

**Arabian Albulids: genetic diversity and life history characteristics  
of bonefish in the Saudi Arabian Red Sea**

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**EXAMINATION COMMITTEE PAGE**

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**ABSTRACT****Arabian Albulids: the genetic diversity and life history characteristics of bonefish in the Saudi Arabian Red Sea**

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The genus *Albula* includes marine fish species, commonly called bonefish, that occur in tropical coastal ecosystems worldwide. Their association to nearshore marine environments makes bonefish especially vulnerable to habitat loss and overharvest. Artisanal fisheries often harvest bonefish, although, in certain areas, bonefish support lucrative catch-and-release recreational fisheries. Bonefish are largely understudied compared to other economically significant fish species, and the presence of cryptic species within the *Albula* genus has further complicated the establishment of conservation measures. In particular, there is no detailed biological information available on bonefish from the Red Sea despite the unregulated harvest of bonefish that occurs there. To facilitate the establishment of management and contribute to the overall knowledge of *Albula* biology, I assessed the genetic diversity, growth, and seasonal reproduction of bonefish in Saudi Arabia. Based on samples collected from local fish markets and coastal waters, my findings provide the first genetically verified records of *A. glossodonta* in the Red Sea and *A. oligolepis* in the northwest Indian Ocean. Moreover, my results indicate a genetically distinct Red Sea population of *A. glossodonta* that reaches smaller sizes than documented for the species in the Pacific Ocean and exhibits distinct seasonal spawning activity over the winter months. This information enables fishery managers to make informed decisions regarding bonefish size limits and seasonal colures around peak spawning activity. My results

may become increasingly relevant as the potential for lucrative recreational fisheries for *Albula glossodonta* will likely increase with the ambitious Red Sea tourism development plans.

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**LIST OF ABBREVIATIONS**

ctyB	cytochrome B
FL	fork length (distance from tip of snout to end of middle caudal fin ray)
GSI	gonadosomatic index
IUCN	International Union for Conservation of Nature and Natural Resources
M	mass
mtDNA	mitochondrial DNA
PCR	polymerase chain reaction



**LIST OF SYMBOLS**

$\pi$	Nucleotide diversity
$F_{st}$	Fixation index (a measure of population differentiation)
$h$	Haplotype diversity
$K$	Body growth coefficient
$L_{\infty}$	Mean length of an infinitely old fish
$n$	Sample size (number of individuals)
$t_0$	Theoretical age at zero length
$t_{max}$	Maximum age in years

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## Chapter 1

### Introduction

The genus *Albula* (Chordata, Actinopterygii, Albuliformes, Albulidae) includes species of silver-bodied marine fishes, commonly known as bonefish (Fig. 1.1). Highly conserved morphology within *Albula* has created phylogenetic complexities and led to the identification of several undescribed species in recent years (Shaklee and Tamaru 1981; Whitehead 1986; Colborn et al. 2001; Bowen et al. 2007; Hidaka et al. 2008; Pfeiler 2008; Wallace and Tringali 2010, 2016; Kwun and Kim 2011). Bonefish remain in a state of taxonomic revision, and there are now 12 accepted species that occur throughout the world's shallow, tropical marine environments with documented instances of sympatric distributions (Colborn et al. 2001; Bowen et al. 2007; Hidaka et al. 2008; Kwun and Kim 2011).



Figure 1.1: A photographed specimen of *Albula* spp. (Thuwal, KSA 2019).

Bonefish inhabit a variety of coastal habitats, including mangrove systems, seagrass beds, sand flats, and coral reefs. As benthivorous mesopredators, *Albula* species may contribute to the functioning of these ecosystems through bioturbation, as they excavate prey, and trophic connections between the benthos and top predators (Gibson et al. 2001; Marley et al. 2019). Bonefish embark on spawning migrations seasonally, leaving shallow-water habitats to aggregate in large numbers over deep water to spawn (Danylchuk et al. 2011). During these spawning aggregations, *Albula* become particularly susceptible to capture in fisheries.

Primarily, bonefish are targeted by subsistence, artisanal, and recreational fisheries (Ault 2007; Allen 2014; Filous et al. 2019b; Rennert et al. 2019). When harvested, *Albula* typically yield low market values, largely due to the hard structures present within bonefish musculature from which the fish gets its name. Conversely, the speed and elusive nature of *Albula* have made bonefish a highly valued sportfish, supporting lucrative recreational fisheries around the world (Ault 2007). In the Florida Keys, where a recreational fishery for bonefish is strictly catch-and-release, it is estimated that a single bonefish has the potential to contribute up to US\$75,000 to the local economy over the course of its lifetime (Ault et al. 2007). This a stark contrast to the mean value of US\$2.56 paid for harvested *Albula* individuals in Saudi Arabian fish markets (Collin Williams, personal observation). In addition to the Florida Keys, other locations that have banned commercial bonefish harvest have seen substantial economic impacts derived from recreational fisheries, including the Bahamas where this contribution is over US\$141 million annually (Fedler 2010). If managed correctly, the establishment of catch-and-release recreational fisheries for *Albula* may be a viable conservation strategy to reduce

harvest and increase the economic contribution of fisheries (Cooke and Philipp 2004; Cooke et al. 2016).

Conservation measures are important to consider as bonefish are at risk of population declines resulting from overfishing and habitat loss (Beets 2000; Friedlander et al. 2007; Adams et al. 2014). Targeted fishing of spawning aggregations has resulted in decreased abundance and size of bonefish (Beets 2000). For instance, the increased harvest of *Albula glossodonta* in Kiribati was marked by a reduction in catch per unit effort (CPUE) (1977: CPUE =  $3.15 \pm 4.39$ , 1992-93: CPUE =  $0.16 \pm 0.83$ ) and mean fork length (FL, cm) (1977: FL =  $46.4 \pm 4.1$ , 1992-93: FL =  $37.6 \pm 7.3$ ) (Beets 2000). Furthermore, the coastal habitats that bonefish inhabit have experienced global declines and degradation over the past century resulting from anthropogenic activities and climate change (Pandolfi et al. 2003; Giri et al. 2011; Short et al. 2011). As the threats of overharvest and habitat loss persist, *Albula* remain considerably understudied relative to other commercially important groups of fishes.

Of the 12 species in the genus *Albula*, half are listed by the IUCN Red List as data deficient, two are vulnerable or near threatened, one is of least concern, and three have not been formally evaluated (Adams et al. 2014; International Union for Conservation of Nature and Natural Resources 2020). The vast majority of bonefish research, especially investigations of molecular ecology and life history, have been geographically concentrated in the tropical Atlantic and Pacific Oceans (Crabtree et al. 1996, 1997; Pfeiler et al. 2000, 2006; Ault 2007; Donovan et al. 2015; Wallace and Tringali 2016; Filous et al. 2019a; Rennert et al. 2019).

Accordingly, there is a lack comprehensive biological information available on *Albula* stocks in the Indian Ocean (e.g., East Africa, Seychelles, Red Sea).

The Red Sea is a semi-enclosed peripheral basin of the Indian Ocean bordering seven countries. A diversity of marine life inhabits the mangrove and coral reef habitats that are prevalent along the coast of the Red Sea. It is understood that unique environmental and biogeographical features have led to high rates of Red Sea endemism, notably 12.9% in fishes (DiBattista et al. 2016b). Commercialized artisanal fisheries in the Red Sea target a variety of species using handlines and gillnets, often harvesting bonefish as both a target species and bycatch (Tesfamichael and Pauly 2016). Fishery regulations are largely absent throughout the Red Sea, and those that do exist are inadequately enforced (Tesfamichael and Pauly 2016). The establishment of a fishery management framework is hindered in part by the lack of regional-specific biological information on exploited fish species. Specifically, no detailed biological information is currently available in published literature on *Albula* from the Red Sea and the status of bonefish in the region remains unclear.

