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Range-Wide Population Structure of 3 Deepwater Eteline Snappers Across the Indo-Pacific Basin

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Abstract

Deep-sea habitats may drive unique dispersal and demographic patterns for fishes, but population genetic analyses to address these questions have rarely been conducted for fishes in these environments. This study investigates the population structure of 3 tropical deepwater snappers of the genus *Etelis* that reside at 100–400 m depth, with broad and overlapping distributions in the Indo-Pacific. Previous studies showed little population structure within the Hawaiian Archipelago for 2 of these species: *Etelis coruscans* and *E. carbunculus*. Here we extend sampling to the entire geographic range of each species to resolve the population genetic architecture for these 2 species, as well as a recently exposed cryptic species (*Etelis sp.*). One goal was to determine whether deepwater snappers are more dispersive than shallow-water fishes. A second goal was to determine whether submesophotic fishes have older, more stable populations than shallow reef denizens that are subject to glacial sea-level fluctuations. Both goals are pertinent to the management of these valuable food fishes. A total of 1153 specimens of *E. coruscans* from 15 geographic regions were analyzed, along with 1064 specimens of *E. carbunculus* from 11 regions, and 590 specimens of *E. sp.* from 16 regions. The first 2 species were analyzed with mtDNA and 9–11 microsatellite loci, while *E. sp.* was analyzed with mtDNA only. *Etelis coruscans* had a non-significant microsatellite global F_{ST}, but significant global mtDNA Φ_{ST} = 0.010 (P = 0.0007), with the isolation of Seychelles in the western Indian Ocean, and intermittent signals of isolation for the Hawaiian Archipelago. *Etelis carbunculus* had a non-significant microsatellite global F_{ST}, and significant global mtDNA Φ_{ST} = 0.021 (P = 0.0001), with low but significant levels of isolation for Hawai'i, and divergence between Tonga and Fiji. *Etelis sp.* had mtDNA Φ_{ST} = 0.018 (P = 0.0005), with a strong pattern of isolation for both Seychelles and Tonga. Overall, we observed low population

structure, shallow mtDNA coalescence (similar to near-shore species), and isolation at the fringes of the Indo-Pacific basin in Hawai'i and the western Indian Ocean. While most shallow-water species have population structure on the scale of biogeographic provinces, deepwater snapper populations are structured on the wider scale of ocean basins, more similar to pelagic fishes than to shallow-water species. This population structure indicates the capacity for widespread dispersal throughout the Indo-Pacific region.

Subject area: tree of life: population structure, phylogeography and phylogenomics
Keywords: dispersal, marine fishes, microsatellites, mitochondrial DNA, demographic history, submesophotic zone

Patterns of genetic connectivity across the Indo-Pacific have been evaluated for many shallow-water marine organisms (e.g., Eble et al. 2015), and to some extent, these investigations extend to organisms inhabiting the deep sea, such as plankton and the pelagic fauna that are captured in commercial fishing operations (e.g., Andrews et al. 2014a; Graves and McDowell 2015; Taylor and Rotterman 2017). While each species shows unique patterns of population structure, some generalities have emerged in broadly distributed species (reviewed in Bowen et al. 2016). Many shallow-water species show a partition at the Indo-Pacific Barrier (IPB) between the Pacific and Indian Oceans, and strong isolation of peripheral habitats in Hawai'i, Fiji, and the Red Sea (e.g., Drew and Barber 2012; DiBattista et al. 2013; Gaither and Rocha 2013; Coleman et al. 2016). In contrast, zooplankton show partitions on the scale of large water masses (Goetze et al. 2017; Iacchei et al. 2017; Wall-Palmer et al. 2018). Many pelagic fishes have isolated populations on the scale of whole ocean basins (Chow et al. 2000; Graves and McDowell 2015; Reid et al. 2016) or global homogeneity (Theisen et al. 2008; Veríssimo et al. 2017). However, few studies have investigated population connectivity of the coastal faunas below the photic zone (>100 m depth), generally recognized as the edge of the continental shelf (Pinet 2003). One prominent question is whether these deep-sea (submesophotic) fauna have population structures similar to the adjacent shallow-water community, or more similar to the wide-ranging pelagic species.

Etelis snappers (Lutjanidae) are large (>65 cm) carnivores that occupy submesophotic habitats (90–400 m, but usually 200–350 m) across the Indo-Pacific. These species are slow-growing and long-lived (up to 32 years for *E. carbunculus*, 55 years for *E. coruscans*, 56 years for *E. sp.*; Williams et al. 2017; Wakefield et al. 2020, Allen H. Andrews, personal communication), and are highly prized as food fish in many regions, prompting the implementation of management plans to assure sustainable fisheries (DeMartini and Lau 1999; Williams et al. 2013; Newman et al. 2015, 2016, 2017; Wakefield et al. 2020; Uehara et al. 2020). Prior to this study, no comprehensive range-wide genetic surveys within this group have been conducted. While the larvae of shallow water snappers generally reside above the continental shelf, the larvae of Eteline snappers reside further offshore and have a longer pelagic phase (Leis 1987), possibly indicating greater dispersal potential.

Until recently, *Etelis coruscans* (Onaga, Deepwater longtail red snapper, Flametail snapper) and *Etelis carbunculus* (Ehu, Deepwater red snapper, Pygmy ruby snapper) were believed to have similar distributions from Africa to Hawai'i, and from the Sea of Japan to New Zealand. However, differences in adult body size across the range of *E. carbunculus* prompted suspicions that there could be 2 or more species within this taxonomic unit. Andrews et al. (2016) demonstrated that *E. carbunculus* is actually 2 species distinguished by subtle morphological differences and a mitochondrial DNA (mtDNA) cytochrome *b* (cyt*b*) divergence of $d = 0.081$. Multivariate analysis of otolith morphometry was also able to discriminate these 2 cryptic species (Wakefield et al. 2014). Although a formal species description distinguishing these 2 species has not yet been published, inspection of the holotype by Andrews et al. (2016) indicated that the valid *E. carbunculus* is widespread across the Indo-Pacific, whereas the new species (*E. sp.*) is known only from the Indian Ocean and southwestern Pacific (Randall et al. 2019; Figure 1).

