connectivity is not straightforward as large scale larval movement being directly related to high

genetic connectivity particularly as self-recruitment and ocean currents can lead to genetic structuring. A recent meta-analysis showed that the length of pelagic larval duration (PLD) did not clearly influence the pattern of genetic structure (Riginos et al 2011). In addition, Selkoe (2011) showed that using the pattern of isolation by distance alongside the pelagic larval duration gave a better indication of genetic structure. Yet there are some cases whereby larval dispersal capacity is suggested to influence connectivity. For example, in a frequently spawning fish, the bluehead wrasse a long PLD was accompanied by panmixia, in comparison to the French grunt which spawn less frequently and had a shorter PLD which showed a well-defined population structure across the Caribbean (Purcell et al., 2006). It is important to state that a direct association between genetic connectivity and larval dispersal duration is rare. In some cases pelagic larval duration time does not correlate to the degree of genetic structure as in the comparative study of the blackbar soldier fish, *Myripristis Jacobus,* which had a shorter PLD but showed higher genetic similarity, than the longjaw Squirrel fish, *Holocentrus ascensionis,* which had a longer PLD but higher genetic differentiation (Bowen, Bass, Muss, Carlin, & Robertson, 2006).

Within the ocean similar habitats can occur separated by vast oceanic distances and if these distances can be crossed by marine organism movement then high connectivity can occur. The combination of large dispersal capability and a life history characteristic of high fecundity and high spawning levels can lead to high connectivity. Such observations of genetic similarity across great distances have been found in Naso (*F. Acanthuridae*) populations over thousands of kilometres throughout the Indo-Pacific (Klanten, Choat, & Van Herwerden, 2007) which supports the idea of connectivity over large distances. Geographical distance can be used to explain patterns of genetic structure as greater genetic differentiation can be found between populations as geographic distance increases. The test of Isolation by Distance (IBD) can be used as a measure of whether observed population structure can be explained through geographic distance between populations. The measure of IBD in marine populations can use larval dispersal distances as an alternative to Euclidean distances and this has been shown to give better explanatory power to understand patterns of population structure (White et al., 2010).

Species specific sensitivity to different barriers has been observed which could be due to a combination of life history and larval traits. Therefore, it can be hard to make predictions or provide explanations for the genetic patterns due to the complexity and synergistic mechanisms

acting together that lead to the degree of structuring of a population. In the Hawaiian Archipelago a pattern of genetic structure was determined for a range of marine species and of those 35 species a high proportion showed regional structuring whilst the rest show patterns of panmixia, isolation by distance or chaotic genetic structure (Selkoe, Gaggiotti, Bowen, & Toonen, 2014). The mechanisms shaping structure do not have an overarching or universal effect on all marine species.

1.5 Evaluating genetic similarity using molecular markers

The field of population genetics has been propelled by ongoing molecular and technical developments that have revolutionised all areas of genetic study. Population genetics has shifted from theoretical and mathematical models to empirical studies due to molecular advancements. The main breakthroughs include the ability to amplify specific DNA regions via PCR and the increased ease of DNA sequencing (Sunnucks, 2000). Developments in molecular markers, in creating universal primer sets or species specific microsatellite production has meant a large selection of markers are now available. The choice of markers is a crucial decision considering the variety available and differences in resolution. The choice in marker depends on the objectives of the study and the level of variation that is desired (Timm et al., 2012). Molecular markers differ due to how different areas of the genome evolve, and differences in the mode of inheritance of markers. The two main categories of markers are biochemical markers such as proteins and allozymes, or genetic markers such as microsatellites. The genetic markers give direct sequence data that allows for allele frequencies and sequence differentiation to be determined. Commonly mitochondrial DNA and microsatellite DNA are used as molecular markers to assess population structure as they show higher variation than other markers.

It can be beneficial to use multiple molecular markers in population analysis considering different marker types vary in the information gained. There have been cases where some markers may reveal genetic similarity where others have missed it, as in the case of *Myriptisis berndti* whereby microsatellites revealed fine scale population differentiation in some areas which had not been found by an earlier mtDNA study concordance of overall wide-scale, global connectivity but also evidence of restricted population differentiation (Muths, Gouws, & Mwale, 2012). Intuitively more information allows for a comparison of data allowing for results to be validated if similar patterns are shown from multiple sources. The use of a combination of mitochondrial and microsatellite markers revealed breaks in the False Anemone

clownfish in the Indo-Malay Archipelago, and the different markers were able to show differences in the process of separation (Timm et al., 2012). There have also been discrepancies whereby a result using one marker type has been called into question when a different marker type is used. This reiterates the importance of choosing the most suitable marker available. Some researchers use multiple markers to combat missing variation because of limitations of certain markers. This may also allow a broader understanding of connectivity by being able to consider both the historical and contemporary connectivity of a population (Sala-Bozano, Ketmaier, & Mariani, 2009).

Genetics studies can be vital in evaluating a pattern of connectivity, albeit the choice of marker will determine the scope of information that can be collected. Recently genetic studies are being coupled with other fields, such as environmental mapping and dispersal dynamics to give a better understanding of which factors influence population structure.

1.6 Study species: *Lutjanus ehrenbergii*

The blackspot snapper (F. Lutjanidae, *Lutjanus ehrenbergii*), belongs to the order Percoidei which is the largest and most diverse order of fish, and contain 145 families (Johnson, 1980). Within the Percoidei there are 3 monophyletic groups Lutjanoidea, Sparoidea and Haemuloidea. The Perciformes are spiny-rayed fishes found throughout tropical and subtropical waters, as well as in coastal areas (Allen, 1985). The family Lutjanidae is composed of 17 genera and 103 species of mostly reef associated marine fishes. The family is divided in four subfamilies; Etelinae, Apsilinae, Lautjaninae and Paradicichthyinae (Johnson, 1980). *Lutjanus ehrenbergii* is morphologically similar to *Lutjanus fulviflamma*, which shares a similar number of spines and rays on the dorsal fin, and has similar colouration. Misidentification can be an issue as both species can also be referred to by the same common name in the Arabian Gulf region which is ‘Naisarah’. *Lutjanus ehrenbergii* is distributed across the Indo Pacific down the coast of East Africa, and up along the Indian coastline (Allen, 1985).

Lutjanids are found in coral reefs in tropical and subtropical waters, whilst juveniles may be found in mangroves or lagoons. Snappers are predatory fish feeding mainly on crustaceans and small fishes. They have high commercial value, which has led to some stocks becoming extremely depleted, and currently *Lutjanus analis* (Mutton Snapper), *Lutjanus campechanus* (Red Snapper) and *Lutjanus cyanopterus* (Cubera Snapper) are listed as

vulnerable by the International Union for Conservation of Nature. The status of *Lutjanus ehrenbergii* has not been assessed for the IUCN Red List.

A characteristic feature of lutjanids is their high dispersal and high fecundity and therefore they have been considered to possibly show high genetic connectivity. A comparison of connectivity between two lutjanid species, *Lutjanus kasmira* and *Lutjanus fulvus*, across the Indo-Pacific found differing patterns of connectivity for the two species. *L. fulvus* showed higher population structure than *L. kasmira* which showed a greater degree of panmixia (Gaither, Toonen, Robertson, Planes, & Bowen, 2010).

1.7 Study area: The Arabian Gulf

The Arabian Gulf is a young sea connected to the Indian Ocean via the Strait of Hormuz. The Gulf contains a diverse range of habitat types such as seagrass beds, mudflats and coral reefs (Price, Sheppard, & Roberts, 1993). The Arabian Gulf is viewed as a unique ecosystem considering the high biodiversity in the face of challenging environmental conditions. The Arabian Gulf is currently the warmest ocean globally reaching temperatures of 34°C (Price et al., 1993). The environmental conditions, particularly the high temperature peaks, would normally kill corals found elsewhere in the world (Riegl, Purkis, Al-Cibahy, Abdel-Moati, & Hoegh-Guldberg, 2011). The temperature is highly variable in the Arabian Gulf, with fluctuations of up to 28°C observed (Price et al., 1993). Specialised marine organisms can be equipped with physiological adaptations to tolerate upper and lower temperature extremities, such as antifreeze glycoproteins found in the notothenoids and Arctic cod which prevent freezing at low temperatures (Harding, Anderberg, & Haymet, 2003). However, the instability of the Arabian Gulf requires organisms to have flexibility in the unpredictable and rapidly changing environmental conditions. The Arabian Gulf is subjected to high rates of evaporation due to the combination of high latitude and shallowness, leading to high salinity reaching 45-50ppt (Price et al., 1993). Marine life in the Arabian Gulf faces multiple stressors that have been proposed to act synergistically, so should be considered together rather than investigating each factor separately (Price et al., 1993). The question of how organisms survive in spite of extreme environmental conditions is particularly relevant to our understanding of climate change predictions. The Arabian Gulf exhibits temperatures similar to the parameters oceans are predicted face over the next 100 years due to climate change (Burt et al. 2014).

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1.7.2 Physical setting

The Arabian Gulf is an area which shows extremes of temperature and salinity as a result of being semi-enclosed, shallow (~35m depth) and at a high latitude leading to high evaporation and increased warming (Riegl *et al*. 2012). The Arabian Gulf not only shows some of the highest thresholds in temperature and salinity which corals and fish are subjected to but also shows dramatic fluctuations in temperature and salinity (Feary et al. 2013). The temperature range of the Arabian Gulf has been recorded to fluctuate between the range of 10°C to 40°C across the seasons (Wilson, Fatemi, Shokri, & Claereboudt, 2002) (Figure 1). Whilst ocean salinity is commonly ~35ppt the salinity in the Gulf fluctuates between 28 to 60ppt from winter to summer (Wilson et al., 2002) . The environmental conditions can be posed as 'extreme' in comparison to the conditions of the neighbouring Gulf of Oman.

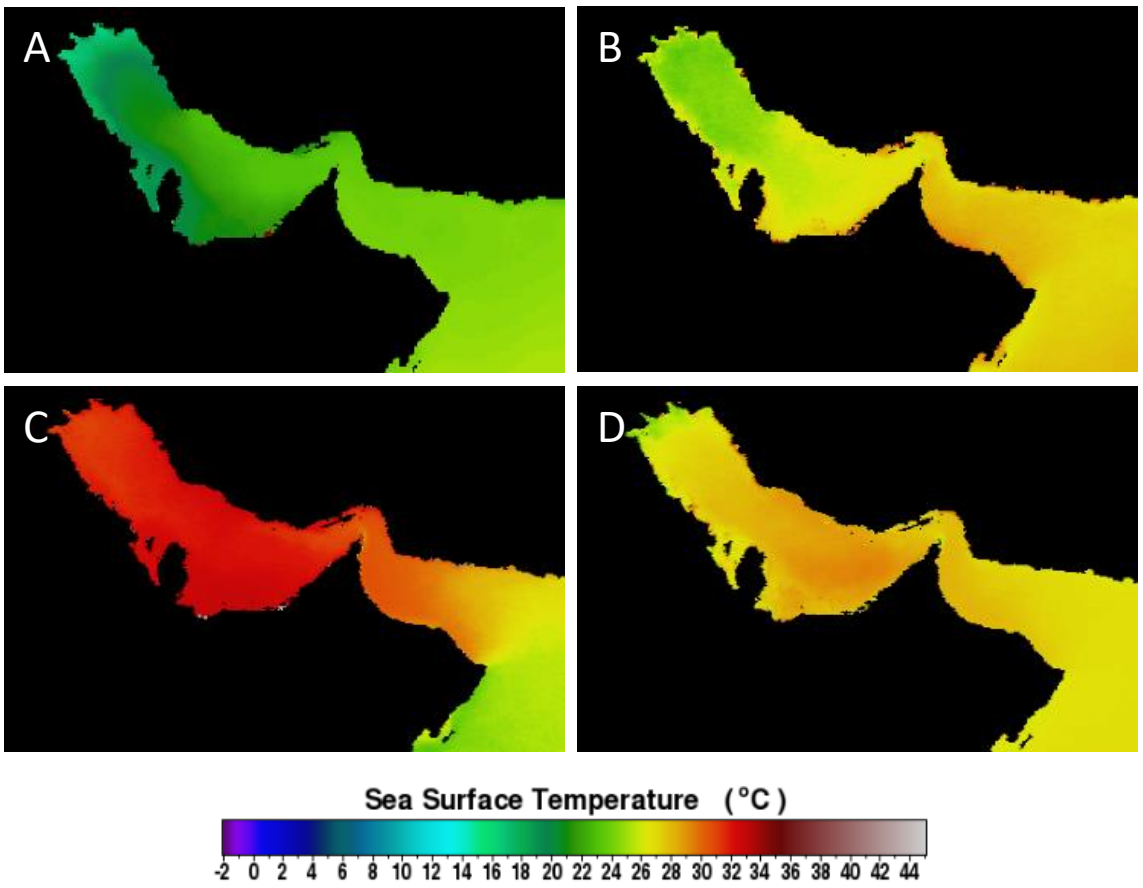


Figure 1: The average seasonal sea surface temperature across the Arabian Peninsula. Data taken over 2010, A) Winter B) Spring C) Summer D) Autumn.

1.7.3 Biological setting

The environmental gradients that exists moving from the Arabian Gulf, across the Strait of Hormuz to the Gulf of Oman are proposed to shape community assemblage. The Arabian Gulf region has lowered coral and fish diversity compared to the nearby Indo-Pacific Ocean. The Arabian Gulf is fairly young compared to the Indo-Pacific and Red Sea, with the sea floor exposed during the last glacial minimum (Lambeck, 1996). The lowered diversity in the Arabian Gulf has been considered to also be due to its youth (Sheppard, 1992). The coral community structure is associated with environmental gradients in chlorophyll-a, salinity and temperature according to multivariate analysis (Bauman, Feary, Heron, Pratchett, & Burt, 2013). The link between environmental gradients and coral reef fish dynamics across the Arabian Peninsula is lesser known. The biodiversity and abundance of reef fish inside the Arabian Gulf is lowered and contains an altered composition of functional groups compared to the Gulf of Oman (Burt et al., 2014). The reduction in diversity and abundance from the Gulf of Oman to inside the Arabian Gulf has been attributed to the restriction of movement across the Strait of Hormuz, isolating the Arabian Gulf (Coles & Tarr, 1990). Therefore the Strait of Hormuz has been coined to act as a 'funnel' due to restricting, or reducing the movement of organisms across this area (Feary et al., 2013). However comparably semi-enclosed environments such as the Red Sea do not show such dramatic reductions in diversity and abundance of marine organism (Burt et al., 2011). Therefore, impediment of marine organisms across the Strait of Hormuz can be considered to be more than solely a physical restriction but potentially due to an environmental gradient between the Arabian Gulf and the Gulf of Oman.

1.8 Research aims and objectives

The aim of this study is to address the gap in understanding of the population genetics of *L.ehrenbergii*, and a broader aim of understanding how coral reef fish populations are structured in the Arabian Gulf which has been a topic that has not received much consideration as of yet.

Understanding the genetic structure of coral reef fish populations across the Arabian Peninsula has currently been overshadowed by a focus on pelagic species. Recent research has shown contrasting patterns in the genetic structure of pelagic fish populations within this region, with strong genetic structuring in sailfish, *Istiphorus platypterus*, populations within the Gulf compared to external populations (Hoolihan *et al.* 2004). A break in gene flow in the

yellow hind, *Cephalopholis hemistiktos,* has been identified between southern Oman near an area of upwelling in comparison to the Arabian Gulf (Priest et al., 2016). Whilst a single panmitic genetic stock of Spanish mackerel, *Scomberomorus commerson,* was found in the Arabian Gulf, Gulf of Oman and Arabian Sea (Hoolihan, 2006). The contrasting results for pelagic fish leaves open the question of whether genetic structure is present for coral reef fish.

