

Genetic population structure and connectivity of four key coastal fisheries species across the Gilbert Islands of Kiribati

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Introduction

Artisanal coastal fisheries play a major role in providing food security and socioeconomic resilience throughout the Pacific (Gillett 2016). Coastal finfish fisheries are particularly important, accounting for up to 60% of catches from nearshore fisheries landings (Dalzell and Adams 1996). Nearly 80% of these landings are primarily for subsistence (Bell et al. 2009), making fish the main protein source in most Pacific Islands (Charlton et al. 2016). Surplus reef fish are traded at local and regional markets, and sometimes internationally. This supports local economies and provides income for communities (Kronen et al. 2010; Gillet 2016).

Rapidly increasing Pacific Island populations with access to better fishing technology and refrigeration options are responding to the increased demand from local and international markets for fresh seafood. This has increased coastal fishing pressure to unsustainable levels in many locations, and highlights the need to effectively manage coastal resources to avoid a continued decline in coastal fisheries catches. Successful management of coastal fisheries requires appropriate data and information from which to make decisions. Unfortunately, in many Pacific Island nations, such data are limited thus constraining countries' ability to make effective management choices. While national coastal fisheries agencies are tasked with collecting the necessary data, there nevertheless remains a severe shortage of information on the life history and demographics of targeted species across the Pacific Islands.

The Republic of Kiribati, in the central Pacific Ocean, is unique in having three separate archipelagoes: Phoenix, Line and Gilbert islands (Alsied 2006; Kiareti et al. 2015). Kiribati's population relies heavily on marine resources and has the highest fish consumption per capita in the Pacific (Charlton et al. 2016). A recently completed (2019–2020) national household income and expenditure survey (Ministry of Finance and Economic Development Government of Kiribati 2021) indicates a total population of ~ 120,000 people across all three archipelagoes, with about 90% or approximately 108,000 people located in the Gilbert Islands chain. Within the Gilbert Islands, the population distribution is also heavily skewed, with about 58% of the population living in South Tarawa, Kiribati's capital.

Unsurprisingly, the fishing pressure around Tarawa (population 63,000) is degrees of magnitude higher than in other atolls where the next most populated atoll (Abaiang) has a population of only 5500 (National Statistics Office 2016). Such a concentration of fishing effort raises an important question: How resilient to fishing pressure are targeted species around Tarawa? One aspect of this question, which is the focus of this study, is understanding the degree of connectivity that exists between resident fish populations of the same species and those from other atolls. Highly connected populations function as meta-populations and have a much higher degree of overall resilience than do isolated and poorly connected populations (Kritzer and Sale 2004).

This study was part of a broader programme looking at the effects of fishing across a human population gradient in the Gilbert Islands. Three atolls – Tarawa, Abemama and Onotoa – were chosen, each with human populations of 70,000, 3200 and 1400, respectively (National Statistics Office 2016). Surveys identified four coastal fish species as being predominant in catches across all three atolls, so our objectives were to determine how genetically isolated the populations around these atolls were from each other, and to gain insights into the level of meta-population resilience that may be intrinsic to the Gilbert Islands.

The four species of interest were: bonefish, *Albula glossodonta*, an inhabitant of sandy lagoons; sweetlip emperors, *Lethrinus nebulosus* and *L. obsoletus*, which inhabit areas with sandy and rubble bottoms inside and outside of lagoons; and the paddletail snapper, *Lutjanus gibbus*, which inhabits areas dominated by coral reef. The genetic structure and connectivity of *A. glossodonta*, *L. nebulosus*, *L. obsoletus* and *Lutjanus gibbus* is either unknown or poorly documented in the Gilbert Islands (Colborn et al. 2001; Friedlander et al. 2007; Wallace 2015). Our principal aim was to determine the degree of population genetic structure and inferred connectivity across three atolls using the highly polymorphic mitochondrial DNA (mtDNA) markers cytochrome b and the control region (Ekerette et al. 2017; Lalitha and Chandavar 2018).

Methodology

Study location

This study focused on the Gilbert Islands with biological samples collected from the three atolls separated by 100 km to 400 km (Fig. 1). Tarawa is the most populated atoll and has the largest lagoon area of 534 km², which is three and seven times larger than Abemama (152 km²) and Onotoa (75 km²), respectively (Ministry of Internal and Social Affairs 2012a, 2012b, 2008).