The specific *Albula* species or number of *Albula* species that occur in the Red Sea have yet to be confirmed with genetic methods. Morphological identification to the species level is inadequate when examining species distributions of most bonefish due to the conserved morphology between cryptic and sympatric species (Colborn et al. 2001; Bowen et al. 2007; Wallace and Tringali 2010, 2016; Wallace 2015). Therefore, genetic species identification is needed to accurately determine which species of *Albula* occur in the Red Sea (Colborn et al. 2001; Wallace 2015).

Two species, *A. glossodonta* and *A. oligolepis*, have been genetically identified in the Indian Ocean, of which only *A. glossodonta* has been documented in the Red Sea via morphological identification (Colborn et al. 2001; Hidaka et al. 2008; Wallace 2015; GBIF 2020). Considering recent changes to *Albula* species delimitations, verification of *A. glossodonta*'s occurrence in the Red Sea is especially significant as it is the type locality of the original species description (Forsskål, 1775, Jeddah, Saudi Arabia). The absence of *A. glossodonta*, the most widely distributed bonefish, in the Red Sea could result in major taxonomic rearrangement (Colborn et al. 2001; Bowen et al. 2007; Wallace 2015). Trends of endemism in the Red Sea and the unique physical environment of the basin warrant further investigation of suggestions from published literature that the Red Sea may harbor a distinct *Albula* lineage (Colborn et al. 2001; Bowen et al. 2007; Wallace 2015; DiBattista et al. 2016a, b).

In addition to the lack of information on the genetic diversity of bonefish in the Red Sea region, no life history data is currently available from the Indian Ocean or Red Sea. Studies focused on the age/growth and reproductive biology of a species enable the establishment of effective fisheries regulations that restrict the harvest of immature individuals and enact seasonal closures around vulnerable spawning times. Because life history characteristics can vary within a species and between locations (Choat and Robertson 2002; Williams et al. 2003; Trip et al. 2008; Berumen et al. 2012; Cappo et al. 2013; Taylor et al. 2018), caution must be taken if using data from other regions (e.g., the South Pacific) as the basis for management decisions. It is much preferred to collect Red Sea-specific life history information if local regulations are to be established for this group of fishes.



The objectives of this work are to contribute to the understanding of *Albula* species distributions in the Indian Ocean and provide the first insight into the biology of bonefish in the Red Sea. I aim to identify I) the occurrence of *Albula* species in the Red Sea using genetic techniques, II) region-specific growth trends of bonefish collected in Saudi Arabia, and III) the seasonal timing of reproduction in Red Sea bonefish. Based upon current species distributions, in the Red Sea, I expect to encounter *A. glossodonta* in sympatry with either *A. oligolepis* or an undescribed species. I further anticipate finding notable differences in growth parameters corresponding to latitudinal gradients within species between the Red Sea and published studies from other locations. However, spawning seasonality is hypothesized to be consistent within species among locations. Ultimately, the results of this study will aid in refining biogeographical uncertainties within the *Albula* genus and provide coastal managers with a comprehensive dataset to support the establishment of a Red Sea fisheries management framework.

## Chapter 2

### Materials and Methods

#### 2.1 Specimen Collection and Processing

Most bonefish specimens utilized in this study were obtained from fish markets, while additional tissue samples were acquired from both field sampling efforts and contributions from collaborating researchers. For all fish collected, length measurements (fork length, FL, mm) were recorded using a tape measure before removing 2 cm<sup>2</sup> of fin tissue from the top lobe of the caudal fin for genetic analysis. Individuals purchased in fish markets were sampled more thoroughly, including measurement of somatic mass (g) and gonad mass (g) as well as the extraction of both sagittal otoliths. Fin tissue was stored in 90% EtOH at -20°C, while otoliths were rinsed with freshwater, dried, and kept in individual envelopes until further analysis.

A total of 304 *Albula* specimens were collected from fish markets in three Saudi Arabian cities along the eastern coast of the Red Sea (Jeddah, Thuwal, and Yanbu) between November 2018 to March 2020 (Fig. 2.1). Fish markets were sampled each month, with the exception of April 2019, and every bonefish encountered was purchased to ensure an accurate representation of the daily catch. Vendors repeatedly assured researchers that bonefish were locally harvested (i.e., landed in one of the respective local catchments of the aforementioned three cities). These claims are supported by the fresh condition of fish encountered and the low value of bonefish, making it unprofitable to transport these fish long distances.

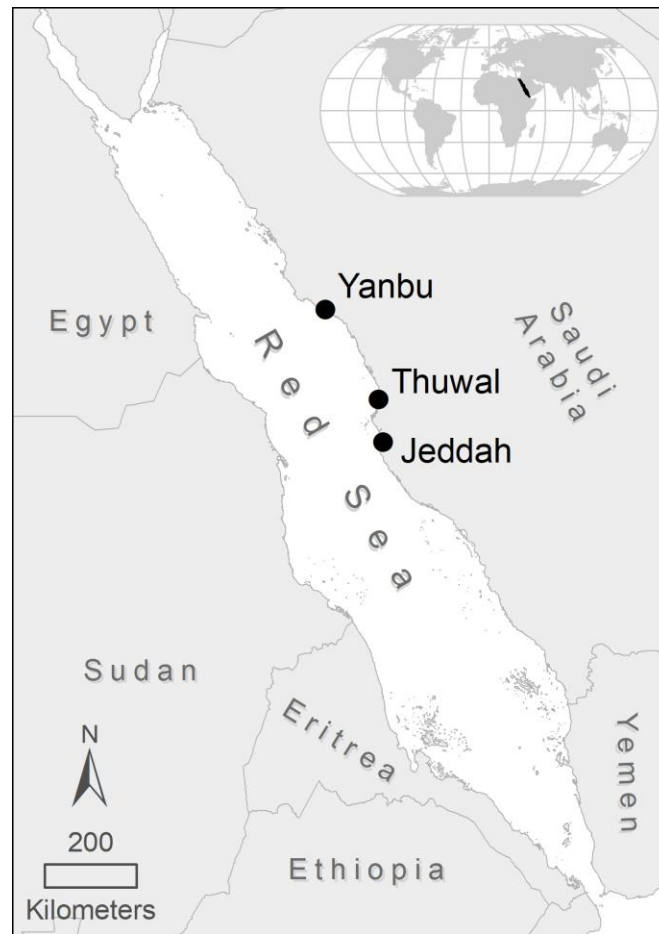


Figure 2.1: Locations of Saudi Arabian fish markets from which specimens of *Albula* spp. examined in this study were collected.

A sample of live *Albula* specimens ( $n=29$ ) were collected to increase the certainty of genetic analyses. Specimens were captured from coastal waters in Thuwal, KSA (Fig. 2.2), using hook-and-line gear (fly tackle or a size 1 hook baited with a live crab, *Metopograpsus messor*) and were released alive after being processed (i.e., FL measurement and collection of a caudal fin tissue sample). Collections occurred exclusively in sandflat environments adjacent to mangroves within 2km of 22.323864, 39.090943 (Fig. 2.2). Fin tissue was taken from the

pectoral fin of one partially preyed upon individual that researchers discovered during collections.



Figure 2.2: Field collection locations of *Albula* spp. on the campus of King Abdullah University of Science and Technology (Thuwal, Saudi Arabia)

Additional *Albula* tissue samples (n=13) were collected by Dr. Joseph DiBattista (Australian Museum, Sydney) from April 2011 to February 2014 (Fig. 2.3) from fish markets in Jeddah, Saudi Arabia, and Hadibo, Socotra Island (Yemen). Additionally, one fish was collected via speargun in the Farasan Banks region of Saudi Arabia (Dolphin Lagoon: 19.088889,

40.380278) (Fig. 2.3). Red gill filaments from each of these additional individuals were stored in 90% EtOH at  $-20^{\circ}\text{C}$ .