The Arabian Gulf environment is characterised by extreme oceanic conditions, including sea surface temperatures reaching 34-36°C in summer (*Hume et al.* 2015), and salinity reaching 40-50ppt (Price *et al.* 1993). Such environmental conditions may be detrimental to performance, or be fatal to Indian Ocean coral and fish species. Alongside the high temperature maximum, the Arabian Gulf also shows large ranges in temperature which fluctuate seasonally (*Hume et al.* 2015), whilst conditions are more stable in the Gulf of Oman. The Gulf is characterised by two environmental filters which may play a role in shaping population structure throughout the region. One is the abiotic environment, with substantial changes in salinity and temperature abiotic variables going from inside the Arabian Gulf area to outside in the Gulf of Oman area. The other is the potential for reduced movement of individuals associated with low coral cover and non-continuous reef structure.

Differences in species richness, species abundance and altered community structure may imply that populations in the Arabian Gulf and the Gulf of Oman are separate units, with the potential to be locally adapted to the environmental gradient between the two areas (Feary et al. 2013). The Strait of Hormuz is viewed as an ecological filter restricting the movement of organisms between the Arabian Gulf and the Gulf of Oman. The biodiversity, and biomass between the Gulf of Oman and Arabian Gulf supports this assertion; the biomass and species richness within the Gulf is reduced in comparison to the Gulf of Oman (Coles, 2009). Many common Indian Ocean fish and coral species are absent in the Arabian Gulf, suggesting they are unable to move into, or to survive in the Arabian Gulf. Zooxanthellae are characteristically temperature sensitive and only 40-50 zooxanthellae species inhabit the Arabian Gulf whilst in the Indian Ocean several hundred zooxanthellae species are found (Price, 1993). The observations of biodiversity and assemblage differences, as well as environmental differences between the Arabian Gulf and Gulf of Oman have led to the widely accepted attribution that there is an area preventing or restricting marine organisms range, or survival.

Despite substantial differences in the structure of biodiversity and community structure between regions, there is no genetic work to investigate the presence or location of a genetic break, or whether populations are genetically isolated across the Arabian Peninsula. I hypothesise that the Strait of Hormuz acts as a genetic break separating *L. ehrenbergii* Arabian Gulf and Gulf of Oman populations. I will address the classical assumption that the Strait of Hormuz is a filter using environmental and oceanographic parameters to characterise how this region is potentially acting a barrier. I will focus on determining whether the spatial pattern of genetic subdivision exists in the Arabian Peninsula in the coral reef fish, *L. ehrenbergii*.

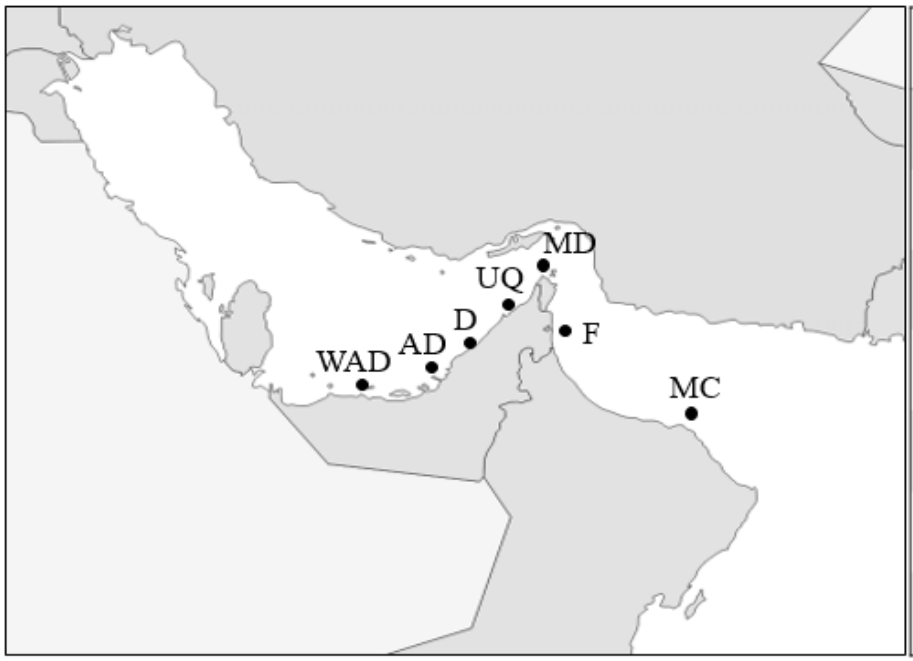
The aim will be achieved by undertaking these three objectives:

1. Determine the degree of genetic structure and level of gene flow between local populations of *L. ehrenbergii* across the Arabian Peninsula, using sequence data from 3 mitochondrial markers.
2. Characterise and determine the role of the spatial distribution of environmental gradients of temperature, salinity and chlorophyll-a across the Arabian Peninsula to characterise the assumed 'filter'
3. Model and quantify larval dispersal range and potential connectivity of a model coral reef fish throughout the Arabian Peninsula to how oceanographic circulation in the region could influence larval connectivity

2.1 Genetic data generation

2.1.1 Study area and sample collection

Tissue samples, sourced from fin or gill tissue, of *Lutjanus ehrenbergii (L.ehrenbergii)* were collected from local fish markets from 7 locations across the Arabian Peninsula (Western Abu Dhabi, Abu Dhabi, Dubai, Um al Quwain, Musandam, Fujairah, Muscat) (Figure 1). The collection of tissue samples from fish markets is a commonly used practice for marine fish population genetics (Spaet, Jabado, Henderson, Moore, & Berumen, 2015). The species *L.ehrenbergii* is a common catch for fish, and due to its inexpensiveness it is rarely moved between markets. Efforts were also made to confirm with fishermen that the fish were caught locally. The samples were pooled together for the genetic analysis into the main geographic areas of the Arabian Gulf, Strait of Hormuz and Muscat, which provides additional precaution to find if differences between these areas. Fin or gill tissue were immediately placed within a separate vial holding 90 – 100% ethanol, and then stored at -20°C within the University of Nottingham.



Locality	Collection	No. samples collected
WAD Western Abu Dhabi	Fish market	20
AD Abu Dhabi	Fish market	20
D Dubai	Fish market	20
UQ Um al Quwain	Fish market	20
MD Musandam	Fish market	20
F Fujairah	Fish market	20
MC Muscat	Fish market	20

Figure 1: Map of sampling locations for collection of *L.ehrenbergii* across the Arabian Peninsula (Western Abu Dhabi, Abu Dhabi, Dubai, Um al quwain, Musandam, Fujairah and Muscat).

2.1.2 DNA extraction

DNA extraction from tissue samples was performed using Qiagen DNAeasy Blood and Tissue kits, following the manufacturer's protocol, or using a modified protocol of the CTAB extraction method (Tel-Zur, 1999). The efficiency of Qiagen kits to that of CTAB is comparable, in that both produce a similar yield of DNA (Zetzsche & Klenk, 2008). The DNA extraction aliquots were nanodropped to quantify the DNA concentration and stored in a -20°C freezer until further analysis.

2.1.3 Polymerase Chain Reaction (PCR) Procedure

To amplify DNA a PCR was run which synthesises billions of copies of a specific DNA sequence in a few hours, through cycles of heating and cooling reactions (Mullis, 1990). In this analysis, we amplified three gene fragments (Cytochrome c Oxidase I, Control region and 12S) using universal primers (Table 2), for 10 individuals from the 7 sampling locations. Each PCR reaction consisted of a total volume of 25 µL, consisting of 1X buffer, 1.5 mM MgCl2, 0.200 µM of dNTPs, 0.2 mM of each forward and reverse primer, 1 U Taq polymerase, 1 µL of DNA template and DNA-free water to fill the tube to the total volume (25ul). Amplification was performed in a thermal-cycler. The optimised thermocycling conditions for each primer set are presented in Table 2. A no template control (sampled with all other chemicals but excluding DNA) was run in every PCR reaction to control for contamination from nucleic acids. PCR products were visualized on 1.5% agarose gel stained with ethidium bromide. A successful amplification of the target region was verified by using a sequencing ladder to determine the product size.

Table 1 The mitochondrial loci amplified for *L.ehrenbergii* individuals from the 7 sampling locations. The primer names and their corresponding sequences (5'-3') for the forward and reverse primers sequences for each loci

Gene fragment	Primer	Primer sequence	Source
Mitochondrial genes			
Cytochrome c Oxidase II	FishF2	TCGACTAATCATAAAGATATCGGCA	(Ivanova, Zemlak, Hanner, & Hebert, 2007)
	FishR2	ACTTCAGGGTGACCGAAGAATCAGAA	(Ivanova et al., 2007)
Control region	Cr-e	CCTGAAGTAGGAACCAGATG	(Lee, Conroy, Howell, & Kocher, 1995)
	Cr-a	TTCCACCTCTAACTCCCAAAGCTAG	(Lee et al., 1995)
12SAR-H	12SAR-H	ATA GTG GGG TAT CTA ATC CCA GTT	(Stephen R Palumbi et al., 2002)
	L16498	CGC CGC CGC CGC CGC CGC ATC TGG TTC CTA CTT CAG G	(P. J. Smith, Gaffney, & Purves, 2001)

Table 2 PCR thermocycling profiles for the amplification of mitochondrial loci of *L.ehrenbergii* from the 7 sampling locations

	Stage 1		Stage 2			Stage 3
	Initial Denaturation	Denaturation	Annealing	Extension	Cycles	Final extension
Cytochrome oxidase I	95 °C, 2 min	94 °C, 30 sec	56 °C, 30 sec	72 °C, 1 min	35	72 °C, 10 min
Control Region	95 °C, 2 min	94 °C, 30 sec	56 °C, 30 sec	72 °C, 1 min	35	72 °C, 10 min
12s	95 °C, 2 min	94 °C, 30 sec	56 °C, 30 sec	72 °C, 1 min	35	72 °C, 10 min

2.1.4 DNA sequencing

20 µL of PCR product from 10 individuals from each of the 7sampling locations were sent to Macrogen for PCR purification and sequencing. Macrogen use a ABI3730XL DNA Analyser for genetic analysis. The results from sequencing from Macrogen were analysed and edited by visualising chromatograms with the sequence editor Trev (James K. Bonfield, Beal, Betts, & Staden, 2002) and manually edited for misreads. Manually-corrected sequences were examined in the multiple sequence editor Gap4 (J K Bonfield, Smith, & Staden, 1995) and manually aligned using the Genetic Data Environment (GDE) program (S. W. Smith, Overbeek, Woese, Gilbert, & Gillevet, 1994) to view regions of similarity in nucleic acid sequences.

2.1.5 Genetic clade characterisation and geographic mapping

The direction of evolution in the samples was constructed through building neighbour-joining trees which were produced on PhyML (Guindon, Delsuc, Dufayard, & Gascuel, 2009). Neighbour joining trees were constructed for each marker individually and also for concatenated sequences, using the following outgroups *Perca fluviatilis, Lutjanus campechanus and Lutjanus fulviflamma*, sequences taken from GenBank. The choice of

Lutjanus fulviflamma was due to it being considered to be in the same species group as *L.ehrenbergii* known as the 'blackspot' group and is found within the a similar geographic range (Miller, Miller, & Cribb, 2007), yet the phylogenetic position of *L.ehrenbergii* has not yet been considered. Whilst *L.campechanus* is in a separate clade within the lutjanids to *L.fulviflamma,* and therefore will provide resolution as to the position of *L.ehrenbergii* as a group within the lutjanids. The species *P.fluviatilis* was used as an outgroup to the lutjanids as it is within the Percidae family. The tree topology was used to define clades, which are groups of haplotypes sharing a common ancestry. The reduction of genetic variation into clade which were supported by a PCA conducted in Jalview (Waterhouse, Procter, Martin, Clamp, & Barton, 2009). The defined clades were mapped spatially onto the area to assess whether geographic isolation of clades exists.

Haplotype networks can be used to examine the evolutionary relationship between haplotypes by joining together haplotypes and mapping out potential pathways to connect sequences. In a haplotype network branches represent mutational steps between haplotypes and can represent the variation and connection between haplotypes, yet does not give an idea of the timing of mutational event (Templeton, 2006). To start haplotype data files for all markers in the form of Roehl Data files were generated on DNAsp (Librado & Rozas, 2009) whereby gaps were not considered, and the invariable sites option was set to removed. Unrooted median joining networks were produced using Network 5 (Bandelt, Forster, & Röhl, 1999), which is based on haplotype frequencies.

2.1.6 Measures of population diversity across the Arabian Peninsula for *L.ehrenbergii*

To understand the degree of variation within each genetic marker at each sampling location a set of summary statistics were produced on Arlequin version 3.5 (Excoffier & Lischer, 2010). The genetic variation in each population was analysed by conducting measures of haplotype diversity *h*, nucleotide diversity analysis and mean nucleotide difference among haplotypes between populations. The haplotypes were mapped spatially across a map of the region to view if spatial subdivision of haplotypes occurred. Due to the high number of haplotypes the mapping was simplified into mapping private and shared haplotypes to give an idea of which geographic areas shared haplotypes and the extent of genetic similarity.

The differentiation between populations was measured through calculating the pairwise F_{ST}. The results for pairwise F_{ST} gives a value between 0 and 1, from panmixia to great population structure respectively. The values were interpreted using the guidelines that 0.0 to 0.05

signifies no to little genetic differentiation, 0.05 to 0.15 indicates moderate genetic differentiation, 0.15 to 0.25 signifies great genetic differentiation and >0.25 signifies very great genetic differentiation. The significance of the result is measured to $p < 0.05$, and presented alongside the F_{ST}. The pairwise F_{ST}s were calculated on Arlequin 3.5 (Excoffier & Lischer, 2010) whereby each sampling location was considered as a 'population'.

2.1.7 Hypothesis testing

The hypothesis outlined in this study centres around a prediction that the Strait of Hormuz could be acting as a barrier to restrict movement, and subsequent gene flow between the Arabian Gulf and the Gulf of Oman. To test this hypothesis pairwise F_{ST}s were calculated between populations according to the groupings of the Arabian Gulf (Western Abu Dhabi, Abu Dhabi, Dubai, Um al Quwain), the Strait of Hormuz (Musandam, Fujairah) and the Gulf of Oman (Muscat). Grouping populations together in this way is also a precautionary step to counteract if the sampling from fish markets were not from the region expected due to movements in fishing activity.