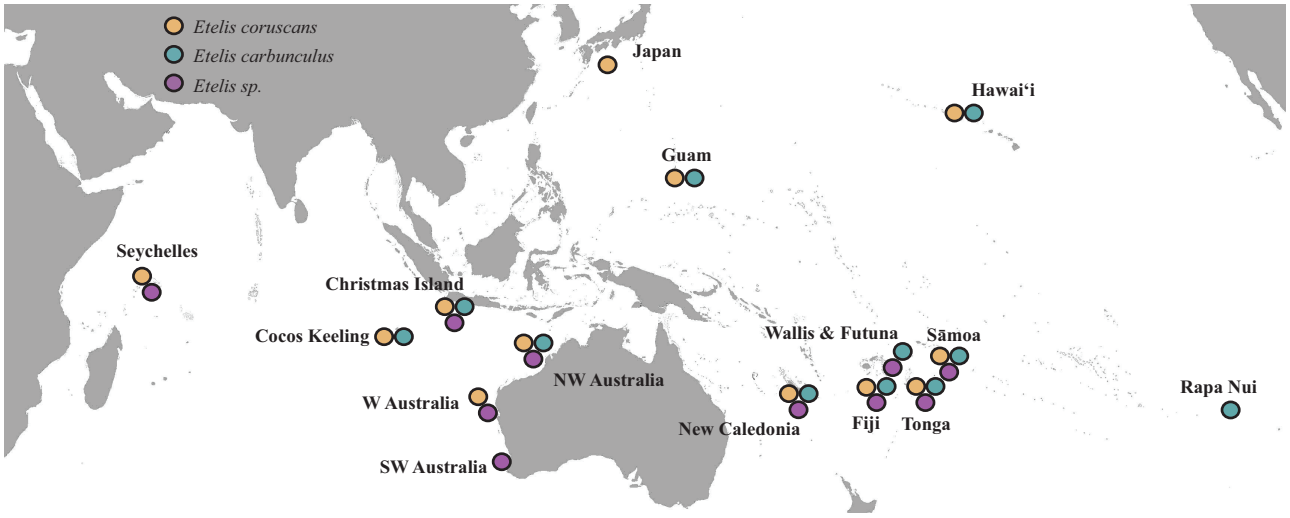

Figure 1. Sampling locations for the 3 species. Colored circles indicate specimens were collected at that location for each given species.

All 3 species inhabit hard substrate with high structural complexity and/or high relief (Ralston 1979). However, these species have different habitat usage, and these differences may influence adult dispersal and genetic connectivity. Adult *E. carbunculus* (and presumably *E. sp.*) are more closely associated with the bottom substrate of crevasses and ledges (Chris Kelley, personal observation) and therefore may exhibit greater genetic structure due to lower dispersal by juveniles and adults. In contrast, *E. coruscans* is more pelagic, feeding up to 50 meters above the bottom, and this species does not show the site fidelity that is typical for most shallow water snappers (Okuyama et al. 2019). This may translate into higher dispersal and reduced population structure in *E. coruscans*.

This study sampled the range-wide distribution of *E. carbunculus*, *E. coruscans*, and *E. sp.* to examine population connectivity and demographic history. For *E. carbunculus* and *E. coruscans*, specimens were surveyed using mtDNA cyt*b* sequences and 9–11 microsatellite loci. Due to funding limitations, *E. sp.* samples were surveyed with mtDNA cyt*b* only. We discuss the results of these analyses in the context of the limited literature on population genetics of deep shelf fishes, to evaluate connectivity and demographic history in the submesophotic fishes relative to the adjacent shallow-water fishes.

Methods

Specimen Collection and DNA Extraction

A total of 1153 specimens were collected from 15 geographic regions for *E. coruscans*, 1064 specimens from 11 regions for *E. carbunculus*, and 590 specimens from 16 regions for *E. sp.* (Table 1, Figure 1). Some of these specimens were used in 2 previous population genetic studies, as described below in the sections on mitochondrial DNA sequencing and microsatellite genotyping (Andrews et al. 2014b; Andrews et al. 2016); in one of these studies, *E. carbunculus* was called "*Etelis marshi*" (Andrews et al. 2014b) due to nomenclatural confusion and the existence of the cryptic species *E. sp.* (Andrews et al. 2016). Tissue specimens consisted of fin clips or muscle tissue collected by commercial fishers, purchased in fish markets, or collected on research cruises, and stored in salt-saturated DMSO buffer (Seutin et al. 1991). Within the Hawaiian Archipelago, specimens were collected between 1997 and 2012. For all other locations, specimens were collected between 2004 and 2012. Genomic DNA extractions were conducted using a phenol-chloroform method (Cummings and Thorgaard 1994), DNeasy extraction kits (Qiagen, Valencia, CA), or the Hotshot method (Meeker et al. 2007).

Table 1. Sample sizes for *Etelis coruscans*, *E. carbunculus*, and *E. sp.* for each marker type (cyt*b* and microsatellites), and sample collection year

	Etelis coruscans			*Etelis carbunculus*			*Etelis sp.*	
Location	cyt*b*	Msats	Years collected	*cyt*b	Msats	Years collected	cyt*b*	Years collected
Seychelles	48	40	2009				31	2009
Cocos (Keeling)	2	2	2009	7		2009		
Christmas Island	5	5	2009	13		2009	2	2009
NW Australia								
Heywood Shoal				1		2009	9	2009
Ashmore Reef							17	2009
Scott Reef	9	4	2009				44	2009
Clerke Reef	10	9	2009				44	2009
Imperieuse Reef	2	2	2009				36	2009
W Australia								
Ningaloo	33	21	2009					
Gascoyne	3	2	2009				25	2009
Coral Bay							54	2009
SW Australia								
Capes							9	2011
Perth							13	2011
Japan	3		2004					
Guam	70	88	2006	69	67	2006		
New Caledonia	52	46	2007	22		2007, 2012	164	2007, 2012
Wallis & Futuna				19		2012	42	2012
Fiji	64	117	2007	42		2007, 2012	48	2007, 2012
Tonga	38	33	2007	61	19	2007, 2012	15	2007, 2012
Sāmoa	27	28	2004–2005	63	47	2004–2005	37	2004–2005
Rapa Nui				1		2011		
Hawaiian Archipelago								
Raita	26	15	2005–2006					
Gardner	104	82	2006	31	32	2006		
St. Rogatien	23	23	2005	31	27	2006		
Brooks Banks	76	65	2005–2006					
All other islands	558	504	1997–2007	704	679	1998–2007		
Total	1153	1086		1064	871		590	