Sampling design

Fin clips were sampled opportunistically from fishers' catches at local boat landing sites during creel surveys conducted between May and December 2019 (Gislard 2020). Samples of *Albula glossodonta* and *Lethrinus obsoletus* were obtained for all three atolls, while samples of *L. nebulosus* were obtained from Tarawa and Abemama atolls, and *Lutjanus gibbus* from Abemama and Onotoa. In total, 241 fin clips were collected and preserved in 95% ethanol: *Albula glossodonta* (n=85), *L. nebulosus* (n=47), *L. obsoletus* (n=52) and *Lutjanus gibbus* (n=57) (Table 1).

Because *A. glossodonta* is morphologically almost indistinguishable from Indo-Pacific sympatric species of the same genus (Wallace 2015) – *A. vulpes*, *A. oligolepis*, *A. argentea*, *A. virgata*, *A. escuncula* and *A. gilberti* – genetic analyses for this species were first concentrated on confirming species identity before connectivity analyses were done.

DNA extraction, mitochondrial DNA (mtDNA) amplification and sequencing

Total genomic DNA was extracted from a 1 cm² piece of fin tissue using a DNA extraction kit. Depending on the species, cyt b or CR markers were used. Such markers (mtDNA) are known to be sensitive to differentiation at the population level (Askari et al. 2013; Grunwald et al. 2002; Imtiaz et al. 2017).

Amplifications by polymerase chain reaction (PCR) and Sanger sequencing were then performed by Macrogen. More details on PCR and sequencing conditions are summarised in Table 1.

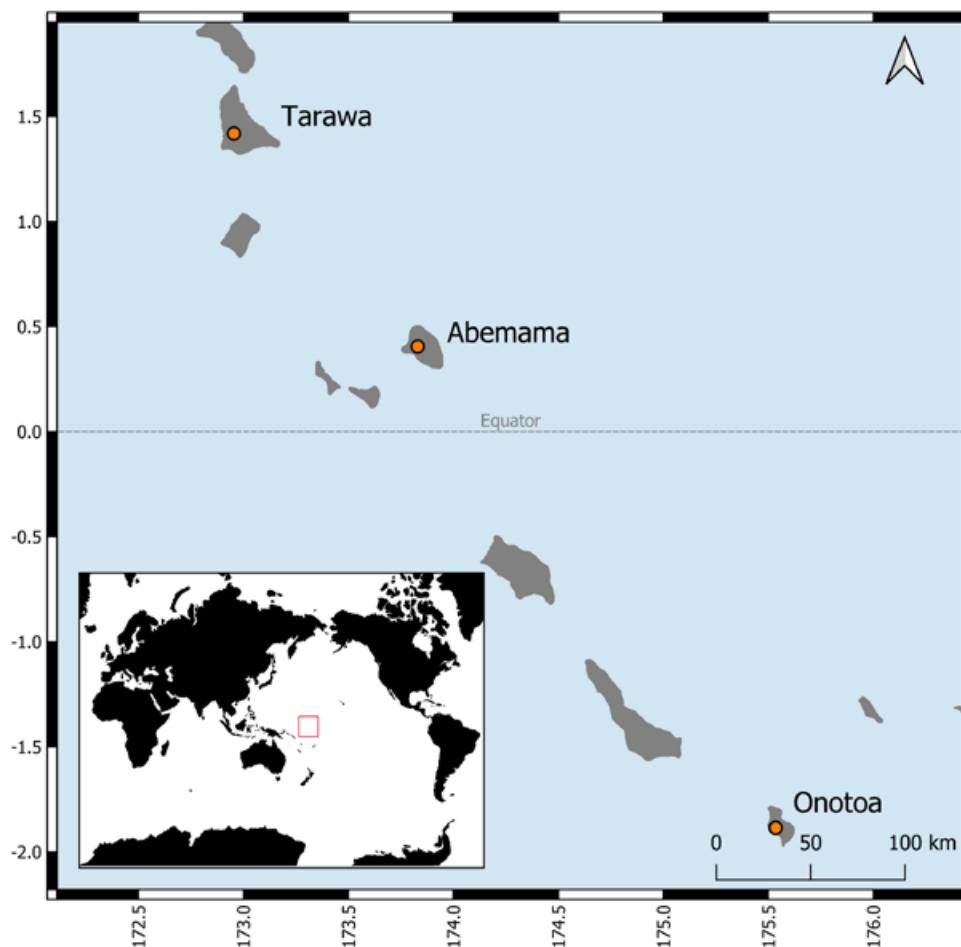


Figure 1. Biological sampling locations in the Gilbert Islands (orange dots). Grey represents land and reef area.