2.1.8 Evidence of demographic changes

To evaluate the presence of population growth tests were conducted testing mutation-drift balance were run such as Tajima's D (Tajima, 1989) and Fu's F (Fu, 1997) and a mismatch distribution. The neutral theory of evolution states that genetic diversity occurs through mutation producing variation, whilst the effect of genetic drift is to remove variation (Hedrick, 2011). Tajima's D is a model which tests the mutation-drift equilibrium by calculating the frequency of variation at different sites and measuring mutational events that lead to differences between variable sites. If mutation-drift is at equilibrium this will give a value of zero, whilst a positive value indicates that balancing selection or a population contraction has occurred leading to a lower than expected frequency of rare alleles. A negative value of Tajima's D would signify a recent population expansion after a bottleneck or positive selection, due to a higher than expected proportion of rare alleles. Tajima's D (Tajima, 1989) and Fu's F (Fu, 1997) tests with 10,000 permutations were conducted on Arlequin (Excoffier & Lischer, 2010).The mismatch distribution conducted on DNAsp (Librado & Rozas, 2009) evaluated the presence of population growth through testing the distribution of the observed pairwise nucleotide differences, against the expected values for a population that is growing Past population growth will give a characteristic shape, with a smooth unimodal distribution expected when a rapid expansion has taken place (Rogers and

Harpending, 1992). A bimodal distribution indicates an expansion in population size, and a multimodal distribution suggests a stable population size over time.

2.2 Environmental analysis to characterise evidence for a presence of a filter separating the Arabian Gulf from the Gulf of Oman

To consider whether the Arabian Gulf and the Gulf of Oman are environmentally distinct units separated by the Strait of Hormuz the environmental parameters across the Arabian Peninsula were investigated. The parameters of sea surface temperature (SST), salinity and chlorophyll *a* were examined to find if there are significant differences between sites. . Sea surface temperature, salinity and chlorophyll data was obtained from SeaWifs, for the locations Western Abu Dhabi, Abu Dhabi, Dubai, Ras al Khaimah, Musandam, Fujairah and Muscat. Locations for environmental data were chosen to match sampling sites for specimen collection. However, as all environmental data from Um al quwain was unavailable, data were taken from Ras al Khaimah, this site is 46km northeast of Um al quwain and therefore should have similar environmental variation. Daily temperature and salinity data from 1997 to 2014, while monthly recordings of chlorophyll *a* data were. To provide a comparison of environmental conditions between sites, the annual mean, the mean of the month with the highest and the lowest SST, salinity and chlorophyll *a*, and the range were calculated for each site To examine the relative importance of temperature, salinity and chlorophyll *a* in providing differences between sites a Principle Component Analysis (PCA) was produced using SPSS.

2.3 Characterising larval connectivity and potential dispersal ability in the Arabian Gulf

2.3.1 Larval dispersal in Arabian Gulf

To determine the movement of larvae across the study area a numerical oceanographic model of larval movement was developed in collaboration with Professor Calvacante[1]. The goal of investigated larval dispersal was to give preliminary findings on the movement of larvae in this area, particularly to see how larvae could move in and out of the Arabian Gulf. As little is known on the larval characteristics of *L.ehrenbergii*, the focus was shifted to how the

[1] I conceived the study with the aim of providing an initial idea of the movement of larvae in this region. The model was developed through an ongoing collaboration with Professor Geórgenes Cavalcante, from Universidade Federal de Alagoas. Professor Calvacante developed and implemented the analyses, undertaking the larval mathematical modelling. The interpretation was discussed together, and I wrote the discussion.

circulation pattern would influence general larval movement in the area. Therefore the characteristics of the larvae were chosen based on an average coral reef fish from the Arabian Gulf. Using ocean circulation patterns and Langrangian particle tracking to simulate larval trajectories, this oceanographic model provided an overview of the pattern of teleost larval dispersal, for a single spawning season across the Arabian Peninsula. The model ran from 27 April to 19 June 2010, coinciding with the summer spawning time for coral reef fish in the Arabian Gulf, including *L.ehrenbergii*.

2.3.2 Larval dispersal model parameters

At each selected time step 1000 particles were released (each equivalent to 100,000 larvae), resulting in 1.6 million modelled larvae being released over the 8 day period across all source areas were released from 8 source areas across the Arabian Peninsula (Western Abu Dhabi, Abu Dhabi, Abu Dhabi, Dubai, Um al quwain, Muscat, Fujairah). The source areas were chosen to gain an idea of movement of larvae into the Arabian Gulf and along the Gulf coastline. Larvae were released over a period of 10 days across all source areas, and the model was run from a total of 45 days; pelagic larval duration of approximately 45 days is considered as an upper threshold over which species are broadly distributed (Brothers & Thresher, 1985). Larvae were modelled as neutrally buoyant, passive particles that followed the prevailing oceanographic currents. The release was started at the peak of the high tide at full moon on 27 April and so continued for 8 days till 4 May 2010. Release time occurred twice a day following each high tide. The dispersal pattern of the larvae at simulation end was then visualized to determine larval dispersion (distance from source) and larval retention. The concentration and number of larvae for each were extracted at various locations to assess the intensity of retention or dispersal of larvae under the influence of fluid transport.

3.1 Analysis of population structure and demographic history of *L.ehrenbergii*

3.1.1 Overview of genetic variation and phylogenetic tree building

The PCR products for COI, control regions and 12S had lengths of 638 bp, 376 bp and 878bp respectively after removing primers and ambiguous sites. The genetic diversity within populations of *L.ehrenbergii* were relatively high, with a high proportion of unique haplotypes. The amino acid sequence of the only coding marker COI was used to view if the genetic variation amounted to a biological change in the amino acid sequence. There was a lack of non-synonymous substitutions between all 69 sequences and 17 synonymous mutations. A nonsynonymous substitution alters the amino acid sequence of a protein, therefore across the COI sequences in the sample all amino acid sequences were identical. Synonymous substitutions are changes in nucleic acid sequence which do not change the sequence of the resulting amino acid sequence, due to redundancy in the genetic code.

L.ehrenbergii was found to be a monophyletic group within the Lutjanidae, apparent within all 3 markers and a concatenated marker tree (Figure1, Figure 2 and Figure 4). The basal split was consistent between the markers COI and control region, and within the concatenated gene tree. Therefore, all further analyses of haplotype and clade mapping within *L.ehrenbergii* populations subsequent trees were rooted on the basal group, clade 1A.

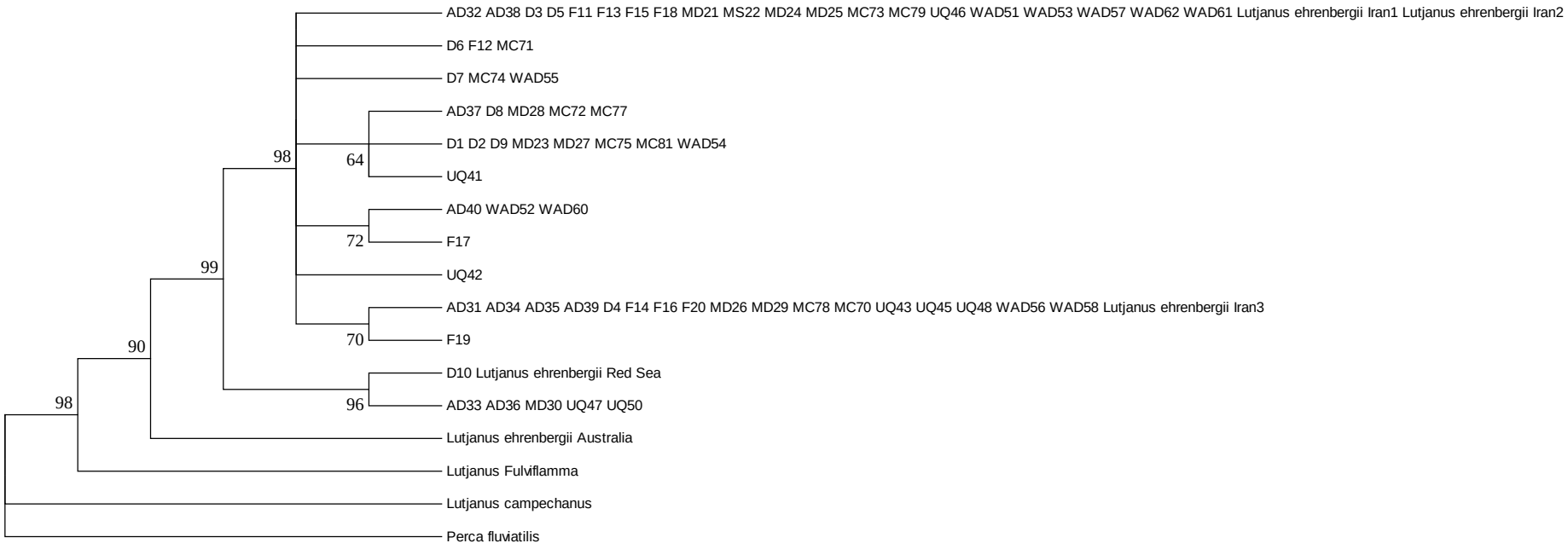


Figure 1. Phylogenetic tree using outgroups*; Perca fluviatilis, Lutjanus campechanus* and *Lutjanus fulviflamma* to root *Lutjanus ehrenbergii* populations for COI

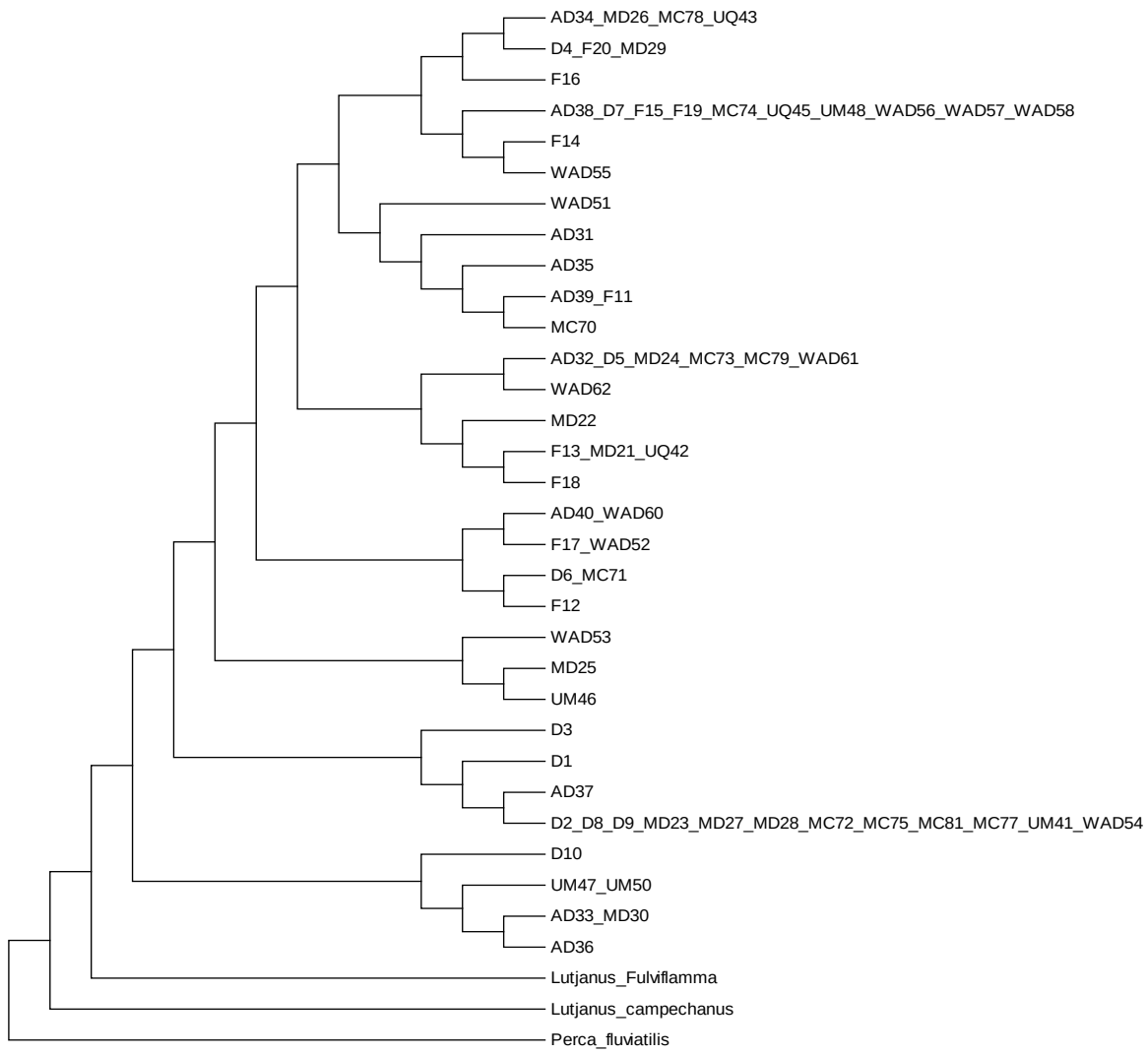


Figure 2. Phylogenetic tree using outgroups *Perca fluviatilis*, *Lutjanus campechanus* and *Lutjanus fulviflamma* to root *Lutjanus ehrenbergii* populations for control region

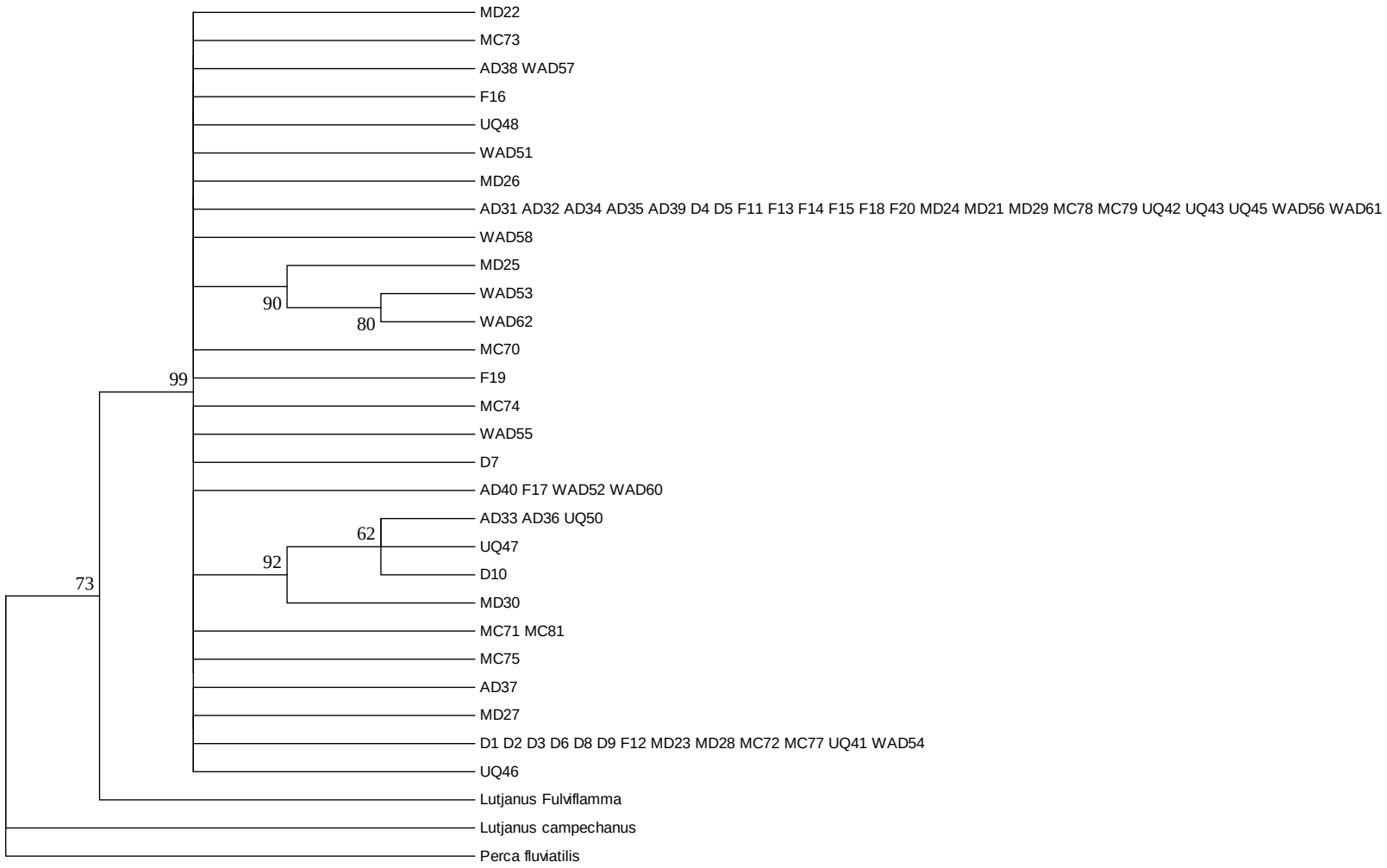


Figure 3. Phylogenetic tree using outgroups *Perca fluviatilis, Lutjanus campechanus* and *Lutjanus fulviflamma* to root *L.ehrenbergii* populations for 12S