Mitochondrial DNA Sequencing

We used cytochrome *b* (cyt*b*) sequence data from 2 previous studies for *E. coruscans* and *E. carbunculus* collected throughout the Hawaiian Archipelago (Andrews et al. 2014b), and for *E. carbunculus* and *E. sp.* collected from 13 additional regions in the Indo-Pacific (Andrews et al. 2016; Table 1, Figure 1). In this study, we also generated cyt*b* sequence data for *E. coruscans* specimens collected from 11 additional regions in the Indo-Pacific (Table 1, Figure 1). PCR conditions and DNA sequencing methods were consistent across all studies. For *E. coruscans*, a 560bp fragment was amplified using the primers Cyb-05 L15020 (GCCAACGGCGCATCCTTCTTCTT; Meyer 1993) and Cyb-07 H15573 (AATAGGAAGTATCATTCGGGTTTGATG; Taberlet et al. 1992). For. *E. carbunculus* and *E. sp.*, a 524bp fragment was amplified using the primers EhucybF (TCAGTCGCACACATCTGCCG) and EhucybR (AGTGCAACAAGGACGGCTGC), both from Andrews et al. (2014b); this region overlaps the region amplified for *E. coruscans*. PCR products were sequenced in one direction using an ABI 3730 automated DNA sequencer (Applied Biosystems, Foster City, CA), and sequences were edited and aligned using GENEIOUS PRO 5.6.2 (Biomatters, LTD, Auckland, NZ).

Microsatellite Genotyping

We used microsatellite data obtained from the study of Andrews et al. (2014b) for *E. coruscans* and *E. carbunculus* specimens collected throughout the Hawaiian Archipelago (Table 1). We also generated microsatellite data from 10 additional Indo-Pacific locations for *E. coruscans* and 3 additional Indo-Pacific locations for *E. carbunculus* (Table 1, Figure 1). Microsatellite PCR and genotyping protocols followed those described in Andrews et al. (2014b), and were conducted by the same person as in the previous study for each species. A total of 10 microsatellite loci were analyzed for *E. coruscans* and 11 microsatellite loci for *E. carbunculus*. PCR products were analyzed on ABI 3730XL or ABI 3130XL genetic analyzers, with all fragments from each primer set run on one machine to avoid bias in fragment length estimates across sequencers. Fragments were scored using GENEMAPPER 4.0 (Applied Biosystems).

GENALEX 6.5 (Peakall and Smouse 2006) was used to identify specimens with identical microsatellite genotypes to determine whether any individual fish were represented more than once in the dataset. Each microsatellite locus was tested for deviations from Hardy–Weinberg Equilibrium (HWE) and linkage equilibrium using ARLEQUIN 3.5.2.2 (Excoffier and Lischer 2010) for all locations outside of the Hawaiian Archipelago with $n \geq 10$. Tests for deviation from HWE and linkage equilibrium for the samples from the Hawaiian Archipelago were reported in Andrews et al. (2014b). Bayesian clustering analyses (described below) were also conducted removing one locus at a time to investigate the influence of each locus on the results.

Population Diversity and Structure

For cyt*b*, we estimated nucleotide and haplotype diversities using ARLEQUIN. For microsatellites, we estimated observed heterozygosity, expected heterozygosity, allelic richness, and total number of alleles for each locus using ARLEQUIN and FSTAT 2.9.3.2 (Goudet 2001). Diversity estimates were calculated for each sampling location with $n \geq 10$.

For cyt*b*, we evaluated the genetic similarity across sampling locations by creating median-joining haplotype networks with NETWORK 5.0 (Bandelt et al. 1999). Unnecessary median vectors and links were removed using the maximum parsimony option. We calculated pairwise and global Φ_{ST} for cyt*b* and pairwise F_{ST} for microsatellites with ARLEQUIN, using sampling locations with $n \geq 13$. Statistical significance was evaluated using 10 000 permutations.

Genetic structure was further evaluated for microsatellite loci using Bayesian clustering analyses in STRUCTURE 2.3.4 (Pritchard et al. 2000). We used the admixture and correlated allele frequency models, with a burn-in of 10^5 steps followed by 10^6 steps. Analyses were conducted 5 times each for $K = 1$ to $K = 9$, both with and without using sampling location as a prior.

Andrews et al. (2014b) used the same cyt*b* and microsatellite markers for *E. coruscans* and *E. carbunculus* across the Hawaiian Archipelago and found evidence for several genetically distinct locations within the middle of the archipelago, but no genetic structure across the remainder of the archipelago. Therefore, for population structure and diversity analyses, we merged all sampling locations within the Hawaiian Archipelago except the locations that had previously shown evidence for genetic structure (for *Etelis coruscans*: Raita, Gardner, St. Rogatien, and Brooks Banks; and for *Etelis carbunculus*: Gardner, St. Rogatien). Notably, Andrews et al. (2014b) found that temporal sampling (from 1997 to 2012) had no influence on the inference of allele frequencies or genetic structure. This temporal range was greater than that for the additional sampling locations included in our study (2004–2012), and therefore it is unlikely that temporal sampling influenced the results of the present study.