Table 1. Parameters of mitochondrial DNA amplification for four reef fish in the Pacific Ocean. The accession number gives access to the sequence on the National Center for Biotechnology Information open data.

Species	Markers	Sense	Primers sequences	Accession number
<i>Albula glossodonta</i>	Cyt b	Forward	5'-GTCTCCAAGAAGGTTAGGCGA-3'	OL542768 OL542781
		Reverse	5'-TGCTAGGGTTGTGTTAATTA-3'	
<i>Lethrinus nebulosus</i>	CR	Forward	5'-CGGTC TTGTAAACCGGATGT-3'	OL580786 OL580794
		Reverse	5'-GTCATGGCCCTGAAATAGGA-3'	
<i>Lethrinus obsoletus</i>	CR	Forward	5'-CGGTC TTGTAAACCGGATGT-3'	OL580795 OL580810
		Reverse	5' GTCATGGCCCTGAAATAGGA-3'	
<i>Lutjanus gibbus</i>	Cyt b	Forward	5'-TGGCAAGCCTACGCAAAC-3'	OL580811 OL580827
		Reverse	5'-TATTCCGCCGATTCAGGTAA-3'	

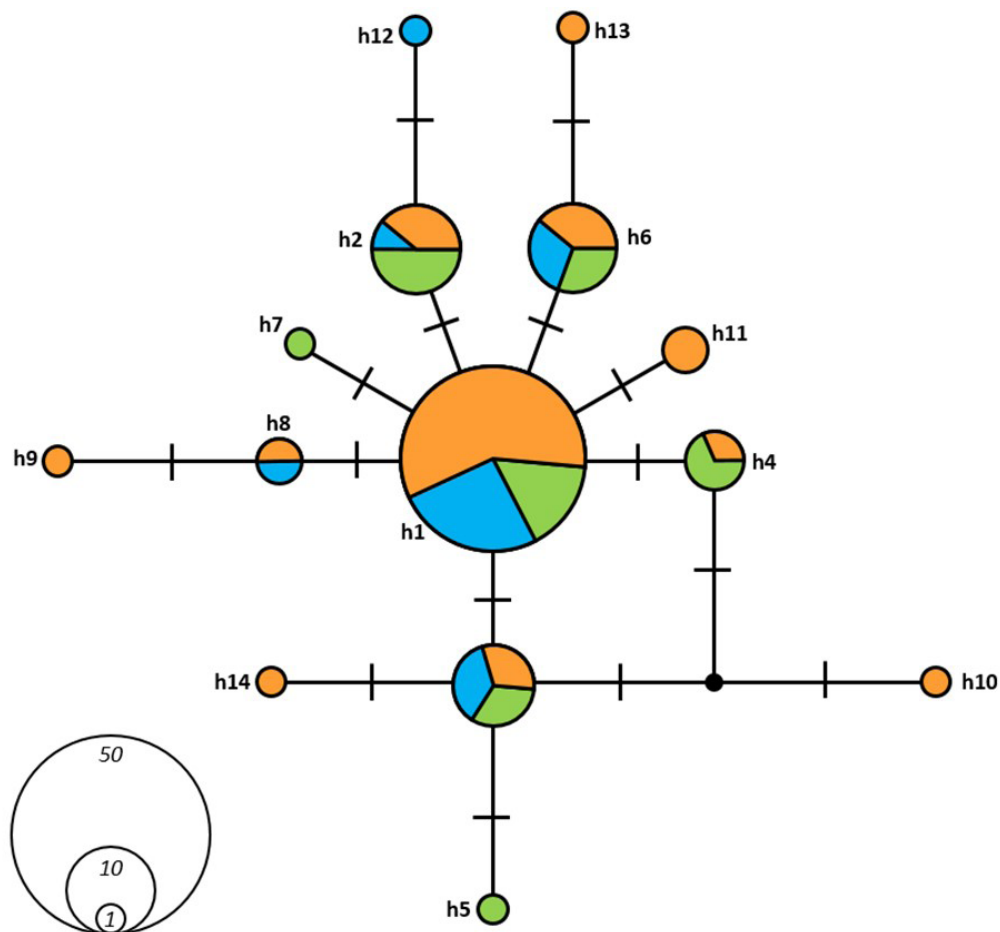


Figure 2. Median-joining haplotypic network among *A. glossodonta* individuals. Circles represent haplotypes with their size proportional to individual frequencies. Colours represent regions of origin (blue: Onotoa; orange: Abemama; green: Tarawa). Length of black lines represent the number of base changes. Black dots represent unsampled median haplotypes.