Sequences of mitochondrial DNA (mtDNA) from *Albula glossodonta* (n=127) collected in the Indian and Pacific Oceans were provided by Dr. Elizabeth Wallace (Florida Fish & Wildlife Research Institute) (Fig. 2.3). This dataset includes 16 bonefish larvae (i.e., leptocephalus) that were collected via light trap from Molokai, Hawaii, in April 2017. The remaining 111 sequences are associated with individual adult bonefish. Collection information regarding these adult fish is described within Wallace (2015).

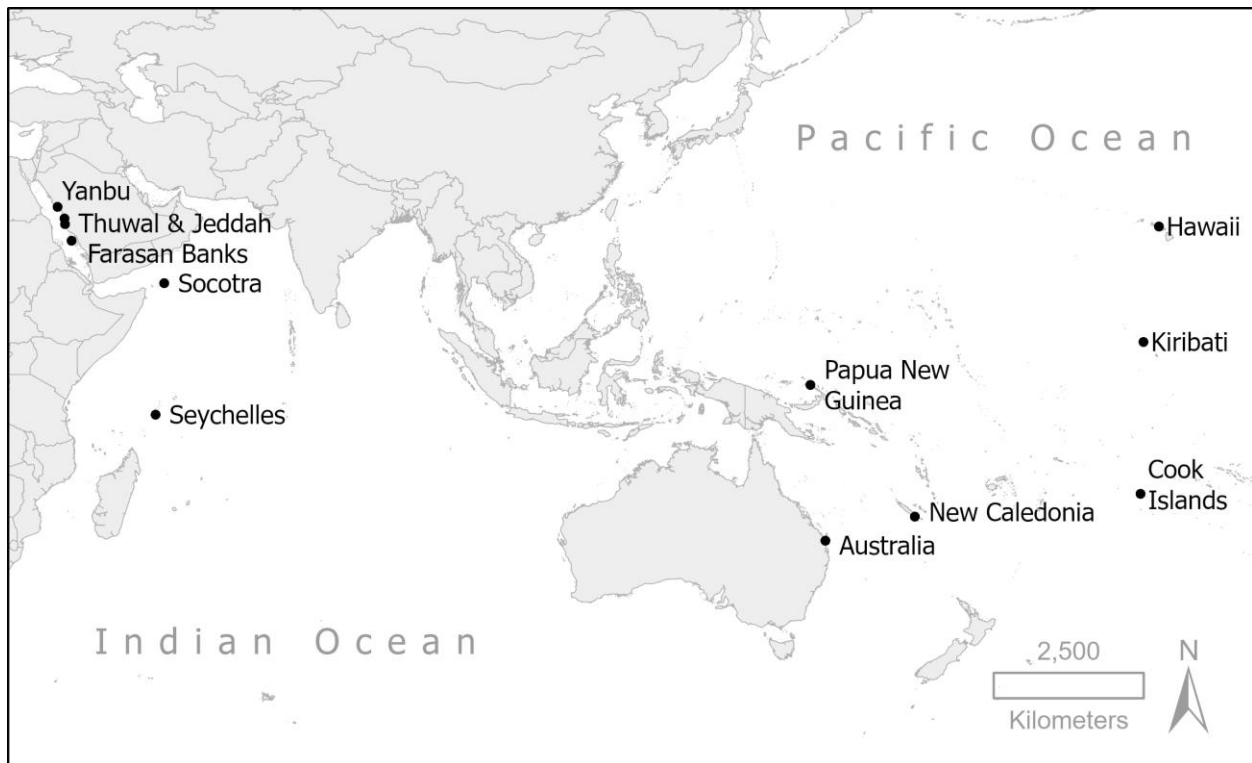


Figure 2.3: Map of locations from which genetic material of *Albula* spp. was analyzed in this study.

## 2.2 Genetic Analyses

Genetic material was extracted from the fin and gill tissues of 323 *Albula* spp from the northwest Indian Ocean with the NucleoSpin® 96 Tissue kit (Machery-Nagel) following the manufacturer's protocols. DNA concentrations were analyzed with a NanoDrop 2000c spectrophotometer (Thermo Scientific).

Polymerase chain reactions (PCR) conducted in SimpliAmp thermocyclers (Applied Biosystems, Thermo Scientific) were used to amplify 568 bp of mtDNA at the cytochrome B region (ctyB). Reactions were carried out in total volume of 15µL containing 2.5µL extraction product, 0.54µL forward primer alb1F (Colborn et al. 2001), 0.54µL reverse primer alb3R (Colborn et al. 2001), 6.8µL Multiplex PCR Master Mix (Qiagen), and 4.62µL RNase-Free Water (Qiagen). Thermocycling began with an initial polymerase heat-activation of 95°C for 15min, followed by 36 cycles of 94°C for 30sec, 55°C for 30sec, and 72°C for 1min 30sec with a single final extension of 72°C for 10min.

PCR products were visualized on a QIAxcel machine (Qiagen) using the QIAxcel DNA Screening kit (Qiagen). Successfully amplified DNA was purified by adding 1.2µL of ExoProStar (GE) to each well before running a single thermal cycle of 37°C for 60min and 85°C for 15min. Sanger sequencing of purified target DNA was conducted using the 3730xl DNA Analyzer (Applied Biosystems, Thermo Scientific).

## 2.3 Age and Growth

### 2.3.1 Otolith Preparation

A subset of 55 *Albula* individuals was used to examine trends of age and growth following general protocols of otolith-derived age estimation (Stevenson and Campana 1992). Collected fish were organized into 11 size classes (5cm FL bins). Five individuals were selected from each bin using a randomized function in Microsoft Excel. Right sagittal otoliths from each fish in the subset were used to estimate an individual's age. If the right otolith was damaged, the left otolith was used.

Otolith cores were marked using a pencil under transmitted light. Marked otoliths were then placed upon a thin layer of previously cured EpoThin2 epoxy (Buehler) in a rectangular casting rubber mold (Buehler), before being fixed by an additional layer of epoxy. An Isomet 1000 precision saw (Buehler) running at  $\geq 200$ rpm was used to make two  $\sim 0.9$ mm transverse sections along otolith cores.

Otolith sections were immediately rinsed in water, trimmed of uneven epoxy fragments, and adhered to a labeled glass microscope slide using thermoplastic cement (Crystalbond, Buehler). Mounted otolith sections were sequentially polished on wet silicon carbide paper with grit sizes of  $25.8\mu\text{m}$  and  $2.5\mu\text{m}$ .

### 2.3.2 Annuli Enumeration

Otoliths were visualized on a modular stereoscope under transmitted light and photographed with an IC80 HD microscope camera (Leica Microsystems). Distinct opaque bands were distinguished as annuli (Fig. 2.4). Of the two sections created for each individual, the section that displayed the clearest banding was used in age estimation. Published literature

on the genus was consulted to determine general trends in annulus shape and spacing (Pfeiler et al. 2000; Larkin 2011; Filous et al. 2019a; Rennert et al. 2019).



Figure 2.4: A polished transverse section of an *Albula* sp. otolith under transmitted light (specimen origin: Thuwal, Saudi Arabia). White dots denote the opaque bands of each annuli.

Annuli were counted twice by the same observer with three months in between readings and without knowledge of the fish's size. A second researcher independently read and assigned ages to each otolith. Afterward, reviewers met to examine any differences observed between reads.



## 2.4 Data Analysis

### 2.5.1 Molecular Outputs

Raw molecular outputs were aligned with MAFFT v.7 (Katoh and Standley 2013) and trimmed using Bioedit v7.2.5. The nucleotide BLAST algorithm (Genbank, NCBI) was used in species determination. A percent identification threshold of >99% was utilized to confidently identify species. Haplotype groups were designated on the DNAsp v6 (Rozas et al. 2017) software and a median joining network was created with the Network software. Arlequin software v3.5 (Excoffier and Lischer 2010) was used to calculate descriptive statistics of molecular data, including haplotype diversity ( $h$ ), nucleotide diversity ( $\pi$ ), and pairwise fixation indices ( $F_{st}$ ).