Demographic History

We evaluated the evidence for recent demographic expansions using Tajima's *D* and Fu's F_S tests (Aris-Brosou and Excoffier 1996; Fu 1997; Tajima 1989a, 1989b) implemented in ARLEQUIN with the cyt*b* sequence data. These analyses test for departures from mutation-drift equilibrium, with large negative values of the test statistics providing evidence for recent demographic expansions or selection. These analyses were conducted for sampling locations with $n \geq 13$.

We used a mismatch analysis to estimate time since coalescence, initial female effective population size (N_{ef}), and current N_{ef} using ARLEQUIN. We used a cyt*b* divergence rate of 2% between lineages (1% within lineages), which is consistent across many teleost fishes (Bowen et al. 2001; Lessios 2008; Reece et al. 2010), and a generation time of 10 years (Andrews et al. 2014b). Notably, the cyt*b* divergence rate and generation time have not been validated for our 3 study species, and therefore we caution against a strict interpretation of coalescence times and N_{ef}.

Results

Editing of mtDNA sequence data resulted in a fragment size of 490 for *E. coruscans* and 436 for *E. carbunculus* and *E. sp.*, as described in Andrews et al. (2016). Microsatellite genotypes generated for this study are reported in Supplementary Tables S1 and S2, and cyt*b* sequences that were new to this study have been deposited in GenBank (accession numbers MT814889–MT815254). For *E. coruscans*, no 2 specimens had identical multilocus microsatellite genotypes. For *E. carbunculus*, matching genotypes were found for 3 pairs of specimens collected from Guam and 4 pairs from Tonga. For subsequent analyses, microsatellite and cyt*b* data were retained for only one specimen from each matching pair, to arrive at the sample sizes reported above.

Microsatellite Quality Control

For *E. coruscans*, one microsatellite locus deviated from HWE after Bonferonni correction in 5 geographic locations (locus EtelisO22O2) and one locus deviated in 4 locations (locus EtelisG23O1). These 2 loci also deviated from HWE at many loci in the Hawaiian Archipelago for *E. coruscans* in the study of Andrews et al. (2014b). In addition, 3 microsatellite loci deviated from HWE for *E. coruscans* in one location (locus EtelisE2E2 in Guam, locus EtelisG8E1 in Fiji, locus EtelisE20O2 in New Caledonia). STRUCTURE analyses conducted removing one locus at a time indicated that locus EtelisE20O2 had a strong influence on population structure, but no other loci influenced the results. Inspection of genotype calls for this locus revealed that the population structure results were likely driven by genotype calling errors associated with inconsistent migration in acrylamide gels. Therefore, locus EtelisE20O2 was removed from subsequent analyses, resulting in a total of 9 loci for this species.

For *E. carbunculus*, one microsatellite locus deviated from HWE after Bonferonni correction in Guam and Sāmoa, but not in Tonga (locus EtelisG8E1). This same locus was found to deviate from HWE at many locations within the Hawaiian Archipelago for this species in the study of Andrews et al. (2014b). One additional locus deviated from HWE in Sāmoa (locus EtelisE2E2). STRUCTURE analyses conducted removing one locus at a time found similar results across all analyses. Therefore, we present here the results of population structure and diversity analyses obtained using all loci for this species. We found no evidence for linkage disequilibrium between any microsatellite loci for *E. coruscans* or *E. carbunculus* after Bonferroni correction.

Genetic Diversity

Standard measures of mtDNA variation (nucleotide and haplotype diversity) for cyt*b* were consistently highest across sampling locations for *E. sp.* and lowest for *E. carbunculus* (Supplementary Tables S3–S5, Figure 2). For *E. coruscans*, cyt*b* diversity was highest at St. Rogatien (near the middle of the Hawaiian Archipelago, haplotype diversity (h) = 0.84, nucleotide diversity (π) = 0.0037) and lowest at Sāmoa (h = 0.65, π = 0.0019) (Supplementary Table S3, Figure 2). Microsatellite allelic richness (A_R) and expected heterozygosity (H_e) for *E. coruscans* were highest in New Caledonia (A_R = 7.19, H_e = 0.763), whereas observed heterozygosity (H_o) was highest for Ningaloo (H_o = 0.729) (Supplementary Table S3, Figure 3a). Allelic richness was lowest for Raita (A_R = 6.32), H_o was lowest for Gardner (H_o = 0.621), and H_e was lowest for Seychelles (H_e = 0.676).

For *E. carbunculus*, cyt*b* diversity was highest at Gardner (near the middle of the Hawaiian Archipelago, h = 0.49, π = 0.0014) and lowest at Tonga (h = 0.16, π = 0.00044) (Supplementary Table S4, Figure 2). In contrast, microsatellite diversity was highest at Tonga (A_R = 6.00, H_o = 0.704, H_e = 0.754) and lowest at Gardner (A_R = 4.34, H_o = 0.563, H_e = 0.615) (Supplementary Table S4, Figure 3b).