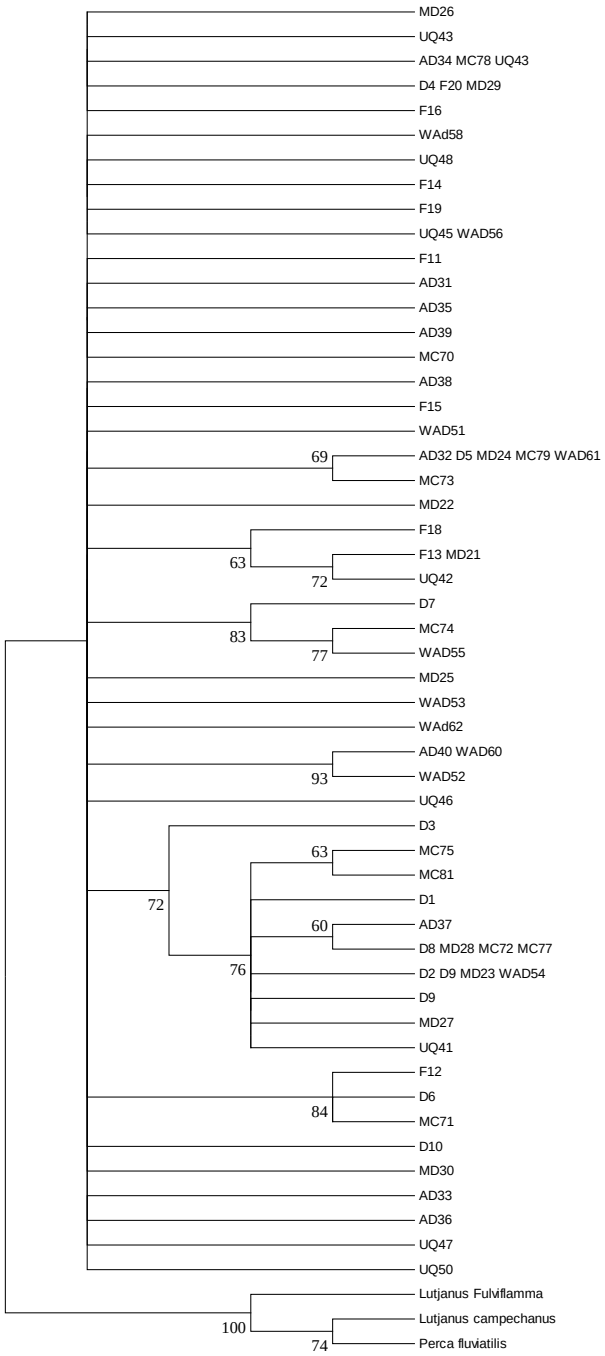


Figure 4: Phylogenetic tree using outgroups*; Perca fluviatilis*, *Lutjanus campechanus* and *Lutjanus fulviflamma*, to root *L.ehrenbergii* populations for concatenated sequences

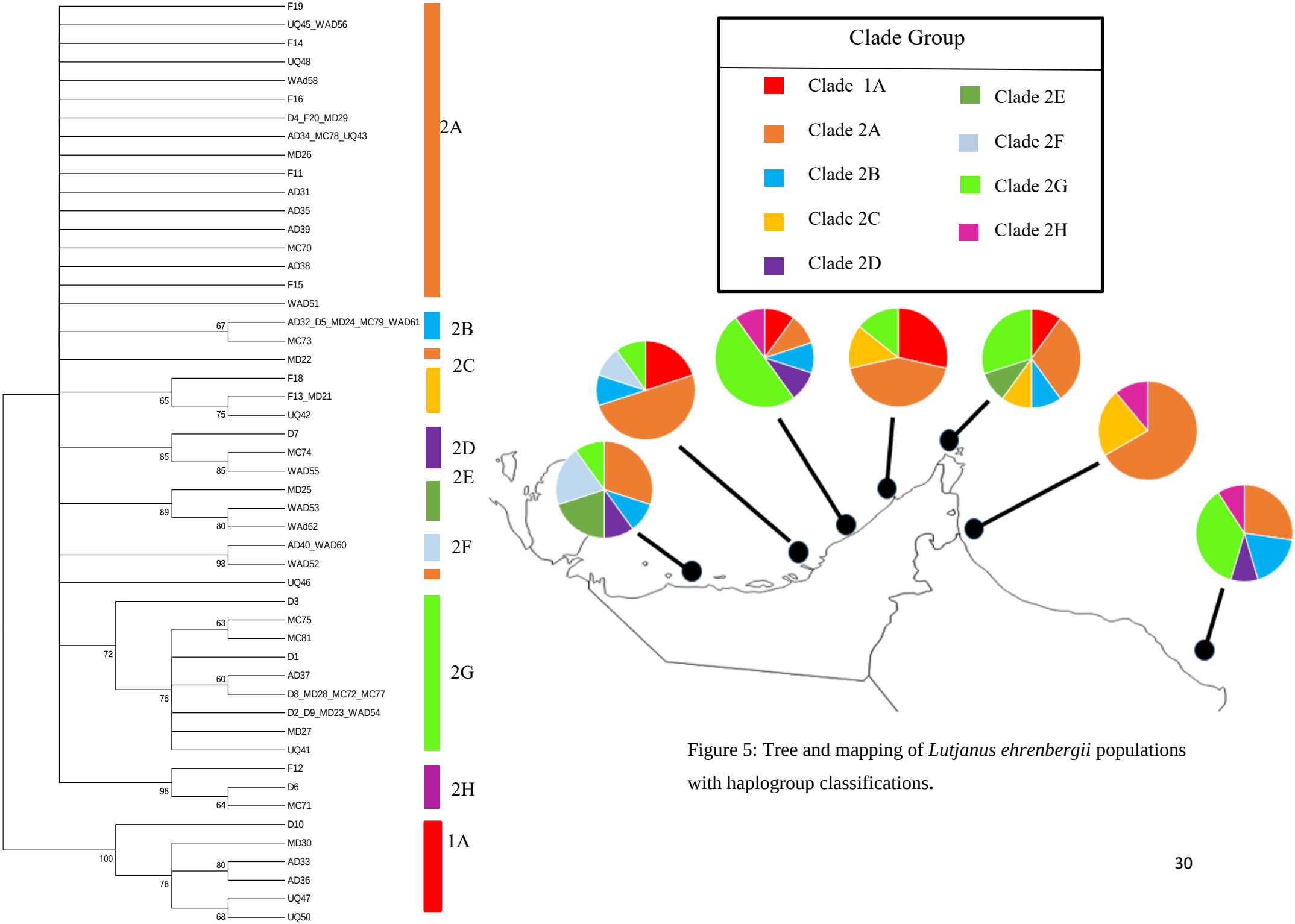


Figure 5: Tree and mapping of *Lutjanus ehrenbergii* populations with haplogroup classifications.

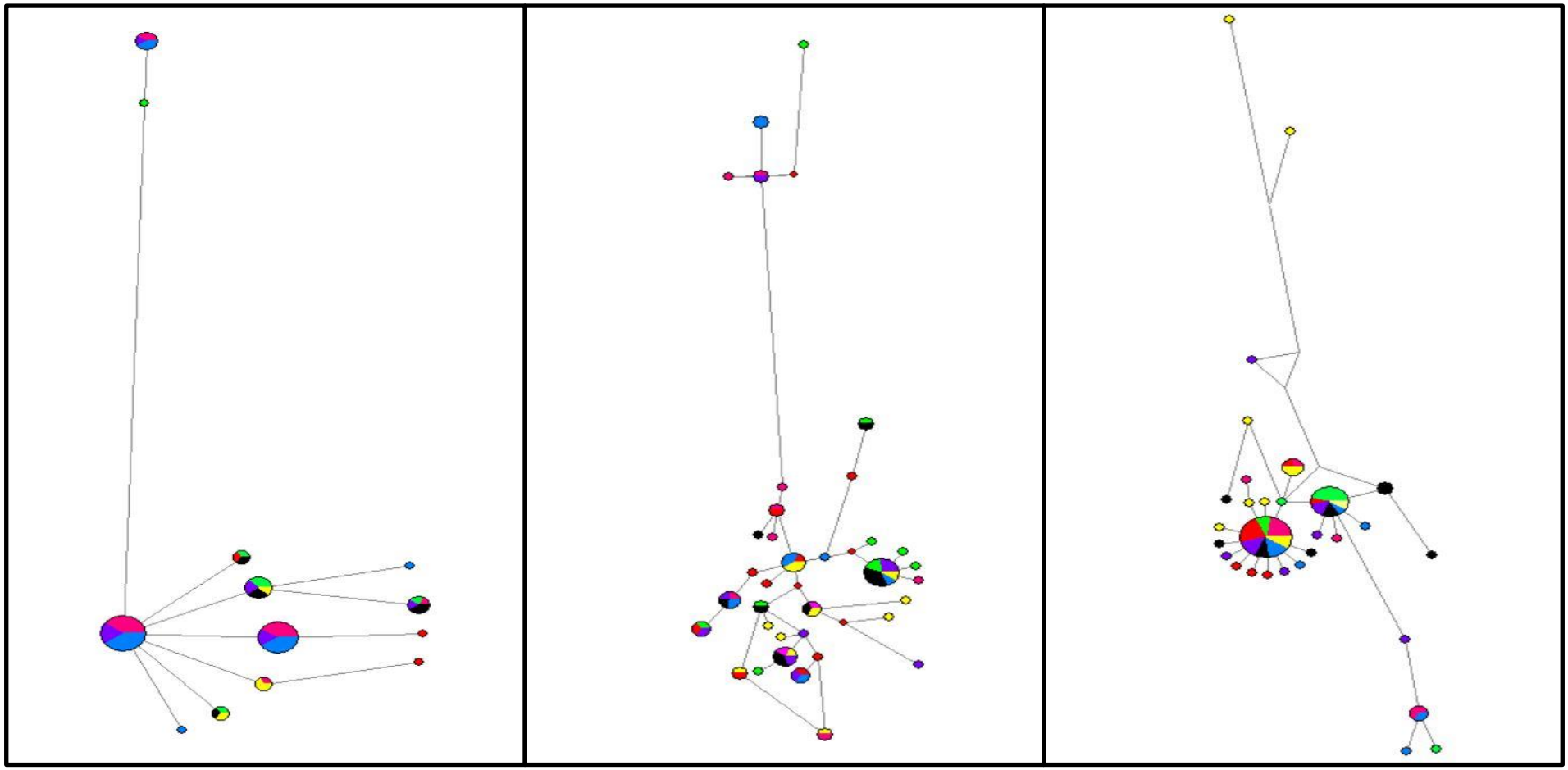


Figure 6 Median joining network of haplotypes. Produced on NETWORK representing the markers A) COI, B) control region and C) 12S. The circle size is proportional to haplotype frequency. The colours correspond to populations (yellow = Western Abu Dhabi, pink = Abu Dhabi, green = Dubai, blue = Um al quwain, purple = Musandam, red = Fujairah, black = Muscat).

3.1.2 Defining clade groupings in populations of *L.ehrenbergii*

Tree building for all three markers and the concatenated trees all showed a similar patterning in the number and size of samples producing groups, with nine main clades distinguished (Figure 5). These nine groups were then taken as the nine clades for further analysis. Clades were supported by high bootstrap values (>60) and validated by the results from the PCA, which produced clusters based on the same clade groupings.

3.1.3 Geographical distribution of clades

The mapping of clades across the sampling area presents the spatial distribution, and can illustrate whether spatial divisions exist. The clade 2A was distributed across all populations (Figure 5). Similarly, a widespread distribution was found in clade 2G, which was present in all populations apart from Fujairah. In comparison, the clades 2B and 2D were not present in all locations but where found across a large spatial distance from inside the Arabian Gulf to outside in the Gulf of Oman. Clade 2C is found in the sites of the Strait of Hormuz at the sites Um al quwain, Musandam and Fujairah. Clade 2E is found within populations in Western Abu Dhabi and Musandam. Clade 2F is found within the Arabian Gulf populations of Western Abu Dhabi and Abu Dhabi. Clade 2H across the either side of the Strait of Hormuz found a sites Dubai, Fujairah and Muscat. Clade 1A was only found present within the Arabian Gulf, and the Strait of Hormuz in the populations Abu Dhabi, Dubai, Um al quwain and Musandam. This clade is absent from Western Abu Dhabi, Fujairah and Muscat. However, using sequences from Genbank of *L.ehrenbergii* for COI found that the clade 1A is also found present in the Red Sea. Clade 1A is restricted to only the Arabian Gulf and Strait of Hormuz in the sampling, however is a clade that is present in a distant area of the Red Sea (Figure 1).

3.1.4 Network analysis of *L.ehrenbergii* haplotypes

Overall all the three networks, for each marker, revealed no pattern of geographic subdivision of haplotypes, supporting the results from clade and haplotype mapping. The median-joining networks constructed for markers COI, control region and 12S showed a similar pattern in terms of clade groupings to the neighbour-joining trees (Figure 6). In all networks the basal clade 1A is separated by the highest number of mutation events to all other sequences. In all of the networks produced there is no separation of haplotypes based on geographic location. The network for COI shows a star-like pattern with many rare haplotype connected in short branches to a predominant haplotype. The network for the control region also shows a pattern of star-like profiles. The network for 12S shows a star-like pattern with one main dominant haplotype connected by short branches to 12 rare haplotypes which correspond to all the sampling localities. The pattern resembling a star like structure indicates that a population expansion has occurred, whereby a dominant ancestral haplotype has given rise to many haplotypes (Ferreri, Qu, & Han, 2013).

3.1.5 Population Diversity Indices

L.ehrenbergii exhibited high levels of haplotype diversity with a total of 13 haplotypes for the marker, the control region had the highest number of haplotypes with 35 and the marker 12S had 30 haplotypes.