Genetics analysis

Sequences were aligned and manually edited using Mega software (Kumar et al. 2018). To confirm *Albula* samples were actually *A. glossodontata*, all sequences were compared to the nucleotide collection from the National Center for Biotechnology Information (NCBI), an international genetics database hosted by the United States National Library of Medicine.

To investigate genetic diversity among atolls, the genetic structures were estimated at both the haplotype (h : haplotype diversity) and nucleotide (π : nucleotide

diversity) levels (Nei 1987) using the software Arlequin v 3.5. (Excoffier et al. 2007). To investigate the evolutionary history of the populations, potential bottlenecks were tested using neutrality tests (Tajima's D test and Fu's FS test). Genetic differentiation between atolls was assessed with a pairwise fixation index for haplotype frequency differentiation (FST).

A haplotypic network of relationships among the Gilbert Islands' mtDNA haplotypes was constructed with Network V10.0 (Fluxus Technology) to visualise connectivity between locations.

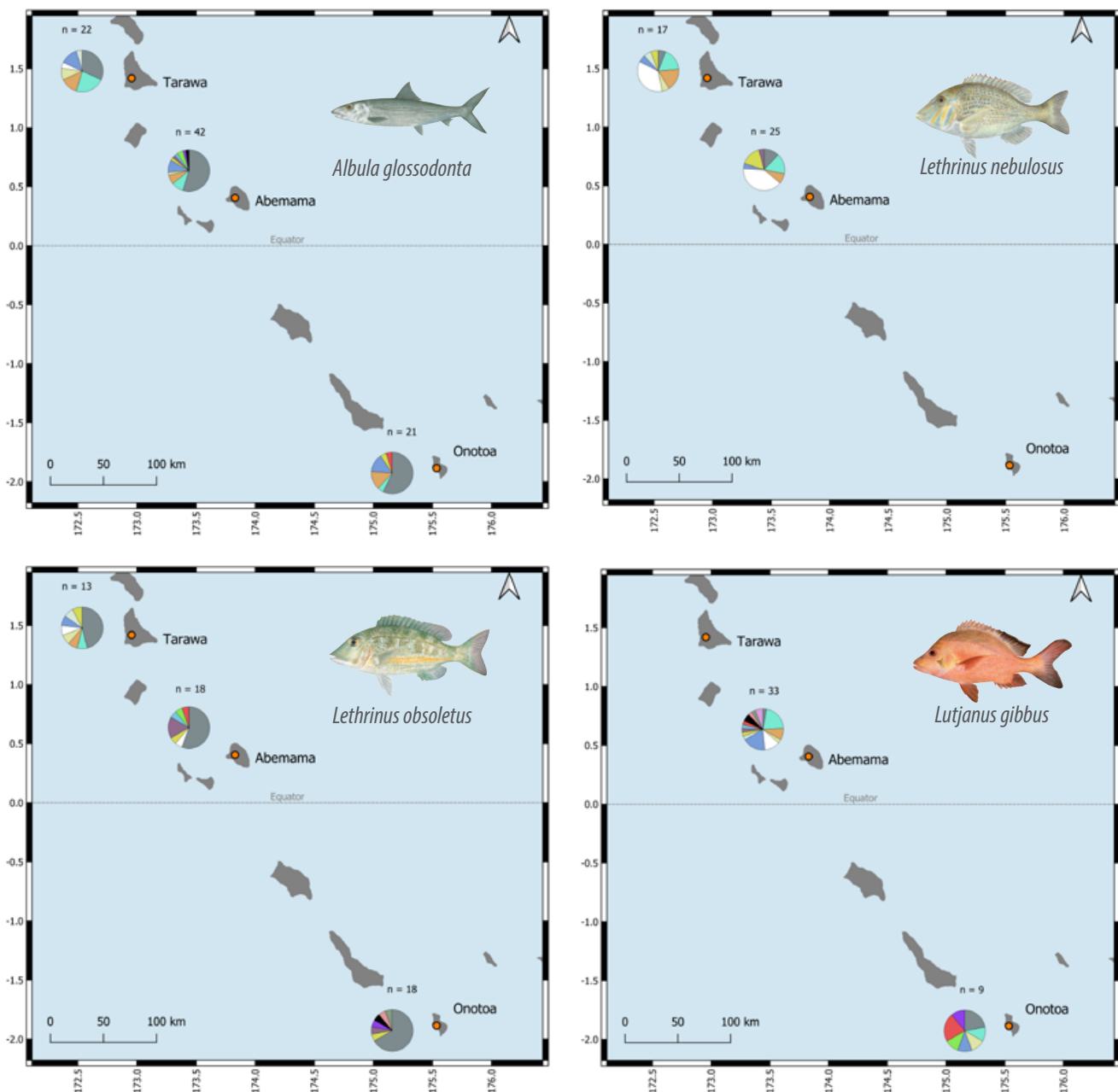


Figure 3. Haplotype map of four reef fish species across the Gilbert Islands. Each haplotype is represented by colour, and n represents the number of specimens sampled.