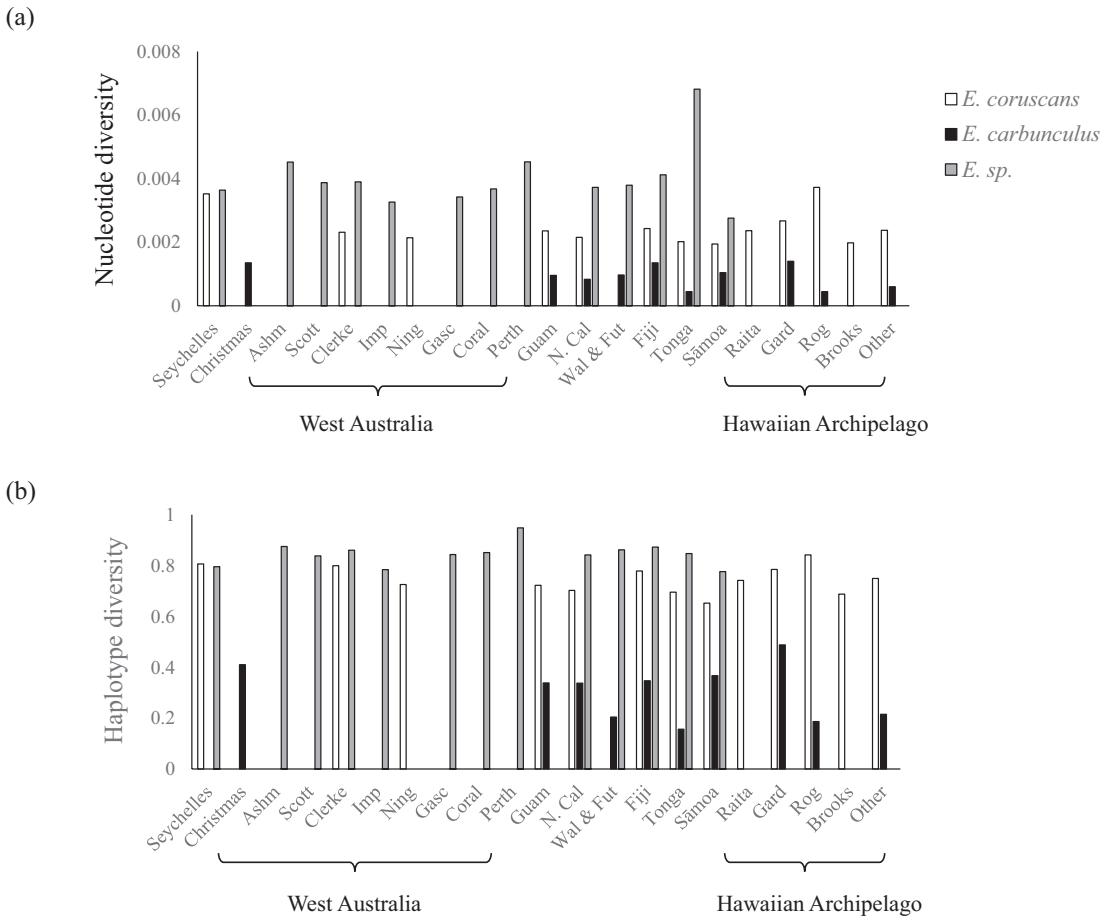

Figure 2. Cytochrome *b* diversity for 3 species across sample sites. (**a**) Nucleotide diversity, and (**b**) haplotype diversity.

For *E. sp.*, cyt*b* diversity was highest at Tonga (h = 0.85, π = 0.0068) and lowest at Imperieuse Reef (h = 0.78, π = 0.0033) (Supplementary Table S5, Figure 2). All the values reported here lie within the range of shallow coastal species.

Population Structure

Global F_{ST} values indicated an overall weak but significant genetic structure for all 3 species. For cyt*b*, global Φ_{ST} values were significant for all 3 species, with the highest value for *E. carbunculus* (Φ_{ST} = 0.021, P = 0.0001), the lowest value for *E. coruscans* (Φ_{ST} = 0.010, P = 0.0007), and an intermediate value for *E. sp.* (Φ_{ST} = 0.018, P = 0.0005). For microsatellites, global F_{ST} values were nonsignificant for both *E. coruscans* and *E. carbunculus*. Haplotype networks showed no clustering of haplotypes by geographic location for any of the 3 species (Figure 4). The haplotype networks for all 3 species had a shallow starburst-like pattern characteristic of rapid demographic expansion, with the strongest starburst pattern for *E. coruscans* and *E. carbunculus* (Figure 4). A starburst pattern resulting from a demographic expansion is characterized by a small number of founder haplotypes and a large number of recently evolved haplotypes that have few mutational differences from the founder haplotypes (Slatkin and Hudson 1991), a common pattern in marine fishes (Grant and Bowen 1998).

For *E. coruscans*, pairwise F_{ST} analyses indicated Seychelles is distinct from all other locations sampled (Table 2); all pairwise comparisons involving Seychelles were significant for microsatellites (F_{ST} values ranging from 0.021 to 0.071), and most were significant for cyt*b* (significant Φ_{ST} values ranging from 0.021 to 0.074, P < 0.05). In addition, the Hawaiian Archipelago was distinct from several locations for cyt*b* (Guam, Tonga, Sāmoa, and Seychelles), although significance was not consistent across Hawaiian sites, with sites in the middle of the archipelago most often distinct from other locations. For microsatellites, no pairwise F_{ST} values were significant aside from comparisons involving Seychelles. STRUCTURE analyses supported the genetic distinction of Seychelles. The highest likelihood occurred at K = 1 for analyses without a location prior and K = 2 for analyses with a location prior (Supplementary Figure S1). Visual inspection of the ancestry proportion plots for all K > 1 showed the Seychelles as a distinct cluster for the analyses with a location prior (Figure 5a, Supplementary Figure S1). Analyses without a location prior showed no evidence for distinct population clusters.

For *E. carbunculus*, pairwise F_{ST} analyses indicated the Hawaiian Archipelago is distinct from many other locations (Table 3). For microsatellites, all pairwise F_{ST} comparisons between Hawai'i and other locations were significant except Rogatien (Hawai'i) versus Guam; the significant F_{ST} values ranged from 0.012 to 0.029 (P < 0.05). For cyt*b*, many pairwise Φ_{ST} comparisons between Hawai'i and other locations were also significant, with significant values ranging from 0.020 to 0.059 (P < 0.05). However, these cyt*b* pairwise Φ_{ST} values were lower for Rogatien than other Hawai'i locations, possibly indicating greater connectivity between Rogatien and locations outside Hawai'i. In addition, no Hawai'i locations were distinct from New Caledonia or Wallis & Futuna for mtDNA, potentially indicating higher connectivity between these locations and Hawai'i (we did not have microsatellite data from these 2 locations). Outside of Hawai'i, the only significant pairwise F_{ST}