The mapping of private and shared haplotypes gives an indication of the distribution of haplotypes between sampling locations. In each population, many sequences were unique haplotypes, found restricted to a single geographic location, these are the private haplotypes (Figure 7). In COI haplotypes were found to be shared across the Arabian Peninsula, with two haplotypes found in every location. Whilst 5 haplotypes were private, and are not found in more than one sampling locations. The haplotypes which were shared only between two to six populations did not show a specific pattern of which location was shared with. For example the 3 haplotype shared between 3 locations each had a different pattern one shared between the neighbours Abu Dhabi, Um al quwain and Musandam, whilst the another haplotype was shared across the mot furthest populations at Abu Dhabi, Dubai and Muscat. In the control region no haplotype was found in every location, but several were found scattered throughout the sampling range, also showing sharing of haplotypes along a large spatial scale. In control region marker, there were 22 haplotypes out of 35 that were unique to a single sampling site. Similarly, to COI the pattern of sharing of haplotypes would portray haplotypes missing from

populations which does not always match neighbouring populations, and could be across from sites within the Arabian Gulf, the Strait of Hormuz and Gulf of Oman. There is therefore not complete sharing of haplotypes between all locations, but sharing of halotypes across large distance and absent from some sampling locations. In 12S there were several haplotypes found scattered throughout the sampling locations, with 1 haplotype found shared between all populations. Whilst 26 of the 30 haplotypes were unique to a single sampling area. Although there was a high frequency of private alleles in all markers the presence of several haplotypes shared across the Arabian Gulf, the Strait of Hormuz and the Gulf of Oman gives no indication of a break at the Strait of Hormuz. The sharing of haplotypes follows that same patchy distribution as COI and control region whereby haplotypes can be shared across a wide range but are absent between neighbouring populations. An example is a haplotype shared between the three populations Western Abu Dhabi, Abu Dhabi and Fujairah. All markers that shared haplotypes between six populations or less showed that there was a patchy distribution of sharing, not necessarily always sharing between neighbouring populations.

The results from the genetic diversity indices showed overall high level of haplotype diversity, and low nucleotide diversity in all populations for each mitochondrial marker (Table 1, 2 and 3). All populations showed high haplotype diversity (*h*) in all mitochondrial markers (Table1, 2 , 3). The haplotype diversity ranges from 0.78 to 0.911 with an average of 0.84 for COI. In comparison, the haplotype diversity in the control region ranged from 0.84 to 1, with an average of 0.95. For 12S the haplotype diversity ranged from 0.64 to 9.33 with an average of 0.83.

Nucleotide diversity was low in all markers, signifying a small proportion of nucleotide sites differ in the populations. For the marker COI the nucleotide diversities ranged from 0.001% to 0.006%, with an average of 0.003%. In comparison the nucleotide diversities control region ranged from 0.01% to 0.02%, with an average of 0.01%. For 12S the nucleotide diversities ranged from 0.002% to 1.35%, with an average of 0.1%. The mean pairwise nucleotide differences between haplotypes ranged from 1.01% to 4.28% with an average of 2.40% for COI. The mean pairwise nucleotide differences between haplotypes ranged from 5.13% to 9.31% with an average of 7.06% for control region. The mean pairwise nucleotide differences between haplotypes ranged from 0.001% to 4.94% with an average of 3.005% for 12S.

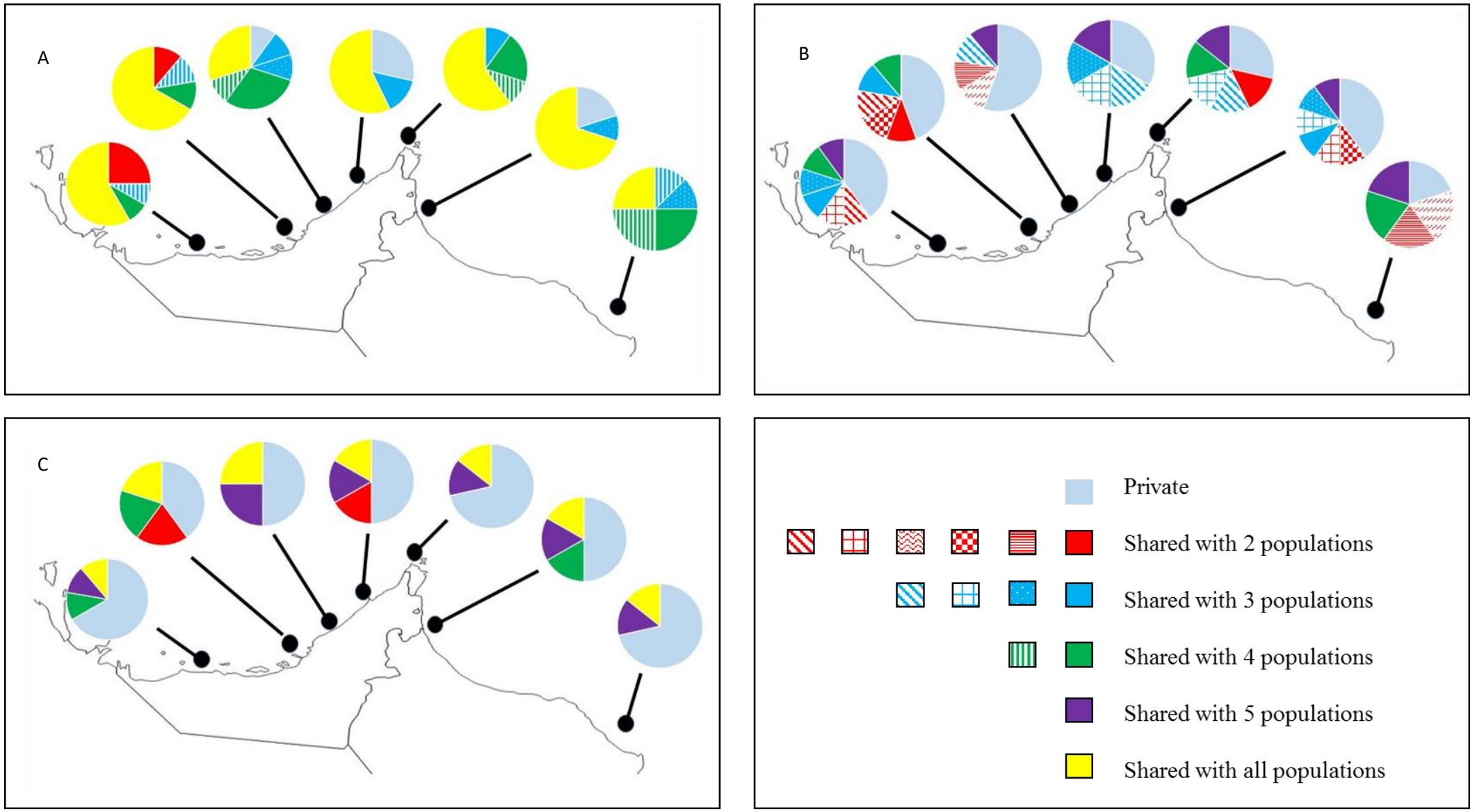


Figure 7: The sharing of haplotypes across the Arabian Peninsula A) COI, B) control region, C) 12S

Table 1 Estimates of genetic diversity. The indices for COI in *L. ehrenbergii.*

COI					
Sampling location	No. of haplotypes	No. of variable sites	Haplotype *h*	Nucleotide (%)	Mean pairwise difference (%)
W. Abu Dhabi	5	4	0.7818 ± 0.1073	0.001596 ± 0.001302	1.018182 ± 0.736308
Abu Dhabi	5	11	0.8222 ± 0.0969	0.005677 ± 0.00355	3.622222 ± 2.003993
Dubai	7	11	0.9111 ± 0.0773	0.003971 ± 0.002633	2.533333 ± 1.485586
Um al quwain	5	11	0.8571 ± 0.1083	0.006717 ± 0.004236	4.285714 ± 2.372374
Musandam	5	10	0.8222 ± 0.0969	0.003797 ± 0.002539	2.422222 ± 1.432292
Fujairah	5	5	0.8000 ± 0.1001	0.002090 ± 0.001598	1.333333 ± 0.901403
Muscat	6	3	0.9111 ± 0.0620	0.002577 ± 0.001871	1.644444 ± 1.055330

Table 2: Estimates of genetic diversity. The indices for control region in *L.ehrenbergii*.

Control region					
Sampling location	No. of haplotypes	No. of variable sites	Haplotype *h*	Nucleotide (%)	Mean pairwise difference (%)
W. Abu Dhabi	10	20	0.9818 ± 0.0463	0.014894 ± 0.008737	5.600000 ± 2.9120444
Abu Dhabi	10	28	1.0000 ± 0.0447	0.024764 ± 0.014069	9.311111 ± 4.677447
Dubai	9	26	0.9778 ± 0.0540	0.019917 ± 0.011501	7.488889 ± 3.823595
Um al quwain	6	33	0.9286 ± 0.0844	0.021847 ± 0.012921	8.214286 ± 4.264830
Musandam	8	27	0.9333 ± 0.0773	0.021158 ± 0.012159	7.955556 ± 4.042376
Fujairah	10	19	1.0000 ± 0.0447	0.013652 ± 0.008173	5.133333 ± 2.717268
Muscat	6	17	0.8444 ± 0.1029	0.015307 ± 0.009053	5.755556 ± 3.009942

Table 3: Estimates of genetic diversity. The indices of genetic diversity for 12S in *L.ehrenbergii.*

12S					
Sampling location	No. of haplotypes	No. of variable sites	Haplotype *h*	Nucleotide (%)	Mean pairwise difference (%)
W. Abu Dhabi	9	19	0.9636 ± 0.0510	0.005633 ± 0.003349	4.945455 ± 2.606757
Abu Dhabi	5	11	0.7556 ± 0.1295	0.004379 ± 0.002717	3.844444 ± 2.109203
Dubai	4	7	0.6444 ± 0.1518	0.002075 ± 0.001471	1.822222 ± 1.14227
Um al quwain	6	10	0.8929 ± 0.1113	0.004759 ± 0.003011	4.178571 ± 2.320511
Musandam	7	14	0.9111 ± 0.0773	0.003974 ± 0.002500	3.488889 ± 1.940794
Fujairah	6	6	0.7778 ± 0.1374	1.355556 ± 0.912491	0.001544 ± 0.001175
Muscat	7	9	0.9333 ± 0.0620	0.003138 ± 0.002050	2.755556 ± 1.591899

3.1.7 Evidence of demographic changes in *L.ehrebergii* across the Arabian Peninsula

In all markers the result of Tajima's D was negative in all populations (Table 4). The only sites with significant departures from neutrality were Dubai (COI), Um al quwain and Muscat (control region) and Abu Dhabi (12S). The negative and significant value of D is a deviation from the neutral model of evolution indicating population expansion, bottleneck or positive selection (Templeton, 2006). The results of Fu's F were negative in all markers for every population. The sites with significant negative Fu's F were in Dubai and Muscat (COI), in Western Abu Dhabi and Fujairah (control region) and in Western Abu Dhabi, Dubai, Fujairah and Muscat (12S). Significantly negative F value indicates an excess of rare haplotypes in the populations over what is expected under neutrality, indicative of population expansion, bottleneck or selection.

Historical demographic changes that have occurred the populations of *L.ehrenbergii* were explored through running a test of mismatch distribution. The results from the mismatch distribution showed a similar profile in all markers, not fitting an equilibrium distribution but with a bimodal distribution (Figure 8).

Figure 8: Demographic changes in *L.ehrenbergii*. The expected and observed data for mismatch distribution model produced on DNAsp for A) COI, B) control region and C) 12S.

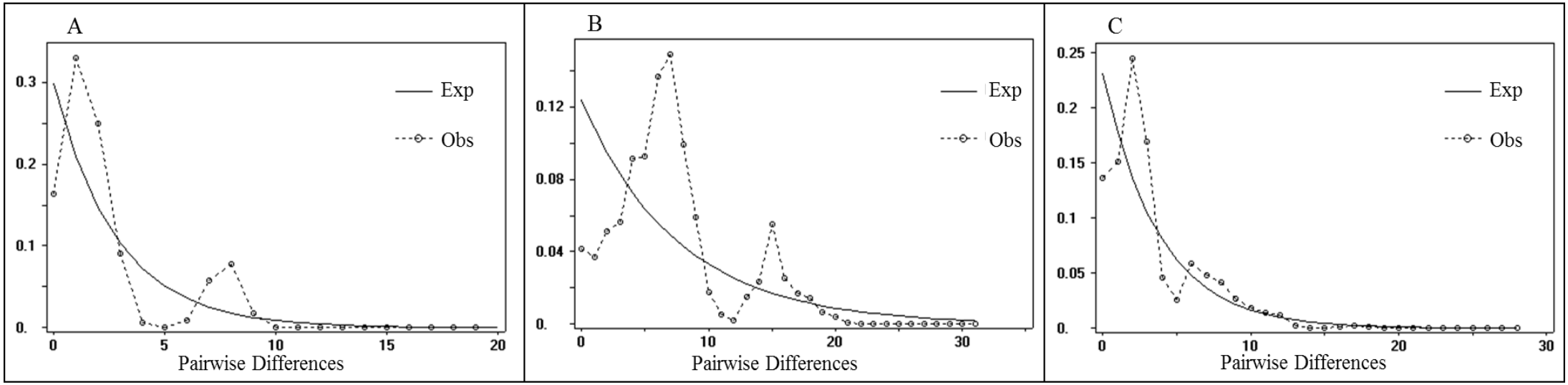


Table 4: Estimates of neutrality tests. Tajima's D and Fu's F for markers A) COI, B) control region and C) 12S produced on Arlequin. P = <0.05 shown in bold.

A) COI

Sampling location	Tajima's D	Fu's F
W. Abu Dhabi	-0.93168	-0.93168
Abu Dhabi	-0.30646	0.76478
Dubai	**-1.56043**	**-2.53669**
Um al quwain	0.05096	0.46302
Musandam	-1.39515	-0.16694
Fujairah	-0.98485	-1.54678
Muscat	-0.27902	**-2.36445**

B) Control region

Sampling location	Tajima's D	Fu's F
W. Abu Dhabi	-0.81500	-4.08681
Abu Dhabi	-0.28365	-3.69296
Dubai	-0.88322	-2.36578
Um al quwain	-0.16682	0.52726
Musandam	-0.79540	-0.82418
Fujairah	-1.10428	-5.80704
Muscat	-0.19631	0.72300

C) 12S

Sampling location	Tajima's D	Fu's F
W. Abu Dhabi	1.07285	**-2.82161**
Abu Dhabi	**-0.05055**	0.90799
Dubai	-1.11638	**0.38768**
Um al quwain	0.41308	-0.86449
Musandam	-1.35110	-1.63996
Fujairah	-1.49289	**-2.92289**
Muscat	-0.58608	**-2.29064**

3.1.7 Population differentiation in *L.ehrenbergii*

The results from the pairwise F_{ST} indicated insignificant genetic differentiation between populations, as there were predominately few departures from 0. The presences of little to no significant structure between the Arabian Gulf and the Gulf of Oman substantiates rejecting the hypothesis that genetic structuring would occur across the filter of the Strait of Hormuz.

There was little to no genetic structure when considering the COI marker, between populations which ranged from -0.085 to 0.065 in which all of the populations showed insignificant pairwise population comparisons ($p< 0.05$) (Table 5). In most populations negative values, or those under 0.05 were found which were insignificant which shows little genetic structure between most populations, and the values could be considered as 0. Moderate differentiation between Fujairah and Muscat at was found at 0.065, however this result was insignificant.