Table 2. Genetic diversity of the four key fish species at the atoll-scale, based on mtDNA.

Species	Atolls	n	Haplotype diversity (h)	Number of haplotypes	Number of unique haplotypes	Polymorphic sites (s)	Nucleotide diversity (π)	Tajima's D test (p-value)	Fu's FS test (p-value)	FST (p-value)		
										Tarawa	Abemama	Onotoa
<i>Albula glossodonta</i>	Tarawa	22	0.835 ± 0.047	8	2	7	0.002 ± 0.001	-0.653 (0.289)	-1.856 (0.105)	x	0.025 (0.107)	0.028 (0.153)
	Abemama	42	0.688 ± 0.075	11	4	11	0.002 ± 0.001	-1.534 (0.043 *)	-5.884 (0.001 *)	x	0.025 (0.107)	0 (0.941)
	Onotoa	21	0.657 ± 0.103	6	1	6	0.002 ± 0.001	-0.988 (0.190)	-1.777 (0.088)	0 (0.941)	0.028 (0.153)	x
	Overall	85	0.722 ± 0.045	14	7	14	0.002 ± 0.001	-1.511 (0.039 *)	-7.490 (0.003 *)			
<i>Lethrinus nebulosus</i>	Tarawa	17	0.846 ± 0.066	8	2	47	0.041 ± 0.021	0.444 (0.719)	5.640 (0.980)			
	Abemama	25	0.797 ± 0.060	7	1	45	0.039 ± 0.020	0.263 (0.656)	11.386 (0.999)			0 (0.855)
	Overall	42	0.805 ± 0.044	9	3	48	0.039 ± 0.020	0.375 (0.701)	13.819 (0.998)			
<i>Lethrinus obsoletus</i>	Tarawa	13	0.808 ± 0.113	8	5	33	0.020 ± 0.011	-1.054 (0.145)	0.947 (0.674)	x	0 (0.598)	0.004 (0.385)
	Abemama	18	0.686 ± 0.112	7	3	55	0.025 ± 0.013	0.212 (0.631)	5.071 (0.969)		0 (0.598)	0 (0.713)
	Onotoa	18	0.569 ± 0.138	7	4	33	0.015 ± 0.008	-1.552 (0.047 *)	2.496 (0.862)		0.004 (0.385)	x
	Overall	49	0.670 ± 0.076	16	12	68	0.019 ± 0.010	-0.832 (0.217)	1.000 (0.149)			
<i>Lutjanus gibbus</i>	Abemama	33	0.911 ± 0.028	15	6	37	0.010 ± 0.005	-0.940 (0.183)	-0.058 (0.537)			0.014 (0.266)
	Onotoa	9	0.944 ± 0.070	7	2	18	0.007 ± 0.004	-0.313 (0.395)	-0.653 (0.304)			
	Overall	42	0.922 ± 0.022	17	8	39	0.009 ± 0.005	-1.004 (0.162)	-0.460 (0.472)			

Results

Genetic identification of *Albula glossodonta*

The 85 sequences obtained from the *Albula* samples were compared to sequences stored in the NCBI database. Among the 100 higher scores of target sequences, the first 27 sequences corresponded to partial sequences of *A. glossodonta* cyt b gene with an identity percentage from 99.4% to 100%. This identity percentage decreased below 95% for *A. esuncula* and below 90% for other species of the same genus (*A. gilberti*, *A. koreana*). Consequently, the 85 *Albula* samples were assigned to *A. glossodonta*.

Sequence descriptive analysis

The 608 base pairs (bp) consensus cyt b sequences of *A. glossodonta* revealed 14 polymorphic sites that defined 14 different haplotypes, with a mean number of pairwise nucleotide differences of 1.282 ± 0.813 (Table 2). The 469 bp and 475 bp consensus CR sequence of *Lethrinus nebulosus* and *L. obsoletus* revealed 48 and 68 polymorphic sites that defined 9 and 16 different haplotypes, with a mean number of pairwise nucleotide differences of 18.167 ± 8.223 and 9.190 ± 4.299 , respectively (Table 2). The 962 bp consensus cyt b sequence of *Lutjanus gibbus* revealed 39 polymorphic sites that defined 17 different haplotypes, with a mean number of pairwise nucleotide differences of 8.667 ± 4.083 (Table 2).