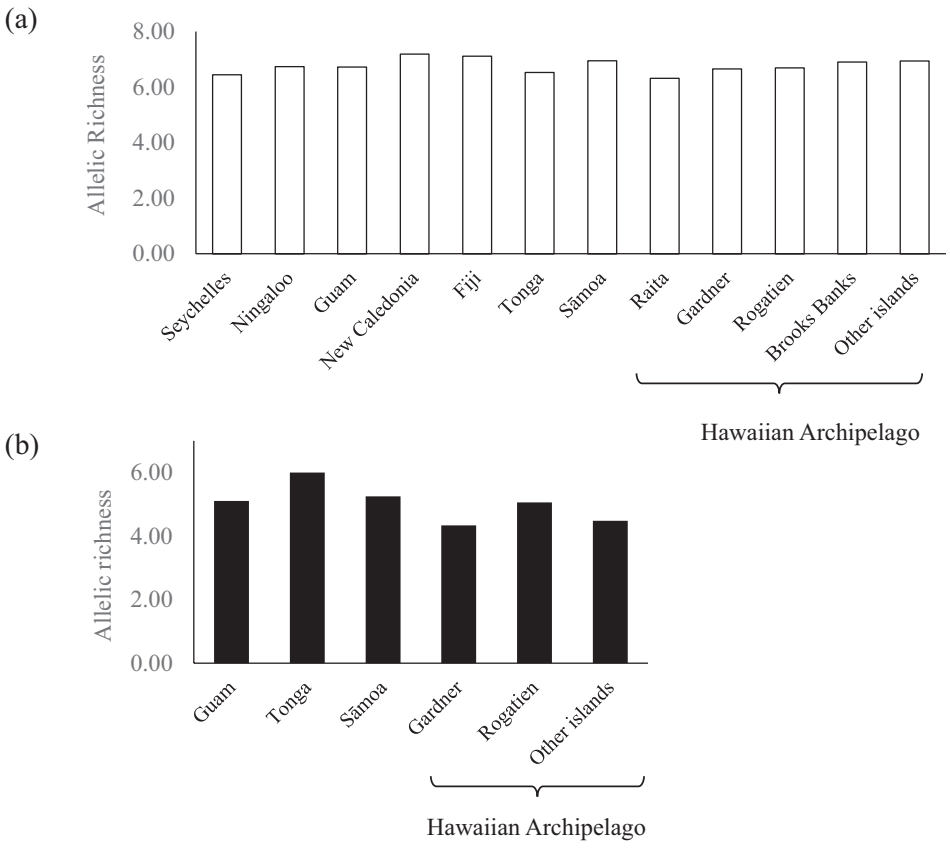

Figure 3. Microsatellite allelic richness for (**a**) *Etelis coruscans* and (**b**) *Etelis carbunculus*.

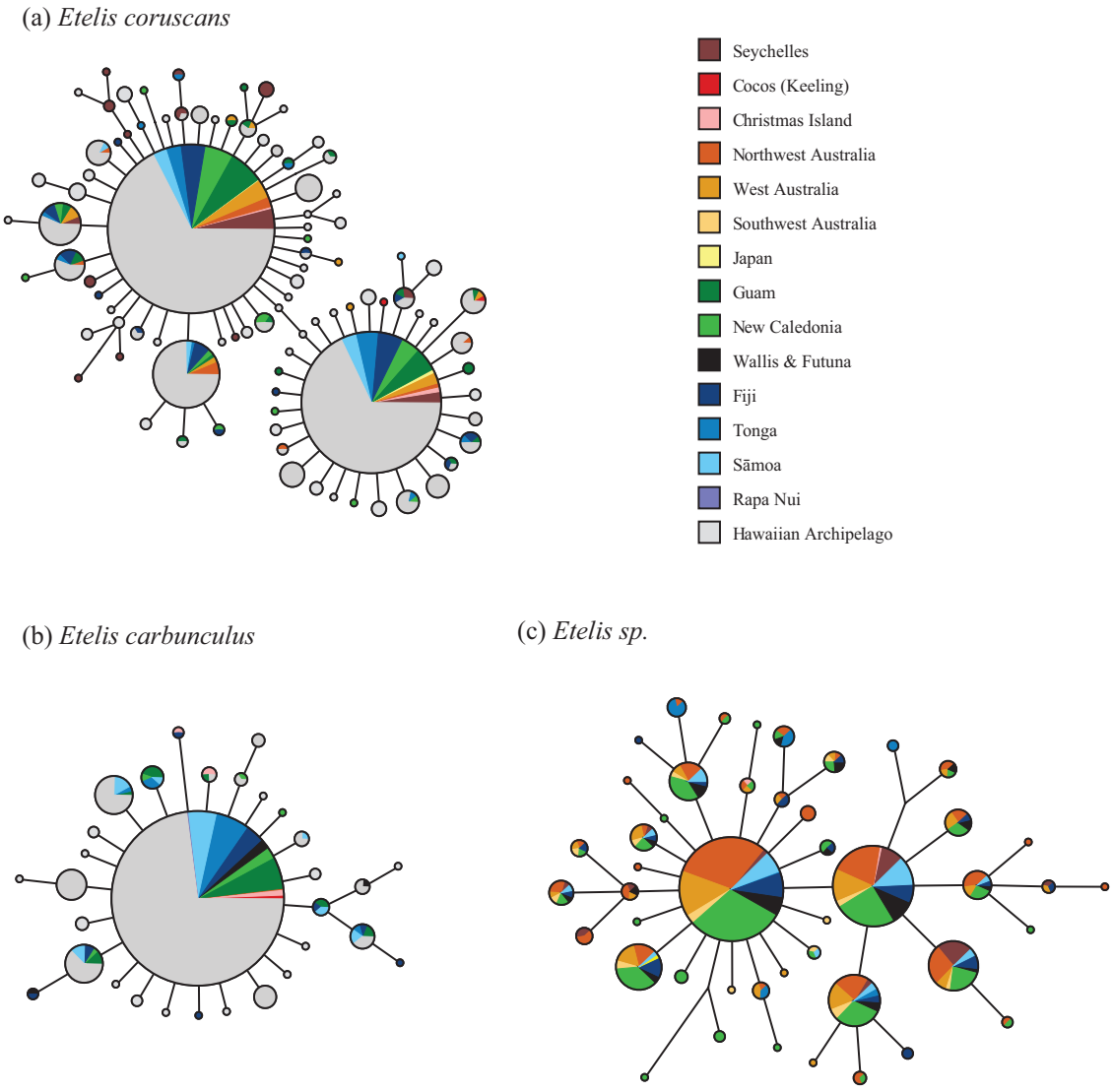

Figure 4. Median-joining networks of cytochrome *b* haplotypes for (**a**) *Etelis coruscans*, (**b**) *Etelis carbunculus*, and (**c**) *Etelis sp.* Each circle represents a unique haplotype, the size of the circle reflects the number of individuals with that haplotype, and the lengths of the lines reflect the number of mutational steps between haplotypes.