In comparison, the control region marker showed mainly little to no genetic differentiation between populations (Table 6). The range was from -0.067 to 0.131 with only 2 out of 21 populations pairs having a significant departure from 0 ($p <0.05$). The 19 population pairs can be considered as a value of 0 which indicate no population structuring. The only significant departures from 0 occurred in the populations Abu Dhabi - Dubai ($F_{ST} =0.093$, $p < 0.05$) and in and Abu Dhabi – Muscat ($F_{ST} = 0.131$, $p <0.05$) which both indicate significant moderate genetic differentiation.

Lastly, there is little to no genetic population differentiation when considering the 12S marker between the majorities of populations (Table7). The range from -0.046 to 0.222 with 3 out of 21 population pairs presenting a significant departure from 0. The 18 population pairs can be considered as a value of 0 indicating no population structure. However, there was a significant moderate level of genetic differentiation ($F_{ST} = 0.05$ to 0.15, $p< 0.05$) between Abu Dhabi and Dubai (0.153, $p <0.05$), Abu Dhabi and Fujairah ($F_{ST} = 0.113$, $p < 0.05$). Lastly, there was a high level of genetic differentiation, found between Western Abu Dhabi and Abu Dhabi ($F_{ST} = 0.222$, $p < 0.05$) (Table 7).

Table 5 Genetic differentiation between populations for COI marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a sampling site (WAD -Western Abu Dhabi, AD -Abu Dhabi D -Dubai, UQ -Um al quwain, MD – Musandam, F – Fujairah, MC- Muscat). P value < 0.05 given in bold.

COI Population Pairwise Fst							
	WAD	AD	D	UQ	MD	F	MC
WAD							
AD	0.04762						
D	-0.01389	0.02778					
UQ	-0.01509	-0.04418	-0.03989				
MD	-0.00775	-0.08466	-0.00654	-0.05691			
F	-0.08305	0.05601	0.01161	0.01271	0.01679		
MC	0.02001	0.01021	-0.03562	-0.05007	-0.00046	0.06540	

Table 6 Genetic differentiation between populations for the control region marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a sampling site (WAD -Western Abu Dhabi, AD -Abu Dhabi D -Dubai, UQ -Um al quwain, MD – Musandam, F – Fujairah, MC- Muscat). P value < 0.05 given in bold.

Control region Population Pairwise Fst							
	WAD	AD	D	UQ	MD	F	MC
WAD							
AD	0.03780						
D	0.01336	**0.09323**					
UQ	0.02049	-0.04354	-0.00684				
MD	0.03666	-0.04782	0.02429	-0.06453			
F	-0.06671	-0.00540	0.02514	-0.04284	0.02813		
MC	0.05910	**0.13143**	-0.02349	0.01557	0.04954	0.09030	

Table 7 Genetic differentiation between populations for the 12S marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a sampling site (WAD -Western Abu Dhabi, AD -Abu Dhabi D -Dubai, UQ -Um al-Quwain, MD – Musandam, F – Fujairah, MC- Muscat). P value < 0.05 given in bold.

12S Population Pairwise Fst							
	WAD	AD	D	UQ	MD	F	MC
WAD							
AD	**0.22222**						
D	-0.03604	**0.15344**					
UQ	0.01961	0.05149	-0.01740				
MD	-0.04468	0.10104	-0.04254	-0.04601			
F	0.03386	**0.11302**	0.01154	-0.01115	-0.00980		
MC	0.06173	0.06085	0.02778	-0.02469	-0.01511	-0.00336	

Hypothesis testing

To test the hypothesis of population differentiation between the Arabian Gulf and the Gulf of Oman, as proposed to be separated by the Strait of Hormuz the pairwise F_{ST}s are shown. Little to no population structure was revealed between the regional groupings (Arabian Gulf, Strait of Hormuz, Gulf of Oman) in all markers (Table 8, 9, 10). Values of pairwise F_{ST}s were predominantly under 0.05, and there were no significant departures from 0 showing a lack of structure been the grouped areas.

Table 8: Genetic differentiation between populations for the COI marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a several sampling sites (Arabian Gulf= Western Abu Dhabi, Abu Dhabi, Dubai, Strait of Hormuz = Um al quwain, Musandam, Fujairah, Gulf of Oman= Muscat). P value < 0.05 given in bold.

COI Population Pairwise Fst			
	Arabian Gulf	Strait of Hormuz	Gulf of Oman
Arabian Gulf			
Strait of Hormuz	-0.01619		
Gulf of Oman	-0.03704	-0.01083	

Table 9: Genetic differentiation between populations for the control region marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a several sampling sites (Arabian Gulf= Western Abu Dhabi, Abu Dhabi, Dubai, Strait of Hormuz = Um al quwain, Musandam, Fujairah, Gulf of Oman= Muscat). P value < 0.05 given in bold.

Control region Population Pairwise Fst			
	Arabian Gulf	Strait of Hormuz	Gulf of Oman
Arabian Gulf			
Strait of Hormuz	0.01968		
Gulf of Oman	-0.03704	-0.01083	

Table 10: Genetic differentiation between populations for the COI marker. Pairwise F_{ST} calculated using Arlequin comparing *Lutjanus ehrenbergii* populations. Each population represents a several sampling sites (Arabian Gulf = Western Abu Dhabi, Abu Dhabi, Dubai, Strait of Hormuz= Um al quwain, Musandam, Fujairah, Outside = Muscat). P value < 0.05 given in bold.

12S Population Pairwise Fst			
	Arabian Gulf	Strait of Hormuz	Gulf of Oman
Arabian Gulf			
Strait of Hormuz	-0.00689		
Gulf of Oman	0.00234	0.01147	

3.2 Environmental analysis and characterisation of the 'filter' hypothesis

3.2.1 Principle Component Analysis

The principle component analysis was used to determine the characteristics explaining differences between the locations, and to determine if there is a distinction between locations. Component 1 accounted for 80% of the variation (Table 11), and the PC1 axis represents an increasing gradient for the features of temperature maximum, salinity minimum, salinity maximum and chlorophyll *a* (Figure 8).

Populations within Western Abu Dhabi, Abu Dhabi and Dubai are characterised by temperature maximum, salinity minimum and salinity maximum. Abu Dhabi is also characterised by chlorophyll *a* minimum. The populations in Um al quwain, Musandam and Fujairah are characterised by temperature minimum and chlorophyll *a* maximum, whilst Muscat is characterised increased temperature minimum and chlorophyll *a* maximum.

Therefore, using the PCA I propose the division between Arabian Gulf, Strait of Hormuz and Gulf of Oman. As the following groupings; Arabian Gulf to contain Western Abu Dhabi, Abu Dhabi, Dubai. The Strait of Hormuz will be grouped as Um al quwain, Musandam, Fujairah. Whilst the Gulf of Oman will contain the population Muscat.

Table 11: Summary of Principle Component Axis Loadings

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6
Standard deviation	2.2111013	0.8986324	0.44225356	0.29988526	0.132286383	0.0217197234
Proportion of Variance	0.8148282	0.1345900	0.03259804	0.01498853	0.002916615	0.0000786244
Cumulative Proportion	0.8148282	0.9494182	0.98201623	0.99700476	0.999921376	1.0000000000

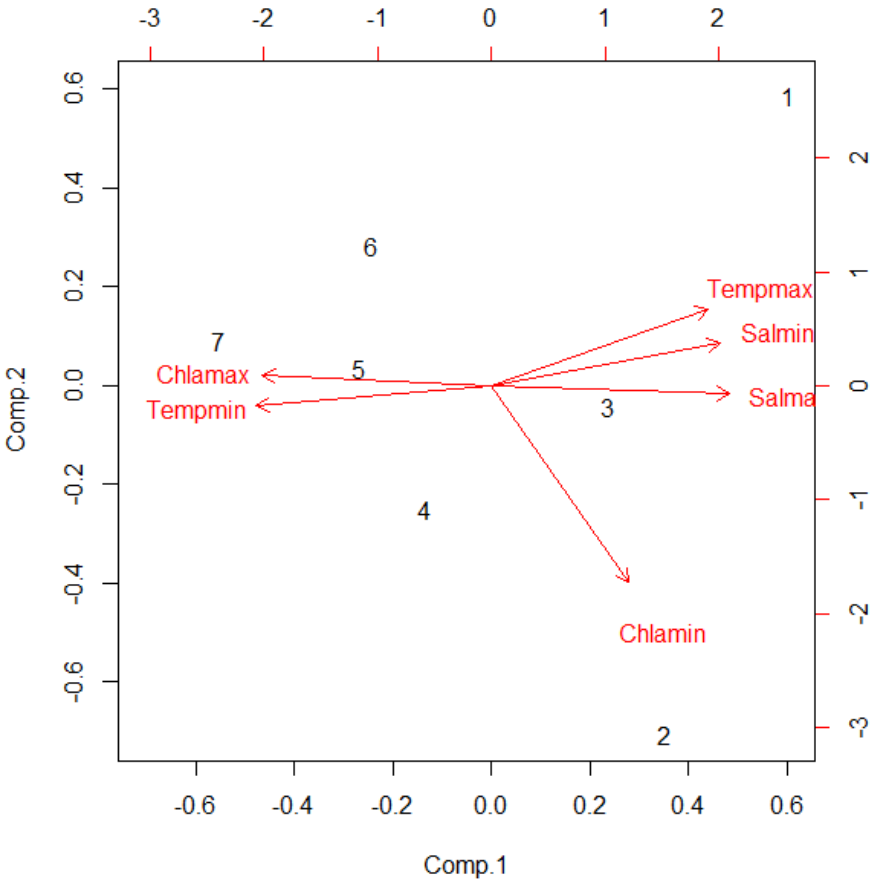


Figure 9: Biplot of PCA

3.2.2 Parameters of sea surface temperature across the Arabian Peninsula

Although mean annual temperature is similar in all sites, at ~27 °C the maximum and minimum temperature at each sites vary moving from the Arabian Gulf, to the Strait of Hormuz and the Gulf of Oman (Table 12). The sites within the Arabian Gulf showed SST reachinh~33°C in the warmest month (August) with 33.97°C at Western Abu Dhabi, 33.55°C Abu Dhabi and 33.33°C at Dubai. In the coldest month (February) the mean sea surface temperatures are variable between Arabian Gulf sites, from 19.76°C in Western Abu Dhabi, 21.39°C in Abu Dhabi and 22.28°C in Dubai. The Arabian Gulf has greater fluctuations in sea surface temperature than in the Strait of Hormuz or the Gulf of Oman. The range in temperature is greatest at Western Abu Dhabi with an annual temperature range of 18.51°C. The range decrease moving along the coastline to the Strait of Hormuz, with the annual range of 15.15°C at Abu Dhabi, 13.96°C at Dubai. In the coldest month the mean sea surface temperature is higher than within the Arabian Gulf, with temperatures of 23.22°C at Ras al Khamiah, 23.31°C for Musandam and 23.52°C at Fujairah. The sea surface temperatures within the Strait of Hormuz are milder and the annual temperature range is reduced at ~10°C. The Gulf of Oman has milder sea surface temperatures than the Strait of Hormuz and is viewed as showing environmental parameters closest to a typical tropical marine ecosystem. The sites within the Strait of Hormuz show lower temperatures than the Arabian Gulf in the warmest month, at 32.23°C in Ras al Khaimah, at 31.74°C at Musandam, and 31.29°C at Fujairah. The Gulf of Oman receives polar water during upwelling events which leads to greater mixing giving milder seasonal changes (Riegl, 2000). The mean sea surface temperature for the warmest month in Muscat was 30.53°C, whilst the mean sea surface of the coldest month was 23.75°C. The range of sea surface temperature at Muscat was smallest at Muscat varying by 9.36°C. T

3.2.3 Parameters of salinity across the Arabian Peninsula

In the Arabian Gulf the mean highest salinity was 41.84psu at Western Abu Dhabi, 40.47psu at Abu Dhabi, 39.83psu at Dubai. The mean highest salinity decreases in the Strait of Hormuz reaching 38 33psu at Ras al Khaimah, 37.94psu at Musandam and 37.29psu Fujairah. The salinity at Muscat is slightly lower than the Strait of Hormuz at 36.82psu. As the mean salinity reduced moving across the coastline from Western Abu Dhabi to Muscat, the range of salinity also reduces. The range of salinity is highest within the Arabian Gulf, at Western Abu Dhabi salinity varies by 5.81psu, at Abu Dhabi the salinity range is 4.43psu, in Dubai

the salinity varies by 4.47psu. In the Strait of Hormuz the salinity range is narrower with variation by 2.83psu at Ras al Khaimah, 1.91psu in Musandam and 1.27psu in Fujairah. The salinity range is lowest in the Gulf of Oman at 0.67psu in Muscat.

3.2.4 Parameters of chlorophyll *a* across the Arabian Peninsula

In the southern Gulf of Oman upwelling brings in cold nutrient rich waters which increase productivity in this area, whilst the Strait of Hormuz and Arabian Gulf have lower chlorophyll *a* in comparison to the Gulf of Oman as shown in Table 12. In the Arabian Gulf the chlorophyll *a* level is lowest, the mean highest chlorophyll *a* is at 0.66 in Western Abu Dhabi, 1.16 at Abu Dhabi, 0.73 at Dubai. In the Straits of Hormuz, the chlorophyll *a* is higher than in the Arabian Gulf, the mean highest chlorophyll *a* is at 2.73 at Ras al Khaimah, 2.81 at Musandam and 3.40 in Fujairah. The highest chlorophyll *a* concentrations are in the Gulf of Oman which is at 6.85. The range of mean annual chlorophyll *a* is narrowest in the Arabian Gulf at 4.41 in Western Abu Dhabi, 5.72 in Abu Dhabi, 4.86 in Dubai. The range increases moving across the Straits of Hormuz reaching 10.54 in Ras al Khaimah, 11.24 in Musandam and 11.49 in Fujairah. The greatest range in chlorophyll *a* is in the Gulf of Oman at 17.41 at Muscat

Table 12: Physical parameters across the Arabian Peninsula. The annual mean, mean of the highest and lowest month and the range is provided for each location for the parameters of temperature, salinity and chlorophyll *a*.

Location	Western Abu Dhabi	Abu Dhabi	Dubai	Ras al Khaimah	Musandam	Fujairah	Muscat
SST (°C)							
Mean annual temperature	27.07 ± (5.25)	27.68 ± (4.63)	27.94 ± (4.29)	27.60 ± (3.66)	27.54 ± (3.39)	27.76 ± (3.23)	27.80 ± (2.91)
Mean coldest temperature	19.76 ± (1.17)	21.39 ± (0.94)	22.28 ± (0.75)	23.22 ± (0.53)	23.31 ± (0.51)	23.52 ± (0.5)	23.75 ± (0.52)
Mean warmest temperature	33.97 ± (0.71)	33.55 ± (0.45)	33.33 ± (0.54)	32.23 ± (0.52)	31.74 ± (0.55)	31.29 ± (0.77)	30.53 ± (0.65
Temperature range	18.51	15.15	13.96	11.95	10.93	10.349	9.396395
Salinity (psu)							
Mean annual salinity	41.80 ± (1.16)	40.72 ± (0.79)	39.77 ± (0.95)	38.27 ± (0.61)	37.49 ± (0.46)	37.09 ± (0.26)	36.71 ± (0.14)
Mean highest salinity month	41.84 ± (1.36)	40.47 ± (0.69)	39.83 ± (0.74)	38.33 ± (0.43)	37.94 ± (0.30)	37.29 ± (0.23)	36.82446 ± (0.09)
Mean lowest salinity month	41.62 ± (0.77)	41.20 ± (0.81)	40.34 ± (0.92)	38.26 ± (0.28)	37.29 ± (0.11)	37.00 ± (0.15)	36.53 ± (0.07)
Salinity range	5.81	4.43	4.47	2.82	1.91	1.27	0.67
Chlorophyll-a (mg m)							
Mean annual chl-a month	1.11 ± (0.75)	1.70 ± (0.81)	1.19 ± (0.74)	2.61 ± (2.01)	2.30 ± (2.11)	2.06 ± (1.94)	2.25 ± (3.15)
Mean lowest chl-a month	0.66 ± (0.10)	1.16 ± (0.16)	0.73 ± (0.12)	2.73 ± (0.97)	2.81 ± (1.55)	3.40 ± (2.52)	6.85 ± (5.10)
Mean highest chl-a month	0.54 ± (0.11)	1.81 ± (0.49)	0.90 ± (0.19)	1.33 ± (0.87)	0.69 ± (0.20)	0.49 ± (0.19)	0.30 ± (0.16)
Annual chl-a range	4.41	5.72	4.86	10.54	11.24	11.49	17.41

3.3 Larval dispersal pattern and retention

The results from the larval dispersal model present a picture of high self-recruitment in the Arabian Peninsula. Whilst low levels of larval dispersal were found in the neighboring populations of Western Abu Dhabi and Abu Dhabi, and Muscat and Fujairah. There was a lack of long distance dispersal between populations far apart, with no larvae moving past their neighboring populations (Figure 10).