Historical demography

Neutrality tests were statistically significant for *A. glossodonta* pooled at the archipelagic level, Tajima's test ($D = -1.511^*$, $p < 0.05$) and Fu's FS ($F_s = -7.490^*$, $p < 0.05$). However, this result is driven by *A. glossodonta* samples from Abemama, the only atoll where neutrality tests were significant ($D = -1.534^*$, $p < 0.05$; $F_s = -5.884^*$, $p < 0.05$).

The median-joining network is star-shaped (Fig. 2), with a central main haplotype (h_1 : $n = 42$) from which other haplotypes derive with one or two mutations.

Tajima's test on *Lethrinus obsoletus* from Onotoa was also significant ($D = -1.552$; $p < 0.05$) but Fu's FS was not. Both neutrality tests were insignificant for *L. obsoletus* pooled across atolls. This was also the case for *Lethrinus nebulosus* and *Lutjanus gibbus* when pooled across atolls. Because the haplotypic networks of *L. nebulosus*, *L. obsoletus* and *Lutjanus gibbus* did not show a genetic trend, the results are not presented in this publication, although they are available on request to the authors.

Genetic diversity and connectivity among atolls

For each species, the main haplotype observed in most specimens was common to all atolls: 83.5% of *A. glossodonta* specimens, 93% of *Lethrinus nebulosus*, 63% of *L. obsoletus* and more than 55% of *Lutjanus gibbus*. Among the 14 haplotypes recorded for *A. glossodonta* and the 16 for *L. obsoletus*, four and two haplotypes were shared among the three atolls, respectively. Similarly, among the nine haplotypes recorded for *L. nebulosus* and the 17 for *Lutjanus gibbus*, six and five were shared, respectively, across Tarawa-Abemama and Abemama-Onotoa (Fig. 3).

Haplotypic diversity (h) increased from the southernmost atoll (Onotoa) to the northernmost (Tarawa) except for *Lutjanus gibbus*, while nucleotide diversity tended to be constant across atolls. For instance, the haplotypic diversity of *A. glossodonta*, *Lethrinus obsoletus* and *L. nebulosus* in Tarawa was, respectively, $h = 0.835 \pm 0.047$, $h = 0.808 \pm 0.113$ and $h = 0.846 \pm 0.066$. This was followed by Abemama, with intermediate to high values ranging from $h = 0.686 \pm 0.112$ to $h = 0.797 \pm 0.060$ and the lowest values in Onotoa with haplotypic diversity ranging from $h = 0.569 \pm 0.138$ to $h = 0.657 \pm 0.103$.



As an indicator of differences in genetic structure across atolls, pairwise comparisons based on haplotype frequencies were investigated for each species between all sampled areas, (Table 2). For each species, pairwise F_{ST} were relatively low, ranging from 0 to 0.028, and were not significantly different across atolls.

Discussion

Our investigation of genetic structure and connectivity of populations of *Albula glossodonta*, *Lethrinus nebulosus*, *Lethrinus obsoletus* and *Lutjanus gibbus* across three atolls within the Gilbert Islands did not uncover the presence of genetically distinct subpopulations. This indicates regular genetic connectivity between Tarawa, Abemama and Onotoa, of these species. Haplotypic diversity, which reflects genetic diversity across the atolls increased from south to north, with samples collected in Tarawa having a higher genetic diversity than samples collected in Abemama and Onotoa. Our analyses also confirmed that our samples of *Albula* belong to a single species, *Albula glossodonta*, and the population of *A. glossodonta* has experienced a historically drastic decline in population size.

Genetic structure and connectivity across atolls

The permutation tests on pairwise F_{ST} for all species showed that genetic structure was not significantly different across atolls, indicating regular gene flow between stocks from Tarawa, Abemama and Onotoa.