Table 2. Pairwise F_{ST} and Φ_{ST} values for *Etelis coruscans*

	Seychelles	Ningaloo	Guam	N. Cal.	Fiji	Tonga	Sāmoa	Hawai'i: Raita	Hawai'i: Gardner	Hawai'i: Rogatien	Hawai'i: Brooks	Hawai'i: Other
Seychelles		0.071*	0.037*	0.021*	0.042*	0.046*	0.035*	0.063*	0.034*	0.057*	0.040*	0.051*
Ningaloo	0.011		−0.039	−0.036	−0.036	−0.004	−0.020	0.000	−0.039	−0.043	−0.034	−0.022
Guam	0.024*	−0.011		−0.014	−0.010	−0.025	−0.016	−0.009	0.001	−0.005	−0.002	−0.009
New Caledonia	0.021*	−0.013	−0.006		−0.006	−0.018	−0.011	−0.012	−0.014	0.000	−0.009	−0.001
Fiji	0.035*	−0.008	−0.003	−0.006		−0.018	−0.012	−0.003	−0.013	−0.006	−0.006	−0.002
Tonga	0.055*	0.014	0.002	0.016	0.008		−0.008	−0.002	−0.023	−0.011	−0.019	−0.007
Sāmoa	0.033*	−0.003	−0.01	−0.003	−0.011	−0.015		−0.001	−0.012	−0.013	−0.016	−0.004
Hawai'i: Raita	0.021	0.019	0.039*	0.018	0.027	0.100*	0.063*		−0.007	0.005	0.001	0.002
Hawai'i: Gardner	0.028*	−0.004	0.007	−0.003	−0.004	0.030*	0.001	0.003		−0.003	−0.001	−0.008
Hawai'i: Rogatien	0.016	0.006	0.016	0.006	0.002	0.048*	0.011	−0.013	−0.009		−0.001	−0.003
Hawai'i: Brooks	0.074*	0.02	0.012	0.022	0.011	−0.009	−0.015	0.099*	0.029*	0.051*		−0.004
Hawai'i: Other	0.046*	−0.004	−0.001	−0.001	−0.001	0.001	−0.013	0.046*	0.009*	0.024	0.004	

Bottom matrix: cyt*b*. Top matrix: microsatellites. Shading and asterisks indicate $P < 0.05$.