### 2.5.2 Life History Information

All life history data was analyzed and graphically represented using R software version 3.5.2 (R Core Team, 2018). A standardized equation for the gonadosomatic index (GSI) was used in calculations ( $\text{gonad mass} * \text{somatic mass}^{-1} * 100$ ) (Devlaming et al. 1982). Age and size data were fit among three nonlinear regression growth models (Gompertz, Logistic, and von Bertalanffy) using the `nls()` function. Analysis of sex-specific trends in age and growth each included three immature individuals.

## Chapter 3

### Results

#### 3.1 Genetic Diversity

Genetic information was analyzed from 450 individuals in 12 locations (Fig. 2.3, Table 3.1). Two *Albula* species were identified based upon mtDNA sequences. Of the 323 individuals genetically analyzed from the northwest Indian Ocean, 322 were identified as *A. glossodonta*, while the only specimen collected outside of the Red Sea (Socotra, Yemen) was identified as *A. oligolepis* (Fig. 3.1). Therefore, all analyses from this point forward focuses entirely on *A. glossodonta*.

A total of 27 haplotypes, including 15 singletons, were obtained from cytB sequences of 449 *A. glossodonta* (Fig. 3.2, Table 3.1). Nine non-singleton haplotypes were geographically restricted, including two in Pacific Ocean (n=2, 7), two in the Indian Ocean (n=2, 2), and five in the Red Sea (n=2, 2, 2, 4, 108) (Fig. 3.2). The most common haplotype was exhibited by 62% of individuals and is the only haplotype shared among sampled basins (Fig. 3.2). Additionally, two haplotypes were shared between locations in the Indian and Pacific oceans (n=8, 16), but were not found in the Red Sea (Fig. 3.2). Overall haplotype diversity was moderate ( $h=0.555$ ), yet measures of nucleotide diversity were very low ( $\pi=0.001$ ) (Table 3.1). Location-specific parameters of genetic diversity are presented in Table 3.1.

Table 3.1: Sample size ( $n$ ), number of haplotypes ( $n_{hap}$ ), number of polymorphic sites ( $n_{ps}$ ), haplotype diversity ( $h$ ), and nucleotide diversity ( $\pi$ ) based on mtDNA (cytB) sequences of *Albula glossodonta* from 12 locations across the Red Sea, Indian Ocean, and Pacific Ocean. (Standard error of the total  $h$  and  $\pi$  is denoted by  $\pm$ )

Location	$n$	$n_{hap}$	$n_{ps}$	$h$	$\pi$
<b>Red Sea</b>					
Yanbu	53	6	4	0.560	0.001
Thuwal (Market)	102	7	6	0.463	0.001
Thuwal (Field)	29	3	2	0.542	0.001
Jeddah	137	9	8	0.529	0.001
Farasan Banks	1	1	1	0.000	0.000
All Red Sea Samples	322	14	12	0.518	0.001
<b>Indian Ocean</b>					
Seychelles	88	9	10	0.291	0.001
<b>Pacific Ocean</b>					
Hawaii	23	6	7	0.747	0.003
Cook Islands	8	3	3	0.464	0.001
Kiribati	3	3	2	1.000	0.002
New Caledonia	3	2	1	0.667	0.001
Papau New Guneaia	1	1	1	0.000	0.000
Australia	1	1	1	0.000	0.000
All Pacific Samples	39	8	9	0.819	0.003
<b>Total</b>					
All Locations	449	27	29	0.555 $\pm$ 0.02	0.001 $\pm$ 0.00

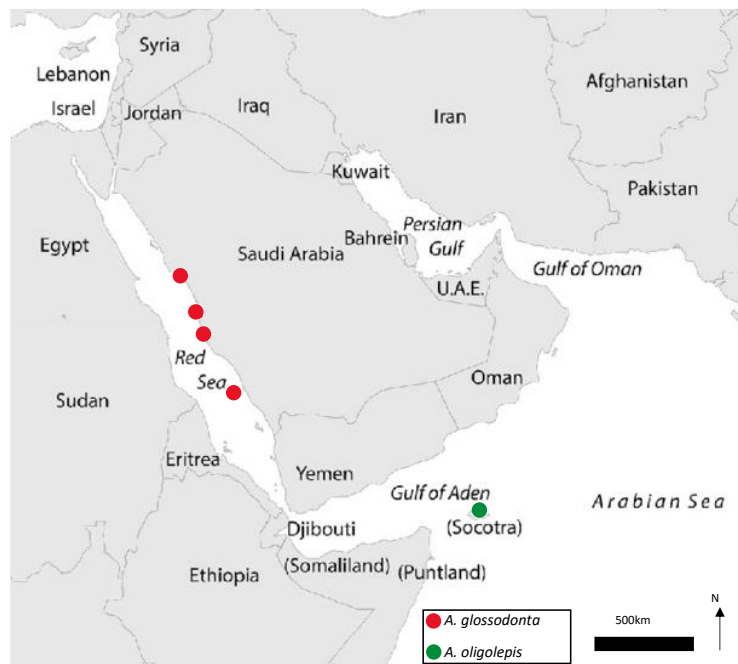


Figure 3.1: Geographic distributions of *Albula glossodonta* and *Albula oligolepis* in the northwestern Indian Ocean identified by cytochrome B sequences.