All four species are pelagic spawners with long pelagic larval durations of between 25 and 58 days on average (Friedlander et al. 2007; Soeparno et al. 2012). Considering the relatively small distances separating the atolls (100 km to 400 km), larvae from one atoll drift long enough to reach other nearby atolls, hence providing sufficient gene flow to maintain the observed genetic similarity between atolls. Similar findings

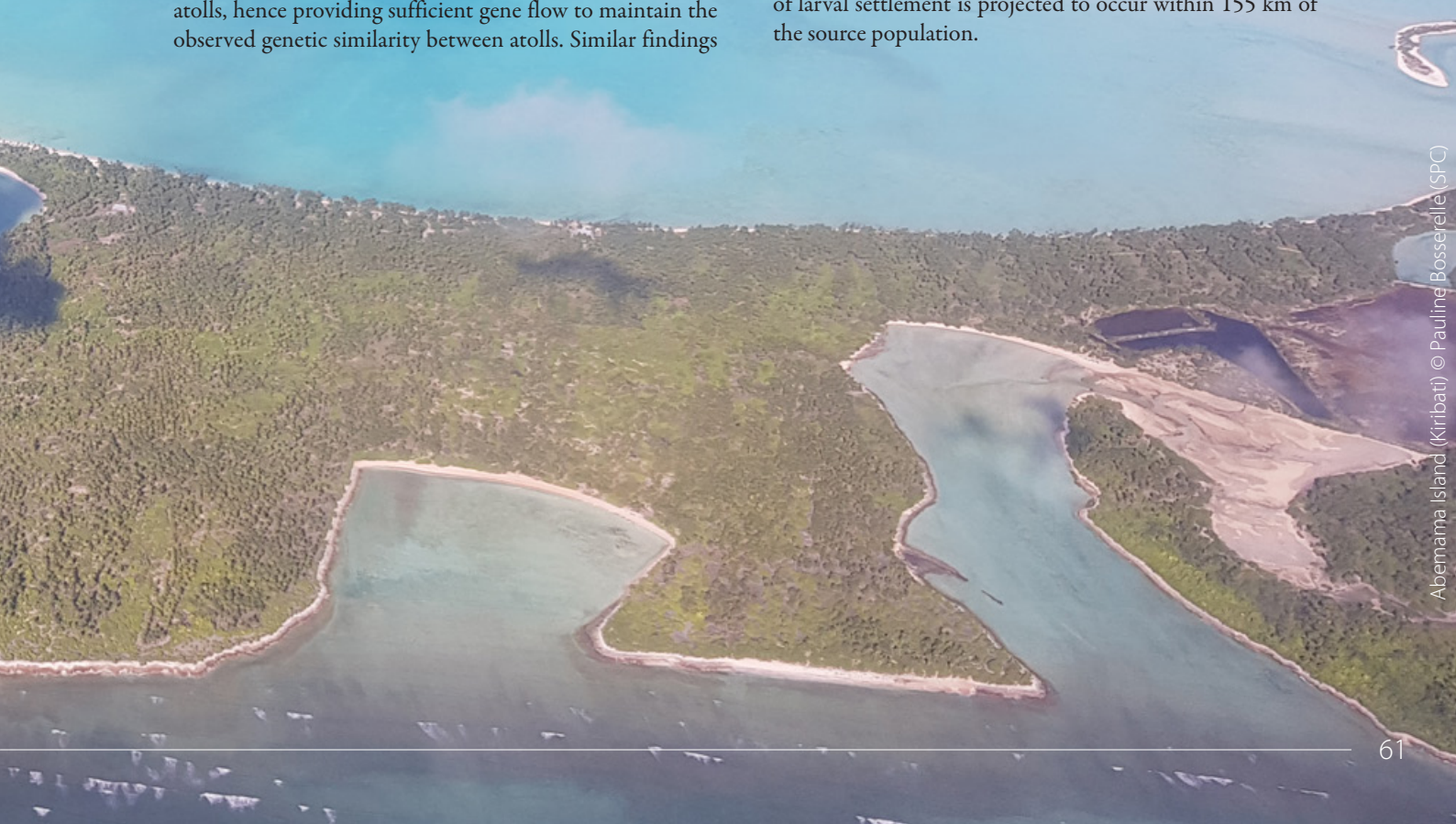
have been reported in the Line Islands, Kiribati where larvae from *A. glossodonta* population in Palmyra Atoll, separated by a distance of 700 km, were recruited from Kiritimati (Friedlander et al. 2007).

In terms of fisheries management, this result suggests that fish stocks from one atoll might be replenished by recruitment of larvae coming from other atolls. However, as only a few individuals are needed to maintain genetic similarity, a genetic analysis such as conducted here is insufficient to distinguish whether larval connectivity is frequent enough and large enough to be demographically relevant. Combining genetics studies with other approaches such as biophysical modelling will provide a much more powerful test of connectivity relevant to fisheries management (Leis et al. 2011). For example, by providing insights into the proportion of larvae that might survive to settle between atolls.