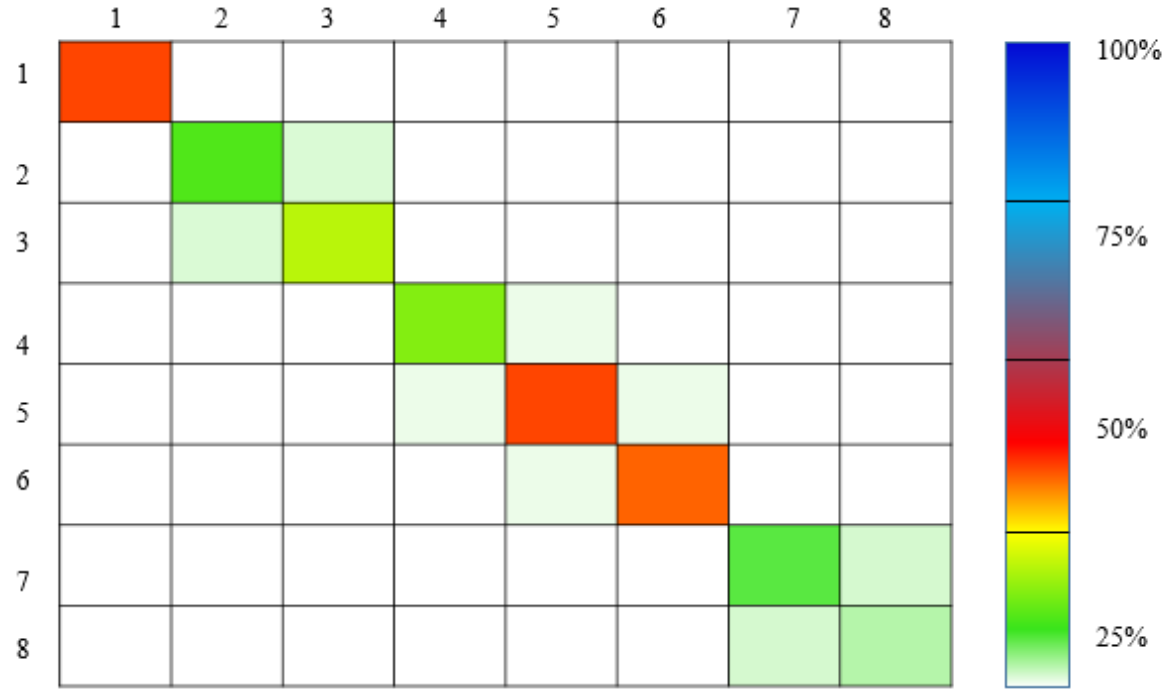


Figure 10: Larval connectivity matrix. The proportion of larvae found in each retention area from the larval released from each sites.

The areas of lowest recruitment were Musandam (S7) and Fujairah (S8) which contained 10.33% and 4.87% respectively. The areas of highest local recruitment were Western Abu Dhabi (S1) with 36.09%, Dubai (S5) with 35.94% and Um al-Quwain (S6) with a retention of 35.64% of the total larvae released. All other sites recruited between 10% - 20% of the total larvae originally released from each source. The maximum potential distance moved varied considerably between locations as shown in Table 13, with the longest dispersal capability in larvae originating from Musandam (S7) and Fujairah (S8), with maximum distance travelled at 140km and 124km respectively. The shortest maximum distance travelled was at Abu Dhabi (S4) travelling 39km, and Um al-Quwain (S6) travelling a maximum of 49km.

Table 13**:** Larval release sites and proportion of larval in retention area at end of model run

Source Areas		No. sites Release	N. of Particle released	Retention Areas (N. of Particles)	Retention Areas (%)	Max distance travelled (km)
S1	WAD	3	1600000	577515	36,09	63,267
S2	AD	3	1600000	214896	13,43	77,223
S3	AD	3	1600000	340935	21,31	112,536
S4	AD	3	1600000	272240	17,02	39,367
S5	D	3	1600000	575015	35,94	94,796
S6	UQ	3	1600000	570078	35,63	49,991
S7	MD	3	1600000	165320	10,33	140,182
S8	F	3	1600000	77953	4,87	124,451

Limited connectivity was found between neighboring source sites, with less than 2% of the larvae released from each site being shared between neighboring sites as shown in Table 14. Connectivity occurred between Abu Dhabi (S2) and Abu Dhabi (S3), Abu Dhabi (S4) and Dubai (S5), Dubai (S5) and Um al quwain (S6), and Musandam (S7) and Fujairah (S8).

Table 14: Larval connectivity between neighboring sites. The release sites and proportion of larval shared between area at end of model run.

Source Stations		Particle released	Retention Areas (Particles)	Retention Areas (%)
S2 - S3	AD - AD	3200000	22154	1,38
S4 - S5	AD -D	3200000	7101	0,44
S5 - S6	D -UQ	3200000	5000	0,31
S7 - S8	MD - F	3200000	22212	1,39

The plot of wind speed during the time period of the model run (Figure10) shows that wind speed rose to highest of 10m/s. There were no abnormalities or sharp increases in wind speed signifying an absence of severe storms or shamal events, characterised by increase in wind speed of over 20 m/s.

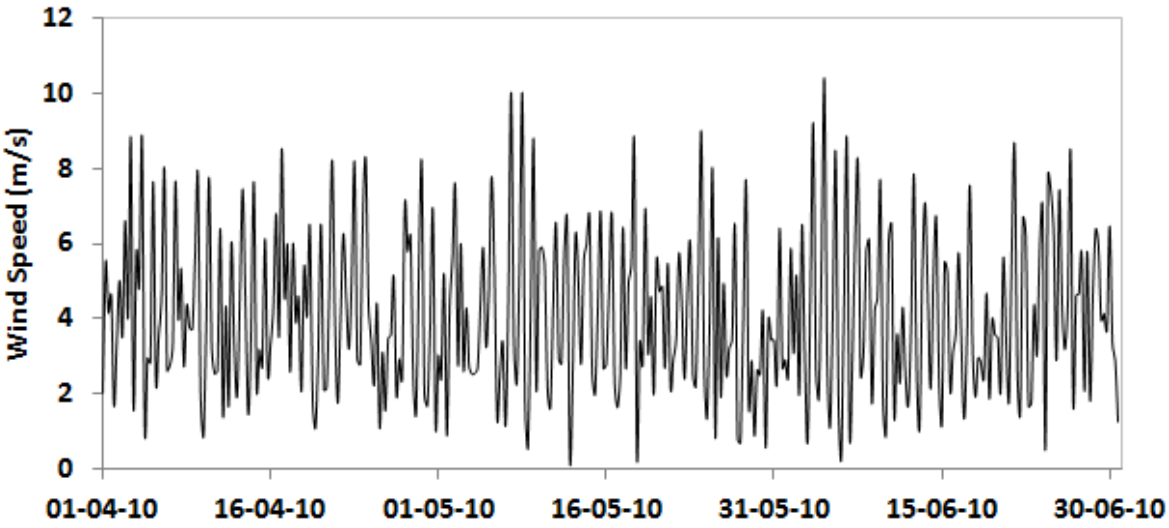


Figure 11: Wind speed across Arabian Gulf during the model run time.

Chapter 4 DISCUSSION

4.1 Evidence for the presence of a 'filter' separating the Arabian Gulf from the Gulf of Oman

The environmental conditions across the Arabian Peninsula follow an environmental gradient which supports the possibility that the Strait of Hormuz acts as an intermediate area between the Arabian Gulf and the Gulf of Oman. The Arabian Gulf showed the highest and lowest values in both temperature and salinity, with the widest range in these parameters. The environmental characteristics of the Gulf of Oman showed narrower variability with a milder temperature and salinity range, but with the highest chlorophyll *a* levels across the Arabian Peninsula. The Strait of Hormuz had a profile of temperature, salinity and chlorophyll *a* conditions between those of the Arabian Gulf and the Gulf of Oman. The idea of a 'filter' or an environmental transition zone in the Strait of Hormuz has been characterised through the environmental analysis. The area of Muscat is near an area of upwelling, which causes temperature to be more stable in this area, in comparison to inside the Arabian Gulf. It has been considered that the upwelling at the Southern Gulf of Oman coast acts as an area of 'thermal refugia' (Rezai, 2004) in that it presents area with a more stable temperature profile. The environmental analysis presented that the Muscat area had a narrower range of temperature and salinity, which would fit into the perspective that this area is an area of thermal refugia.

4.2 Pattern of genetic spatial structure in *L.ehrenbergii* across the Strait of Hormuz

This thesis examined the pattern of population structure in *L.ehrenbergii* across the Arabian Peninsula and found that predominantly a pattern of high genetic similarity existed across the region. Although the environmental analysis provided evidence to suggest an environmental gradient between the Arabian Gulf and the Gulf of Oman, little significant population differentiation was found between the Arabian Gulf, the Strait of Hormuz and the Gulf of Oman. The hypothesis of an environmental filter structuring populations genetically can be rejected and instead this work can be interpreted as an overall pattern of connectivity between populations of *L.ehrenbergii* from the southern Arabian Gulf to the northern Gulf of Oman. There is also evidence that there are fine scale differences between populations in terms of haplotype frequency and in clade mapping.

The filter hypothesis which predicted a barrier to gene flow across the Strait of Hormuz can be rejected as the populations show little genetic differentiation between the population groupings of the Arabian Gulf, Strait of Hormuz and Gulf of Oman. The pairwise FST values were predominately non-significant and showed a lack of significant departure from 0 among localities, distinctive of a lack of population differentiation across sampled populations. These results signify the presence of genetic homogeneity between populations, which would imply that there is sufficient gene flow between populations to counteract genetic divergence between populations (Gibson, Atkinson, & Gordon, 2009). In many Lutjanidae species similar patterns showing a lack of population structure have been found, such as in the Northern Red snapper, *Lutjanus campechanus* (Pruett, Saillant, & Gold, 2005), the yellowtail snapper, *Ocyurus chrysurus* (da Silva, Sampaio, Schneider, & Gomes, 2016), and the Red snapper *Lutjanus purpurues* (da Silva et al., 2016; Gomes, Sampaio, & Schneider, 2012). This is often attributed to the high fecundity and swimming capability of lutjanid larvae.

The haplotype mapping showed high haplotype diversity, with a large proportion of unique haplotypes which were isolated to a single population. Although there was haplotype sharing across all sites, there was also a high degree of haplotypes found only at a single site. There were also many haplotypes that were shared across only a few sites. The sharing of haplotypes did not just occur between neighbouring sites but could occur between populations that are widely spaced. Although an overall picture of haplotype sharing occurred there were population differences in the frequency of haplotypes, which showed a pattern that could be considered as non-random. This pattern could present differences in haplotype frequency because of haplotype loss between sampling locations. Although overall there is little to no genetic differentiation between locations, the clade mapping presented 3 out of 9 clades which showed geographical restriction. The Clade 1A and 2F were restricted to only the Arabian Gulf, whilst Clade 2C only occurred in sites within the Strait of Hormuz. This also points towards the idea that although no significant genetic differentiation occurred there is a degree of differences in haplogroups which show geographical restriction.

The populations that do share haplotypes, or clades were found across the most distant locations (~600km) which suggests that there has been, or may continue to be gene flow between *L. ehrenbergii* populations. The scale of spatial genetic structure can vary considerably between species. In the three spot reef fish, *Dascyllus trimaculatus*, the amount of genetic differentiation was determined around an island, between island archipelagos, and across a greater

geographical distance across the Indo-Pacific (Bernadi *et al.* 2001). Strong population structure was only found at the highest level of spatial distance, and in my study of the Arabian Peninsula the distance between sites may not be considered far in terms of marine connectivity. In lutjanid species genetic structure can be present at distances of over thousands of kilometres (Bernal-Ramirez et al. 2003). This project could be continued to extend the sampling area to consider how the populations within the Arabian Peninsula fit into the population structure across the Indo-Pacific or into a global distribution. The inclusion of a sample from the Red Sea and from Australia in COI tree building hints that there is the possibility for haplotype sharing between the Arabian Gulf and the Red Sea. Whilst the sequence from *L.ehrenbergii* from Australia showed strong support to be designated as a separate group to the samples collected. A full sample set from far spread locations would be required to fully understand population structure across an increased geographic area. The COI tree would suggest that this would be a fruitful area to pursue for further analysis with samples from a global distribution.

Although *L.ehrenbergii* presents high genetic similarity across the Strait of Hormuz the direction of gene flow still needs to be determined and may show that the Strait of Hormuz causes restricted gene flow in a single direction. The Red Sea can be used as a comparison to the Arabian Gulf as it is similarly an enclosed body of water restricting water inflow, which also has an environmental gradient across the region. The gene flow in in the lionfish, *Pterois miles,* was revealed to flow unidirectionally towards the Northern Red Sea and the Gulf of Aqaba, proposed to be due to oceanographic circulation (Kochzius & Blohm, 2005). In the anemonefish, *Amphiprion bicinctus*, across the Red Sea a pattern of a stepping stone model of gene flow occurred, with difference across environmental gradient moving from South to Northern Red Sea (Nanninga et al., 2014). The direction of ocean circulation can influence gene flow in panmitic populations, as well as environmental gradients. A lack of population structure was revealed across a 1300km stretch of African coastline for the goby, *Caffrogobius caffer*, but unidirectional gene flow was found suggesting some populations are effectively isolated (Neethling, Matthee, Bowie, & von der Heyden, 2008).

A further consideration of this work is that is currently considers mitochondrial markers, which are uniparentally inherited. The data presented only considers the female populations level of genetic differentiation and gene flow. Sex-biased dispersal can occur whereby one sex shows site fidelity, known as philopatry, whilst the other sex disperses to alleviate competition (Moritz, 1987). Sex biased dispersal has been well documented in mammals and birds, and in

marine systems has been noted particularly in sharks (Portnoy et al., 2015). This pattern has not yet been documented in reef fishes and receives little attention. A case of sex bias in dispersal has not been observed in lutjanids using genetic markers whilst in the case of *L.kasmira* the mitochondrial and nuclear markers showed similar patterns of genetic divergence (Gaither, 2010). The movement of L.*ehrenbergii* has been focused on juvenile movement and has not yet considered differences in male and female patterns of dispersal. The presence of sex biased dispersal could be determined by comparing nuclear and mitochondrial markers (Moritz, 1987; Prugnolle, 2002). In further work on *L.ehrenbergii* comparing this work to nuclear data could determine whether sex bias dispersal is occurring.