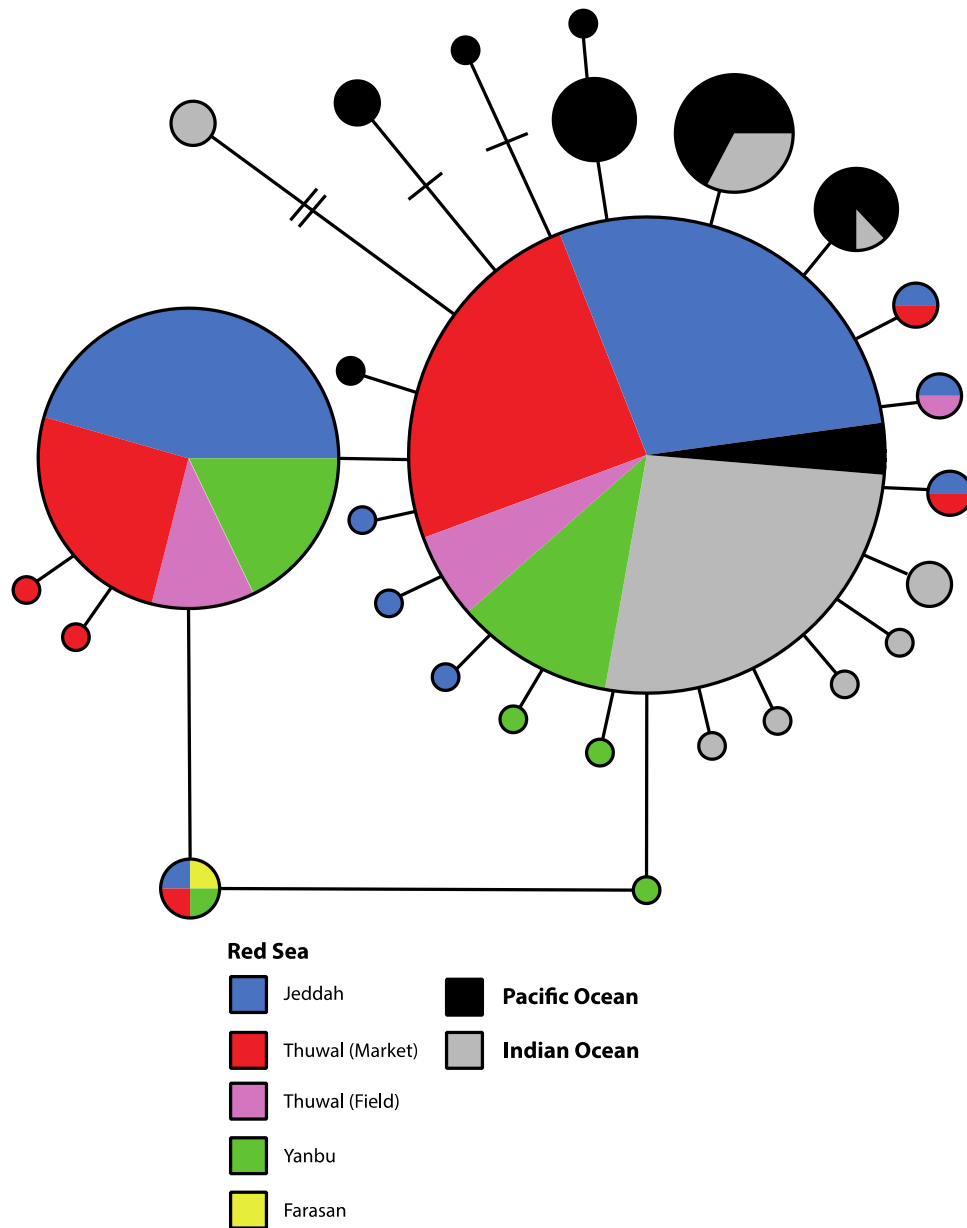


Figure 3.2: Median-joining network based on 568 bp of mitochondrial sequence data (*cytB*) from *Albulaglossodonta* ( $n=449$ ). Circles represent haplotypes and are sized in proportion to frequency. Branches represent a single nucleotide change with crossbars indicating an additional nucleotide difference. Colors denote collection sites in the Red Sea, Pacific Ocean (Hawaii, Kiribati, Cook Islands, New Caledonia, Papua New Guinea, Australia), and Indian Ocean (Seychelles) indicated by the key.

Fixation index values derived from mtDNA sequences provide evidence of population structuring in *A. glossodonta* between but not within basins (Table 3.2). Population comparisons of individual locations excluded collection sites from which fewer than 20 samples were available (Farasan Banks, Cook Islands, Kiribati, New Caledonia, Papua New Guneaia, and Australia) and included pooled samples from the Red Sea and Pacific Ocean independently (Table 3.2). Individuals from the Red Sea exhibited genetic differentiation compared to locales in the Indian and Pacific Oceans (Table 3.2). Inter-basin population structure was also found between Indo-Pacific locations (Table 3.2). Conversely, no population differentiation was observed within the Red Sea or between Hawaii and samples pooled across the Pacific Ocean (Table 3.2).

Table 3.2 Pairwise statistics of genetic differentiation based upon mtDNA sequences (cytB) of *Albula glossodonta* between six locations with samples sizes greater than 20 as well as pooled samples from basins with samples from more than one location (Red Sea and Pacific Ocean). Fixation index ( $F_{st}$ ) values are reported above the dashed line in the right side of the table. Corresponding p-values indicating a significant differentiation from zero are given below the dashed line in the left side of the table. Significant values ( $p < 0.05$ ) are denoted in bold.

Location	Yanbu	Thuwal (market)	Thuwal (field)	Jeddah	Red Sea	Seychelles	Hawaii	Pacific Ocean
Yanbu	-	0.002	-0.019	-0.010	-0.008	<b>0.227</b>	<b>0.306</b>	<b>0.225</b>
Thuwal	0.300	-	0.008	0.003	0.000	<b>0.159</b>	<b>0.338</b>	<b>0.233</b>
Thuwal (field)	0.748	0.253	-	-0.016	-0.011	<b>0.275</b>	<b>0.288</b>	<b>0.218</b>
Jeddah	0.822	0.238	0.789	-	-0.004	<b>0.217</b>	<b>0.368</b>	<b>0.273</b>
Red Sea	0.773	0.305	0.577	0.920	-	<b>0.193</b>	<b>0.393</b>	<b>0.295</b>
Seychelles	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	-	<b>0.263</b>	<b>0.141</b>
Hawaii	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	-	-0.012
Pacific Ocean	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.623	-

### 3.2 Collection Demographics of *A. glossodonta*

Collections of *A. glossodonta* from three Saudi Arabian fish markets yielded a total of 304 fish of which 124 were male, 172 were female, and eight were designated as immature with underdeveloped gonads (Table 3.3). Males ranged in length from 26.2-52.2cm and females from 22.8-57.9cm (Fig. 3.3). Mean length measurements between sexes did not differ (t-test:  $p=0.763$ ) nor did mean body weight (t-test:  $p=0.586$ ) (Table 3.3). However, females were found at marginally greater sizes than males (Fig. 3.3).

Table 3.3 Sample size (n), mean fork length (FL (cm)), and somatic mass (M (g)) of male, female, and immature *Albula glossodonta* collected from fish markets in Saudi Arabia. Values for FL and M are means  $\pm$  standard error.

Sex	n	FL (cm)	M (g)
Male	124	36.8 $\pm$ 0.5	770.8 $\pm$ 32
Female	172	37.2 $\pm$ 0.5	812.7 $\pm$ 34
Immature	8	22.2 $\pm$ 1.7	175.6 $\pm$ 33
Total	304	36.6 $\pm$ 0.4	778.9 $\pm$ 24

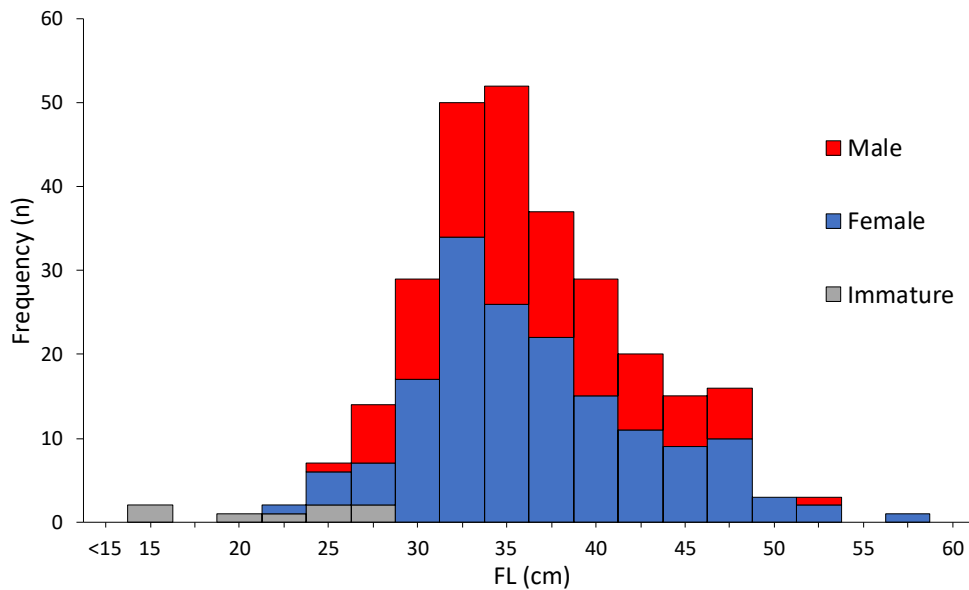


Figure 3.3: Length frequency distributions of male, female, and immature *Albula glossodonta* collected from fish markets in Saudi Arabia (n=304).

### 3.3 Age and Growth

#### 3.3.1 Age distribution

Age estimates were obtained from three immature, 21 male, and 31 female genetically identified *A. glossodonta*. In 8 cases, age assignments differed between readers by 1 year and were subsequently jointly resolved for each individual analyzed. Overall, fish ranged from 1-12 years old with an average age of  $3.6 \pm 0.3$  (Fig. 3.4). All immature individuals (FL = 15-24cm) were one year old, while males ranged from 1-9 years old with a mean age of  $3.7 \pm 0.5$  and females ranged from 1-12 years old with a mean age of  $3.8 \pm 0.5$  (Fig. 3.5). There are no apparent differences in age between sexes (t-test:  $p = 0.840$ ), although females were found at older ages than males (Fig. 3.5).