Therefore, under current levels of knowledge, the species we have investigated should be managed at the atoll level.

Genetic diversity gradient across atolls

For all species except *Lutjanus gibbus*, haplotypic diversity analysis revealed a descending genetic diversity gradient from Tarawa to Onotoa. One hypothesis to explain this gradient is that the proximity of an atoll to more adjacent reefs would favour more diverse larval recruitment. Within a 155 km radius, Tarawa, Abemama and Onotoa are, respectively, surrounded by six, five and four neighbouring atolls with a mean distance of 75 km to 80 km. According to the biophysical model by (Trembl et al. 2012), the greater the distance, the lower the probability of connection, 95% of larval settlement is projected to occur within 155 km of the source population.



Another recognised influence on genetic diversity is habitat size and fragmentation (e.g. Rauch and Bar-Yam 2005; Manel et al. 2020). Total lagoon area is two to four times larger in Tarawa than Abemama and Onotoa, which correlates positively to the genetic diversity gradient.

Irrespective of the drivers underlying the observed patterns, genetic diversity has been used in fisheries as an indicator of population declines (Smith 1994). The observed genetic diversity of these four species should be considered a reference point that can be periodically monitored to assess the longer term stability of stocks (Bruford et al. 2017).

Confirmation of bonefish species

All bonefish specimens collected for this study were confirmed to be *Albula glossodonta*. This aligns with previous work on bonefish species diversity in the region, which has found only *A. glossodonta* across numerous locations in Kiribati (Friedlander et al. 2007; Wallace 2015).

Historical population reduction hypothesis

Owing to the significant non-neutrality tests and the diagnostic star-shaped Median-Joining haplotypic network, we suggest that *A. glossodonta* has undergone a significant population reduction, known as a bottleneck effect, at some stage in its evolutionary history (Bouzat 2010; Nei et al. 1975). This trend has been observed on a larger geographic scale in the Indo-Pacific Ocean (Friedlander et al. 2007; Williams et al. 2020).

While the cause of bottleneck effect has been mainly attributed to anthropogenic and ecological factors such as environmental variations, introduction of non-native species, habitat destruction and overexploitation, the consequences and its management implications remain unclear (Atarhouch et al. 2006; Bouzat 2010; Parra et al. 2018).

According to the paradigm of inbreeding depression, a reduction in the genetic diversity of a population caused by a bottleneck effect can have a deleterious impact on its fitness and affect the viability of the population in the long term, and increasing its risk of extinction (Bouzat 2010; Charpentier et al. 2005; Da Silva et al. 2006).

While the paradigm of inbreeding depression suggests that the loss of genetic diversity resulting from a bottleneck effect can directly lead to extinction, this relationship may be oversimplified. Some researchers argue that other factors, such as phenotypic adaptation, could play a critical role in a population's survival (Bouzat 2010). Therefore, a more complex approach may be necessary to fully understand the dynamics between genetic diversity and extinction risk.

Limitations of the study

Sampling

Sampling was opportunistic from fishers at the time, hence there are low numbers or missing samples from some combinations of atoll and fish species (e.g. the lack of *Lutjanus gibbus* samples from Tarawa, and the relatively low sample size from Onotoa). Missing or small sample sizes limits the inferences that can be made from analyses of the genetic material. Further sampling will be undertaken in the near future to fill in these gaps and to add additional species to the investigations.

Genetic method

It is known that the *cyt b* gene is more conserved than the mtDNA CR (Ardura et al. 2013), and may fail to detect different subpopulations at small geographic scales. It nevertheless remains a widely referenced universal gene that is technically straightforward to investigate without the need for developing prior sequencing and proven trials, which makes it a practical choice for many genetic studies (Cantatore et al. 1994). Further investigations using microsatellite approaches and/or developing mtDNA CR primers for *Albula glossodonta* and *Lutjanus gibbus* would, therefore, be necessary to confirm the presence or absence of genetically different populations.

Conclusions

As coastal fisheries species continue to be heavily fished and as (human) Pacific Island populations continue to grow, the need for effective management remains as urgent as ever. In order for management to be effective, it needs to be driven by decisions that are informed by scientifically rigorous data. This study provides foundational evidence of linkages between fish populations across the atolls making up the Gilbert Islands, and confirms the existence of a single species of bonefish in the region. These results should be thought of as a starting point from which further targeted work can be done to obtain the necessary data on which to implement sustainable coastal fishing approaches for Kiribati.

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