4.3 Presence of localised genetic structure *L.ehrenbergii* acorss the Arabian Peninsula

Whilst the overall pattern of genetic differentiation between pairwise populations showed little genetic differentiation, there is evidence that population structure occurring between some sites. In lutjanids such as *Lutjanus kasmira* and *Lutjanus fulvus* a pattern of large scale connectivity has been inferred alongside some degree of population differentiation at a few sites across the Indo-Pacific (Gaither et al., 2010). In marine systems, the presence of non-geographically related pockets of genetic structure has been noted to exist, and is termed chaotic genetic patchiness. The existence of genetic patchiness can be due to temporal changes in population structure, and this may be linked to stochasticity in larval movements over time (Selkoe, 2006). The modelling of larval distribution has shown to be variable between seasons, and between years and this is proposed to add an element of variability in population structure (White, 2010). Whilst the larval dispersal model showed high self-recruitment, no shamals were present during the running period of the model. Yet it is known that shamals can occur that could temporarily enhance larval movement and could be further analysed as a potential driver of genetic patchiness observed in this study. The role of sweepstake recruitment is also considered to influence the presence of patchiness in genetic structure (Hellberg, 2009). Sweepstake recruitment refers to how marine organisms produce a larger quantity of offspring, and have high mortality rates which can lead to a few individuals contributing to much 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 (Selkoe, 2006). Therefore, the presence of patchy genetic differentiation may be due to temporal variation due to circulation, or may be due to uneven genetic contribution of successful larvae.

The clade mapping from the concatenated sequences found that there is a high proportion of clades which were widespread across the Arabian Gulf to the Gulf of Oman. However, there are some clades composed of few rare haplotypes which seem to show some degree of spatial restriction. Clade 1A is restricted to only the Arabian Gulf and Strait of Hormuz in the sampling, however is a clade that is present in a distant area of the Red Sea. Clade 2F is found within the Arabian Gulf populations of Western Abu Dhabi and Abu Dhabi. Clade 2C is found in the sites of the Strait of Hormuz at the sites Um al quwain, Musandam and Fujairah. The designated clade groupings could be subject to adjustment depending on the stringency and parameters of defining a clade group. Some clade groupings also consist of few rare haplotypes, and therefore larger sampling could find the presence of these haplotypes at additional locations. If this was the case it is still important to note that there are certainly differences in the frequency of clades between locations.

4.4 Demographic history in *L.ehrenbergii*

The demographic changes in all populations showed deviations from the expectations under a model of neutrality, and point towards to possibility of a bottleneck, population expansion or a signature of purifying selection (Grant & Bowen, 1998). In a population that has undergone a bottleneck the expectation is that there would be low nucleotide diversity, high haplotype diversity, negative Tajima's D, and negative Fu's F; all characteristics of the populations sampled within the present study. In a genetic bottleneck event a large proportion of haplotypes are lost, then as the population recovers and expands new mutations stay in the population rather than being lost increasing haplotype diversity (Hedrick, 2011). The high haplotype diversity, and the presence of star-like networks also suggest that a bottleneck has occurred.

4.5 A signature of historical or contemporary connectivity in *L.ehrenbergii*?

The pattern of genetic structure examined in this study could be representing contemporary patterns of gene flow, or it may be a reflection of historical patterns of gene flow (Benzie, 1999). Distinguishing between past and present patterns of population structure is difficult and the effect of past dispersal can mask present population isolation, or restrictions to movement. Alternatively historical barriers can influence present population structure, known as the ‘ghost of landscape past’ (Landguth et al., 2010), which can be considered in relation to the ‘ghost of dispersal’ past. Past population structure can be considered to be lost over several hundred generations, and is lost at a faster rate when dispersal potential is high (Landguth et al., 2010).

The presence of shared haplotypes, and low genetic differentiation between distant conspecific populations can be indicative of gene flow occurring recently in evolutionary time, whilst it might be due to historical movement, and subsequent gene flow. The lack of high genetic differentiation could possibly be reflecting the historical movement of *L.ehrenbergii* from the Indian Ocean into the Arabian Gulf. The reef associated fish biodiversity inside the Arabian Gulf is comprised entirely of fish species that colonised the region from the Indian Ocean between 6,000 to 9,000 years ago (Riegl, 2012). Before this time the Arabian Gulf was dry, and the basin was an area where humans settled before being forced to move as it began to flood (Teller, 2000). The recent colonisation of the Arabian Gulf poses the question of whether enough time has passed to view genetic differences between populations, independent to if population subdivision has occurred. The pattern of low genetic differentiation may therefore be reflective of historical movement of *L.ehrenbergii* into the Arabian Gulf. The sharing of the clade 1A with the Red Sea could be the result of ancestral movement, whereby not enough evolutionary time has passed for genetic differentiation to have occurred between populations. The Red Sea is older than the Arabian Gulf and contains species that would have originated from the Indian Ocean, and so would expect to have a potentially historical connection between these areas. The movement of individuals between the Red Sea, the Arabian Gulf, the Indo-Pacific and the West Indian Ocean does occur, and evidence shows an area of hybridisation occurs where these four regions meet (DiBattitsta, 2015). This suggests that widespread movement of marine fish is still occurring between these regions. Alternatively, there may be a break in connectivity between the Red Sea and the Arabian Gulf in which clade 1A could be an ancestral clade, and its absence in from Fujairah and Muscat is due to differing frequencies between the Gulf of Oman and the Arabian Gulf over time. The work of Priest (2015) concluded that populations of the yellowfin hind grouper, *Cephalopholis hemistiktos*, between the Gulf of Oman and Arabian Gulf were isolated from the Red Sea. Yet one shared nuclear haplotype between the regions was found, as the marker was suggested to be in the process of segregating. Therefore, it cannot be definitive that there is genetic connectivity with the Red Sea based on a single haplotype in the Red Sea. Therefore, more sequences to make a full population would be required to make conclusions about the connectivity or isolation with the Red Sea, and would give an idea of whether the observed pattern is due to historical or contemporary connectivity.

4.6 Contemporary larval distribution in the Arabian Peninsula

The larval dispersal model provides a preliminary description of the potential movement and larval connectivity across the Arabian Peninsula due to oceanographic circulation in this region. In this study the results from the larval dispersal component showed that local recruitment dominated with a small degree of larval connectivity between neighbouring populations. This result did not reveal a restriction of larval movement in one direction, or a restriction of larvae across the Strait of Hormuz. Yet the larvae reaching the Strait of Hormuz retention sites showed some of the lowest levels of larval concentrations. Although the results of the larval model are not specific for *L.ehrenbergii* they give an idea of potential movement. In members of the Lutjanidae family have characteristically fast swimming larvae therefore demographic connectivity may be potentially enhanced by swimming ability. As considered earlier the oceanographic circulation pattern can vary over time, and this can lead to changes in connectivity, reflecting changes in adult and juvenile movement which can cause genetic patchiness. In the current model a snapshot of a single spawning season is present, and this may be variable between different years. For example rare climatic events have the potential to alter dispersal (R. K. Cowen, 2000), and few movements are sufficient to homogenize populations and prevent genetic differentiation from occurring (Hedrick, 2011). In the Arabian Gulf infrequent yet strong winds known as shamals occur from November to March and June to August, which overlaps with the spawning season of *L.ehrenbergii*. Shamals influence fluctuations in water temperature and salinity, as well as driving changes in circulation patterns (Cavalcante, Feary, & Burt, 2016). The winds are temporary but have a significant effect by changing circulation patterns in the Arabian Gulf (Aboobacker, Vethamony, & Rashmi, 2011). During the course of the model no shamals, or anomalous wind events occurred. Yet it has been predicted that shamal events have the possibility to greatly enhance the potential movement of coral larvae by up to 35km which has been predicted to lead to high patterns in connectivity of corals (Cavalcante et al., 2016). Therefore, there is the possibility that the variability between years, and the occurrence of shamals may increase the likelihood of rare long distance dispersal events. In both modelling and physical measuring of larval dispersal, the dynamic and stochastic nature of larval movement can be difficult to characterise, yet can provide a major role in the pattern of genetic connectivity.

4.7 Implications of population connectivity in presence of environmental gradient

Biogeographical breaks can have a greater influence on some species over others, such as the lack of a genetic break in *Lutjanus kasimira* compared to *Lutjanus fulvus* across the Indo-Pacific Barrier (Gaither et al., 2010). There is the possibility that the environmental gradient across the Strait of Hormuz may impact certain species more than others, particularly considering many species present in the Gulf of Oman are absent from the Arabian Gulf, suggesting that some species are unable to survive within the Arabian Gulf. Coral reef fish inhabiting the Arabian Gulf have been predicted to live near the upper limits of their thermal capacity (Price et al., 1993). The tolerance window of coral reef fish larvae is narrower than in adults. Therefore, coral reef fish larvae may play an important role in restricting movement between the Arabian Gulf and the Gulf of Oman, as the environmentally sensitive larvae may exhibit mortality moving across the environmental gradient through the Strait of Hormuz in some species. Infrequent extreme weather events are important in the Arabian Gulf as these increase temperature and salinity are implicated in the survival and temperature thresholds of marine life. In the Arabian Gulf severe shamals, and environmental disturbances have been linked to mass coral death (Cavalcante *et al.* 2015;Coles & Riegl 2013)), and are considered to influence biodiversity, leading to variability in fish assemblage structure (Ghazilou, Shokri, & Gladstone, 2016). The mechanism behind coral resilience to heat is unknown, yet one proposal is that exposure to unstable temperatures may play a role in increasing the potential survival to further elevations in temperature. The lowest and highest temperature fluctuations lead to repeated coral deaths in the Arabian Gulf, known as hot-kills and cold-kills, which have both been attributed to lead to corals adapted to a greater tolerance window rather than specifically hot or cold specialised corals (Riegl & Purkis, 2012). Experimentally stressing coral thermal tolerance has found that prior exposure to variable environments can enhance thermal tolerance, such as seen in *Acropora hyacinthus* and in *Acropora aspera* (Middlebrook, Hoegh-Guldberg, & Leggat, 2008; Oliver & Palumbi, 2011). Corals that have naturally undergone variable conditions over many generations show higher resilience to elevated temperatures, such as coral *Pocillopora damicornis* from upwelling versus non upwelling areas showing different responses (D'Croz & Maté, 2004). The organisms in the Arabian Gulf have been proposed to have resilience to survive in an environmentally stressful and unstable area. The presence of genetic similarity between *L.ehrenbergii* populations in the Arabian Gulf and the Gulf of Oman presents that then Arabian Gulf fish populations may be showing plasticity in

their responses to an environmentally challenging environment rather than being genetically distinct. *Symbiodinium thermophilium* is a zooxanthellae partner that is adapted to both heat and salinity tolerance (Hume *et al.* 2015) and its adaptation to thermal tolerance is considered to have arisen from the attributes of an ancient and widely distributed group (Hume *et al.* 2016). *S. thermophilium* was revealed to be distributed in the Arabian Gulf and the Gulf of Oman, but was distinct to other areas (D'Angelo *et al.* 2015). The researchers conclude that the Gulf of Oman could present an area whereby selection occurs on preadapted traits. The genetic connectivity of *L.ehrenbergii* is seemingly unaffected by the environmental gradient, and in light of the work on coral the suggestion could be made that the Gulf of Oman provides a site where traits are selected for which can survive in the Arabian Gulf. The physiological or behavioural mechanisms by which Arabian Gulf *L.ehrenbergii* can survive and tolerate the extreme salinity and temperature is yet to be elucidated. The ability to survive in this extreme area could be due to phenotypic plasticity and acclimation. In the USA the spatial distribution and abundance of the grey snapper, *Lutnaus griesus*, is predominantly caused by cold temperatures in winter leading to high overwinter mortality (Wuenschel, Hare, Kimball, & Able, 2012).

4.8 Implications for conservation and management of *L.ehrenbergii*

The reduction of genetic diversity puts populations at higher risk to extinction, and reduces their capacity to adapt to environmental change (Frankham *et al*. 2004). The loss of biodiversity is occurring at an unprecedented speed, and marine environments are particularly vulnerable because of overfishing, habitat loss and the effects of climate change. The Arabian Gulf is an area facing anthropogenic stressors, as well as the natural environmental challenges (Rezai, 2004). Particularly damaging has been the large-scale development activities in the area which has led to habitat loss through reclamation and dredging (Naser, 2014). The Arabian Gulf has also been subjected to pollution from desalination plants, industrial chemical waste, and oil spills (Naser,2014). As climate change continues sea surface temperature will increase but the coral reefs of the Arabian Gulf are already considered to be showing detrimental effects with increased frequency of bleaching events. Whilst the marine organisms inside the Arabian Gulf are currently surviving whilst facing extremes of high and low temperatures, it is considered that Arabian Gulf organisms are living near the upper threshold of their tolerance. Therefore, being able to survive in a currently extreme set of environmental conditions does not necessarily preclude that Arabian Gulf organisms will be able to respond to increasing

temperatures in the future, particularly at the speed of change. However, some researchers have an optimistic view that marine organisms being subjected to stress will provide an area where juveniles with higher resilience will be produced, with the ability to move to and colonise nearby areas facing temperature increases (Riegl, 2003).

The findings of this study show a pattern of high genetic diversity and predominantly low genetic structure. The presence of high genetic structure, isolating populations, could lead to the loss of genetic diversity. Therefore this work suggests that high gene flow could be occurring and therefore the *L.ehrenbergii* populations across the Arabian Peninsula are not at a high risk of genetic loss. In terms of managing the population the presumed connectivity would suggests the population could potentially be considered as a single unit.

4.9 Future work

As a pattern of some non-spatially occurring structure was found, this would either be that there is some level of structure, or that genetic patchiness is occurring. To differentiate which of these explanations best represents the genetic structure in the Arabian Gulf further analysis of population could take place using a marker with higher sensitivity to detect genetic variation such as microsatellites. When this project began there were no microsatellites developed for *L.ehrenbergii* and their development went outside the scope of this project. However mitochondrial DNA has been shown to be able to find genetic structure in lutjanid species, and considering the youth of the Arabian Gulf microsatellites may not be able to reveal genetic structure. Some researchers measure genetic population structure over a period of years to view the temporal variation alongside any patterns of spatial structure. Long term monitoring of population structure can help elucidate the overall pattern of genetic structure when chaotic genetic patchiness occurs.

To determine if a pattern of geographic restriction in the clade 1A exists adding more populations inside the Arabian Gulf as well as outside beyond Muscat, potentially in the Red Sea would help resolve the pattern of clade 1A distribution. This could also answer a potential next question of whether the Arabian Gulf and Gulf of Oman populations are genetically connected or distinct to the wider region across the Indian Ocean.

The larval dispersal model provides a starting point to understand how the oceanography of the region can potentially move larvae inside the Arabian Gulf. As larval dispersal can show stochasticity over time it could be beneficial to extend the model run time over several years,

to view how the pattern changes over time and to detect any potential wide dispersal events if they were to occur.

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