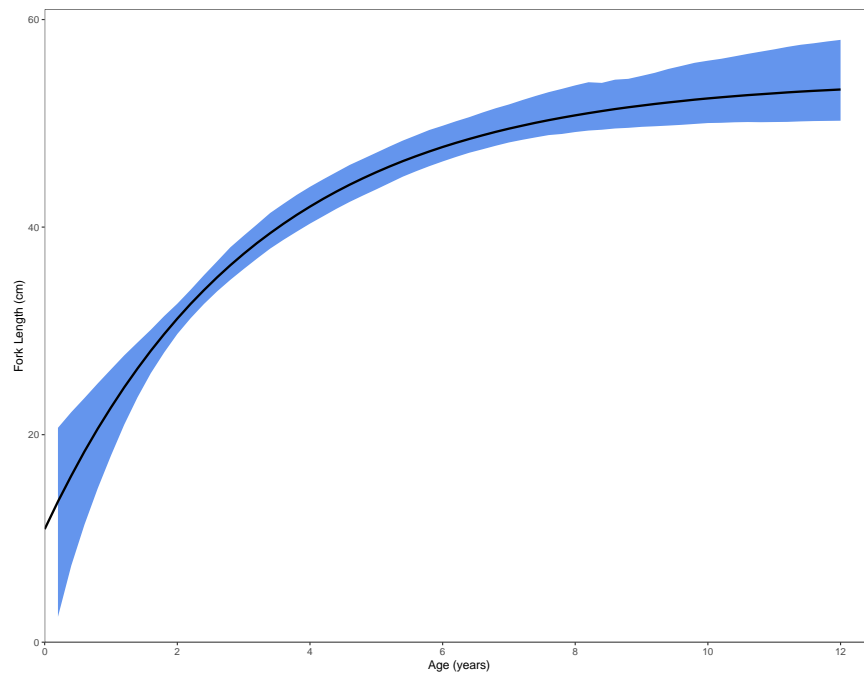


Figure 3.4: von Bertalanffy growth curve (black line) for *A. glossodonta* collected in the Red Sea (Saudi Arabia). The upper and lower bounds for a 97.5% confidence interval of the model are shaded in blue. Observed age-at-length values are represented by opaque grey circles.

### 3.3.2 Growth Models

Age-at-length data of *A. glossodonta* was best fit to the von Bertalanffy growth model (AIC= 576.9) in comparison to the Gompertz (AIC= 577.8) and Logistic (AIC= 578.9) models (Fig. 3.4, Fig. 3.5). Pooled age information from all individuals were used to determine the age of an infinitely old fish ( $L_{\infty} = 54.2\text{cm} \pm 2.8$ ), body growth coefficient ( $K = 0.32 \pm 0.07$ ), and theoretical age at zero length ( $t_0 = -0.71 \pm 0.40$ ) (Fig. 3.4). Sex-specific models revealed minimal variation in asymptotic length and growth rates between males ( $L_{\infty} = 51.2 \pm 4.5$ ,  $K = 0.33 \pm 0.12$ ) and females ( $L_{\infty} = 54.9 \pm 2.9$ ,  $K = 0.37 \pm 0.07$ ) (Fig. 3.5). Estimates of age at a length of zero indicate that female ( $t_0 = -0.24 \pm 0.30$ ) age-length data is slightly better fit to the model than that for males ( $t_0 = -0.78 \pm 0.62$ ) (Fig. 3.5).



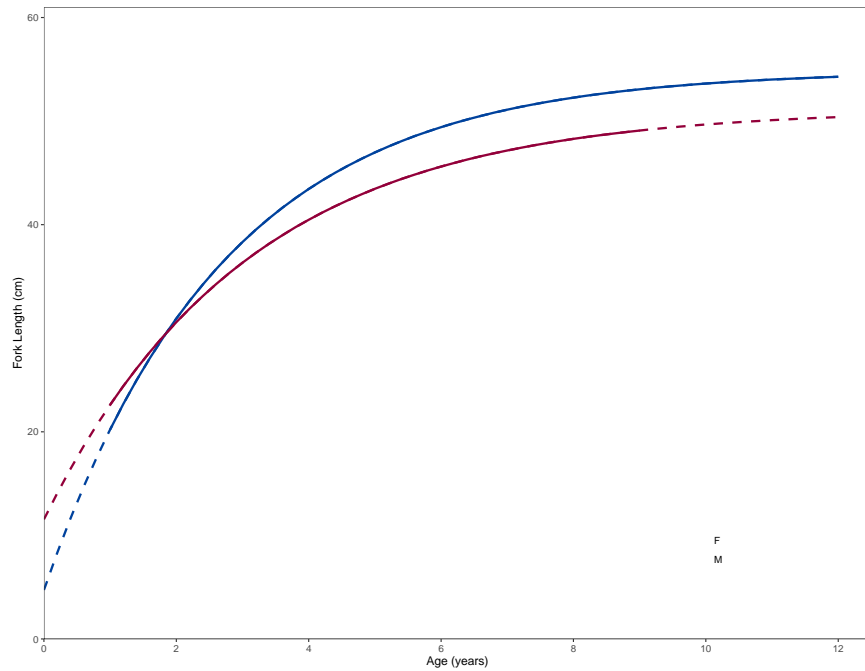


Figure 3.5: von Bertalanffy growth curve for male (red) and female (blue) *A. glossodonta* collected in the Red Sea (Saudi Arabia). The upper and lower bounds for a 97.5% confidence interval of the model are shaded in corresponding colors. Observed age-at-length values are represented by sex-associated colored circles.

### 3.4 Reproductive Seasonality

Measures of gonadosomatic index (GSI) in *A. glossodonta* varied significantly throughout the year (ANOVA:  $p \leq 0.001$ ) (Fig. 3.6). Mean monthly values of GSI for both sexes ranged from 0.1-5.8, with the highest values occurring in December and lowest in July (Fig. 3.6). Females (max GSI = 7.8) exhibited higher GSI values than males (max GSI = 3.8) (Fig. 3.6). Data was not available for either sex during the month of April and immature individuals, for which a sex could not be determined, were excluded from GSI analysis.

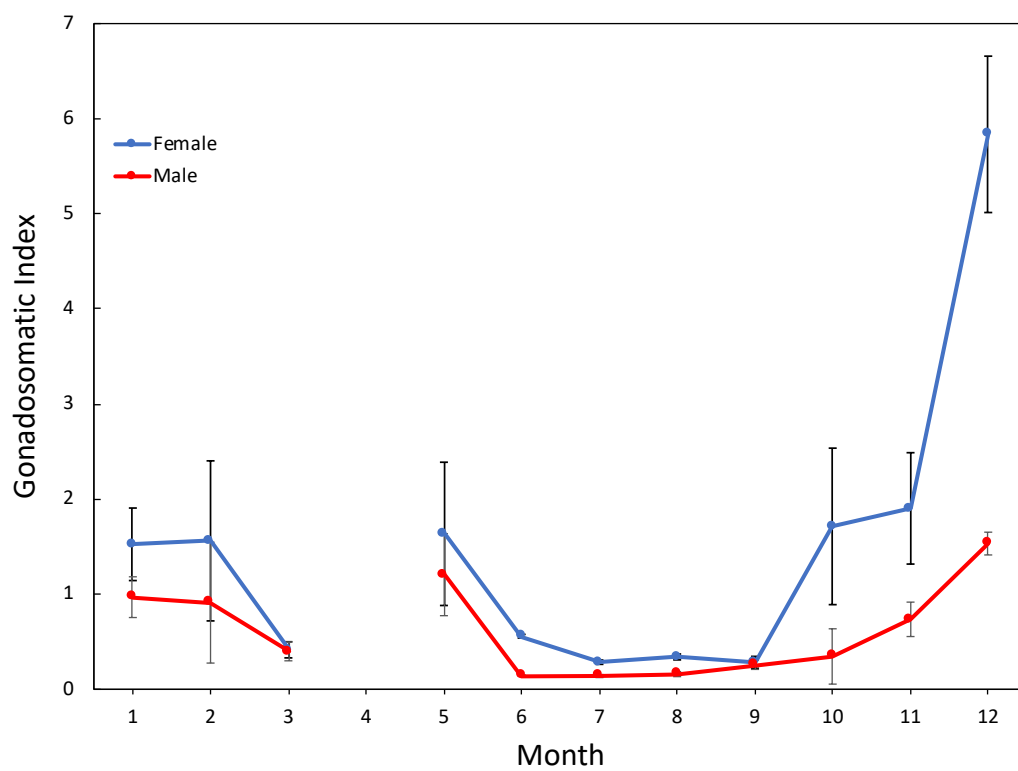


Figure 3.6: Mean monthly gonadosomatic index values of male and female *Albula glossodonta* collected from fish markets in Saudi Arabia. Bars represent Standard Error.

## Chapter 4

### Discussion

#### 4.1 Species Distributions and Population Connectivity

My results provide the first genetic identifications of *Albula* species in the northern Indian Ocean. Based on mtDNA sequences, *A. oligolepis* was documented in Socotra, Yemen, and *A. glossodonta* was documented from several locations within the Red Sea. These findings support morphology-based records of both species from this region (Hidaka et al. 2008; GBIF 2020).

The identification of a single *Albula* species in the Red Sea was unexpected as several species within the genus exhibit sympatric distributions in the Atlantic and Pacific Oceans (Shaklee and Tamaru 1981; Colborn et al. 2001; Adams et al. 2007; Wallace and Tringali 2010, 2016; Donovan et al. 2015; Wallace 2015). The two bonefish species identified from the Indian Ocean in this study, *A. glossodonta* and *A. oligolepis*, occur sympatrically in the southwestern Pacific Ocean, although localized sympatry between these species has yet to be verified in the Indian Ocean (Colborn et al. 2001; Wallace 2015). While albulid sympatry may occur in the Seychelles, where *A. oligolepis* has been identified morphologically and genetic material of *A. glossodonta* has been collected, genetic identification of both species from the same location is needed to substantiate this observation (Colborn et al. 2001; Hidaka et al. 2008; Wallace 2015).

Sampling effort and habitat availability are potential explanations as to why *Albula* sympatry was not observed in the Red Sea. Low sample sizes or biased collections may produce

inaccurate estimates of species composition. However, the current study employed considerable sampling efforts in the central Saudi Arabian Red Sea. Sampling included both fisheries independent and dependent collections of fish from varying habitats and depths with different gear types across multiple years. All of the specimens collected were identified as *A. glossodonta*, indicating an unlikelihood that *A. oligolepis* or another undescribed *Albula* species commonly occurs in the area of the Red Sea sampled here.

Observed distributions of *A. glossodonta* and *A. oligolepis* may be better explained by regional heterogeneity of habitat types and differences in habitat preferences between species. Spatial partitioning between shallow sandflats and deeper channels has been documented in sympatric bonefish species, with *A. glossodonta* commonly encountered in shallow water (Adams et al. 2007; Donovan et al. 2015). It is possible that *A. glossodonta* is associated to the expansive shallow-water sandflat environments found both in the Seychelles and Saudi Arabian Red Sea, while *A. oligolepis* inhabits the rocky coastlines influenced by seasonal upwelling that occur in Socotra and around the Gulf of Aden. To further assess patterns of *Albula* distribution and sympatry in the Indian Ocean, future studies will need to implement diversified and extensive sampling protocols to genetically identify species from undersampled areas.

Molecular identification of *A. glossodonta* from the Red Sea in the current study provides only the second location within the Indian Ocean from which the species has been genetically documented (Colborn et al. 2001; Friedlander et al. 2007; Wallace 2015). The occurrence of *A. glossodonta* in the Red Sea is especially significant as it is the type locality of the species and the Red Sea has been suspected of harboring an endemic *Albula* species

(Colborn et al. 2001; Bowen et al. 2007). My results provide support for the continued, widespread use of Forsskål's original *A. glossodonta* description from the Red Sea suggesting that further taxonomic revision of the species in the region is not needed.

The presence of *A. glossodonta* in the Red Sea is not surprising as the species exhibits a relatively long pelagic larval duration (57 days) and is the most widely distributed species in its genus (Colborn et al. 2001; Friedlander et al. 2007; Wallace 2015). While there is clear evidence that *A. glossodonta* can disperse across major biogeographical barriers (e.g., Sunda Shelf & Bab al Mandab straight) and across great distances, these potential barriers may still limit or restrict gene flow (Colborn et al. 2001; Wallace 2015).

My results describe distinct populations of *A. glossodonta* in the Pacific Ocean, Indian Ocean, and Red Sea. These findings align with previously published mtDNA derived measures of genetic differentiation within *A. glossodonta* that describe structuring between the Pacific and Indian Oceans (Colborn et al. 2001; Friedlander et al. 2007). Analysis of microsatellite DNA in *A. glossodonta*, however, has shown weak, nongeographic population structuring across the Indo-Pacific (Wallace 2015).

Inconsistent results between studies may be explained by sample size and methodology. The findings of Wallace (2015) are based on a smaller sample size that pooled individuals throughout the Pacific Ocean. While I also pooled individuals within basins for comparisons of genetic differentiation, population comparisons were also conducted using specific locations that yielded greater levels of differentiation than comparisons between pooled groups. This aspect of sample design may yield a more accurate representation of an area by reducing the

level of genetic diversity within a designated group that may arise between specific locations. Additionally, larger sample sizes produce more accurate results by increasing the certainty of analysis. Regardless, there are limitations to drawing conclusions of population structure from mtDNA alone (Hoarau et al. 2004). Further investigations utilizing multiple classes of molecular markers (e.g., microsatellite DNA and next generation sequencing) are needed to confirm the trends of population structure in *A. glossodonta* observed here.

#### **4.2 Life History Characteristics**

The current study presents the first life history information from an albulid in the Indian Ocean and the Red Sea. I expected to find differences in life history characters between the Red Sea and previously published studies from the Pacific Ocean corresponding to broad geographic thermal patterns of growth and longevity in marine fishes. Tropical reef fishes are generally observed to exhibit slower growth, larger body size, and increased longevity along gradients of increasing latitudes, presumably due to the changes in temperature regimes associated with the latitudinal gradient. (Fowler 2009; Trip et al. 2014; Morais and Bellwood 2018). However, consistent latitudinal trends in life history parameters were not clearly observed in *A. glossodonta* between the Red Sea and Pacific Ocean. In fact, the fastest growth and largest asymptotic size documented for *A. glossodonta* comes from Anaa Atoll, French Polynesia (-17.402344, -145.499757), the lowest latitude location among published studies on the species (Filous et al. 2019a) (Table 4.1). Age structure of *A. glossodonta* conformed to predicted trends, as sampled populations from comparable latitudes in the central Red Sea (22.297442, 39.091440) and Oahu, Hawaii (21.438564, -158.003514) exhibited older maximum

ages than Anna Atoll at a lower latitude despite smaller sample sizes (Donovan et al. 2015; Filous et al. 2019a) (Table 4.1). Interestingly, faster growth and smaller asymptotic size, and younger maximum age were recorded for *A. glossodonta* in the Red Sea compared to Hawaii (Donovan et al. 2015) (Table 4.1). High temperatures within the Red Sea complicate latitudinal comparisons and may account for the life history differences in *A. glossodonta* relative to Hawaii (Sofianos and Johns 2007; Tesfamichael and Pauly 2016).

Table 4.1: Comparative life history parameters of *Albula glossodonta* from the Red Sea, Hawaii (Donovan *et al.* 2015), and French Polynesia (Filous *et al.* 2019). (Standard error is denoted by  $\pm$ )

	Saudi Arabia	Hawaii	French Polynesia (male)	French Polynesia (female)
n	55	56	225	249
K	$0.32 \pm 0.07$	$0.18 \pm 0.06$	$0.38 \pm 0.06$	$0.21 \pm 0.7$
$t_{\max}$	12	14	8	10
$L_{\infty}$	$54.2 \pm 2.8$	$67.3 \pm 6.3$	$58 \pm 2.5$	$78 \pm 5.0$

There is increasing evidence to suggest that temperature is not only factor driving life history variation within tropical marine fish species, especially in regard to growth rate (Trip et al. 2008; Berumen et al. 2012; Cappo et al. 2013; Morais and Bellwood 2018; Taylor et al. 2018). It has been suggested that local environmental features (e.g., habitat quality, food availability, etc.) varying across large geographic scales have considerable influence on the growth rate of tropical fishes (Trip et al. 2008). If true, localized environments could partially describe the differences in *A. glossodonta* growth demographics between the compared studies. Regardless,

influential complexities of fish life history characters warrant consideration of other non-environmental factors that could explain the variation observed in *A. glossodonta* specifically.

Fishing pressure can directly induce changes to life history parameters of marine fish species (Ruttenberg et al. 2011). Reports have shown that harvest of *A. glossodonta* may reduce the abundance of older fish and the overall size of individuals (Beets 2000; Filous et al. 2019a). Filous et al. (2019) collected a small, supplementary sample of *A. glossodonta* from an unexploited atoll in French Polynesia (-17.005569, -149.562369), demonstrating that the species can reach 20 years of age and further complicating a latitudinal explanation of age structure. Harvest fisheries for *A. glossodonta* persist in all locations from which the life history characters of the species have been described in detail (sample size >50) (Table 4.1). Maximum ages of *A. glossodonta* reported from these locations range from 8-14 years, well below the oldest documented individual of the species (20 years) (Table 4.1). This suggests that the age structure and possibly other aspects of the *A. glossodonta* biology are influenced by fishery exploitation at all compared locations (Filous et al. 2019a).

Varying levels of fishing effort and capture methodologies could further complicate geographic comparisons of the life history information currently available for *A. glossodonta*. For example, unique stone fish traps are commonly used to harvest bonefish on Anaa Atoll, but are not utilized in the Saudi Arabian Red Sea reef fisheries. In my study area, gill nets and handlines are the more prominent gear. If different gear types disproportionately capture particular size classes or sexes of bonefish it could lead to demographic shifts in local stocks.



Another considerable non-environmental influence on tropical marine fish life histories is the abundance of predatory species (Ruttenberg et al. 2011). Removal of marine top predators (i.e., sharks) can reduce size, decrease longevity, and increase growth rates of mesopredatory fish (Ruttenberg et al. 2011). Sharks are documented predators of bonefish, thus the low abundance of overexploited shark stocks in the Saudi Arabian Red Sea likely has an effect on the demographics and life histories of *A. glossodonta* in the region (Danylchuk et al. 2007a, b; Spaet and Berumen 2015). Additional investigations would be needed to develop a better understanding of growth dynamics in *A. glossodonta* throughout its range accounting for temperature, localized habitat features, and trends in mortality.

There were no definitive differences in age, size, and growth found between sexes of *A. glossodonta* in the Red Sea (Fig. 3.5). This finding conflicts with the sexually dimorphic growth previously documented in *A. glossodonta* (Filous et al. 2019a). Still, comparisons of age and growth in this study were restricted by low samples sizes, especially in the male subset. The occurrence of females at older ages and slightly larger sizes than males suggests that differences may occur between sexes, but were not confirmed here given the low number of individuals aged for each sex. Age determination of the remaining individuals in the current dataset would enable further examination of growth between sexes with increased certainty.

The timing of *A. glossodonta* reproduction during winter months in the Red Sea matches the reproductive seasonality documented for the species in the Pacific Ocean (Donovan et al. 2015; Filous et al. 2019a). Values of GSI collected throughout the year in Saudi Arabia indicate that Red Sea *A. glossodonta* demonstrates spawning activity from October to February and

then again in May, with the highest GSI values observed in December. Donovan et al. (2015) examined temporal patterns in *A. glossodonta* recruitment in Hawaii and estimated two distinct periods of peak spawning activity between November to December and March to June. Multiple peaks of reproductive activity in *A. glossodonta* from the Red Sea could explain low values of GSI recorded in March before a second increase in GSI was documented in May. The absence of GSI from the Red Sea in the month of April hinders a definitive examination of a second spawning cycle. Still, the specific months at which *A. glossodonta* in the Red Sea are most likely to spawn have been identified by the current study and may be foundational to the establishment of fishery regulations in the region that protect these fish at a time when they are most vulnerable to overexploitation.

#### **4.2 The Future of Red Sea *Albula* Fisheries**

There is a pressing need to establish conservation measures regarding bonefish in the Red Sea due to the lack of regulations on harvest and large-scale planned coastal development in Saudi Arabia that may reduce habitat availability (Nurunnabi 2017). Oddly enough, the anticipated tourism motivating coastal development in Saudi Arabia poses a potential threat to the health of coastal habitats but, ultimately, may bring attention to the conservation needs of bonefish as the species becomes increasingly targeted by foreign recreational anglers. Bonefish, among other species, are already targeted by a recreational fishery along the western Red Sea in Sudan (personal communication: African Waters Fishing). Communities of recreational anglers already exist in Saudi Arabia and foreign fishing outfitters are taking steps to establish operations in the Saudi Arabian Red Sea with the recent enactment of tourist visas in the

country (personal communication: Jeddah Fishing Club, Wild Sea Expeditions). Red Sea fisheries in Saudi Arabia may soon see an influx of recreational anglers targeting bonefish. Continued biological investigations of *A. glossodonta* in the Red Sea, including the identification and distribution of key habitats, the distribution and abundance of individuals, and rates of harvest, are necessary to accurately construct fishing regulations. Effective restrictions on the harvest of bonefish in the Red Sea will help establish a balance between traditional artisanal fisheries and the healthy fish populations needed to support rapidly developing recreational fisheries.

## Chapter 5

### Conclusions

To conclude, *A. glossodonta* was genetically documented in the Red Sea, refining biogeographical uncertainties in the genus. The identification of a single species of bonefish in the Red Sea despite extensive sampling suggests that claims of *Albula* sympatry should not be generalized across regions, especially in the Indian Ocean. Evidence is presented here for a distinct population of *A. glossodonta* in the Red Sea indicating that dispersal of new individuals into the basin is low and that stocks of Red Sea bonefish may be sensitive to overexploitation. Furthermore, life history characters of *A. glossodonta* in the Saudi Arabian Red Sea varied from reported values for the species in the Pacific Ocean, highlighting the need for local information of fish stocks to accurately build fishery measures upon. The highest spawning activity of *A. glossodonta* in the Red Sea occurred in December. Therefore, at a minimum, I recommend a seasonal *Albula* fishery closure around the month of December to prevent the overharvest of *A. glossodonta* spawning aggregations.

Unfortunately, the extent to which the Red Sea population of *A. glossodonta* is exploited remains unclear. Further investigation into the distribution, abundance, and harvest of bonefish in the Red Sea is needed to formulate an effective conservation strategy. Biological information on coastal fishes targeted by fisheries, including the results of the current study, will become increasingly vital in the future as Saudi Arabia seeks to protect its marine resources, but lacks much of the detailed information needed to do so (Nurunnabi 2017).

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