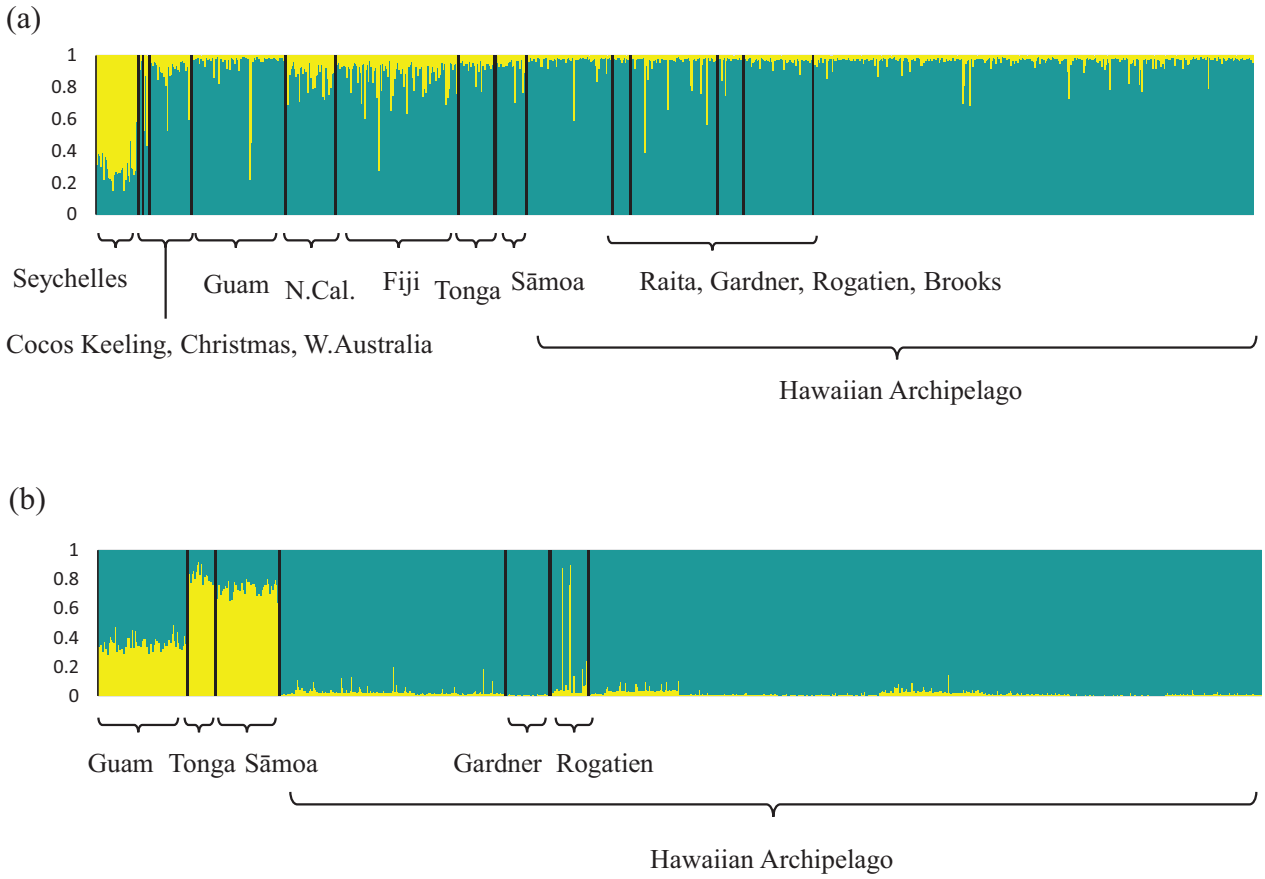

Figure 5. Bayesian clustering analysis results obtained with the program STRUCTURE 2.3.3 (Pritchard et al. 2000) at $K = 2$ using sampling location as a prior for (**a**) *Etelis coruscans* and (**b**) *Etelis carbunculus*.

Table 3. Pairwise F_{ST} and Φ_{ST} values for *Etelis carbunculus*

	Guam	N. Caledonia	Wallis & Futuna	Fiji	Tonga	Sāmoa	Hawai'i: Gardner	Hawai'i: Rogatien	Hawai'i: Other
Guam		*NA*	*NA*	*NA*	−0.002	−0.009	0.021*	−0.043	0.015*
N. Caledonia	−0.008		*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
Wallis & Futuna	−0.010	−0.012		*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
Fiji	−0.001	0.004	−0.019		*NA*	*NA*	*NA*	*NA*	*NA*
Tonga	0.001	−0.008	0.009	0.032*		−0.005	0.029*	0.015*	0.019*
Sāmoa	−0.004	0.003	−0.010	−0.002	0.014		0.021*	0.019*	0.012*
Hawai'i: Gardner	0.048*	0.013	0.022	0.040*	0.059*	0.047*		−0.056	0.002
Hawai'i: Rogatien	0.021	0.004	0.002	0.029	0.009	0.024	0.011		−0.048
Hawai'i: Other	0.023*	0.005	0.005	0.044*	0.003	0.020*	0.055*	−0.004	

Bottom matrix: cyt*b*. Top matrix: microsatellites. Shading and asterisks indicate $P < 0.05$.

comparisons for either microsatellites or cyt*b* was Tonga versus Fiji (cyt*b* $\Phi_{ST} = 0.032$).

STRUCTURE analyses provided further support for the genetic distinction of Hawai'i for *E. carbunculus*. The highest likelihood occurred at $K = 4$ for analyses without a location prior and $K = 2$ for analyses with a location prior (Supplementary Figure S2). However, visual inspection of the ancestry proportion plots for all $K > 1$ indicated a relatively consistent partitioning of population clusters across analyses, with the strongest partitioning between Hawai'i and all other locations, but also evidence for partitioning of Guam, Tonga/Sāmoa, and Rogatien (Figure 5b, Supplementary Figure S2).

For *E. sp.*, mtDNA pairwise Φ_{ST} comparisons indicated Seychelles & Tonga are distinct from all other locations (Table 4). All pairwise comparisons with Seychelles were significant ($P < 0.05$), with Φ_{ST} values ranging from 0.060 to 0.235. Most pairwise comparisons with Tonga were also significant, with significant values ranging from 0.085 to 0.235. The only nonsignificant comparisons for Tonga were Ashmore Reef and Perth.

Demographic History

For all 3 species, Fu's F_S values were negative and significant ($P < 0.05$) for most sampling locations, with the only exceptions being Wallis &

Table 4. Pairwise Φ_{ST} values for *Etelis sp.* for cyt*b*

	Seychelles	Ashmore Reef	Scott Reef	Clerke Reef	Imp. Reef	Gascoyne	Coral Bay	Perth	N. Cal.	Wallis & Futuna	Fiji	Tonga	Sāmoa
Seychelles													
Ashmore Reef	0.112*												
Scott Reef	0.062*	−0.007											
Clerke Reef	0.060*	0.007	−0.010										
Imperieuse Reef	0.156*	0.008	0.008	0.012									
Gascoyne	0.126*	−0.016	−0.003	0.007	−0.010								
Coral Bay	0.092*	−0.012	−0.010	0.003	0.004	−0.002							
Perth	0.131*	−0.023	−0.010	−0.008	−0.028	−0.034	−0.015						
New Caledonia	0.106*	−0.002	−0.003	0.002	−0.006	−0.009	−0.004	−0.017					
Wallis & Futuna	0.090*	−0.020	−0.012	−0.006	0.005	−0.009	−0.014	−0.021	−0.007				
Fiji	0.090*	−0.001	−0.008	−0.002	−0.009	−0.008	−0.011	−0.024	−0.008	−0.011			
Tonga	0.235*	0.058	0.124*	0.122*	0.111*	0.085*	0.138*	0.051	0.135*	0.102*	0.112*		
Sāmoa	0.080*	0.006	−0.013	−0.006	0.016	0.008	−0.006	0.004	−0.003	−0.013	−0.003	0.151*	

Shading and asterisks indicate $P < 0.05$.

Futuna for *E. carbunculus* and Tonga for *E. sp.* (Tables 5–7). Results were more variable across species for Tajima's *D* tests; the proportion of sampling locations with negative and significant ($P < 0.05$) Tajima's *D* values was 9 out of 11 for *E. coruscans*, 5 out of 8 for *E. carbunculus*, and 6 out of 13 for *E. sp.* (Tables 5–7).

Most coalescent time estimates for all 3 species were between 100 000 and 350 000 years (Tables 5–7). Values were lowest for *E. coruscans* (mean 132 653 years; range 102 041–193 878 years), intermediate for *E. sp.* (mean 223 183 years; range 149 083–481 651 years), and highest for *E. carbunculus* (mean 282 875; range 57 339–344 037 years). Estimates of initial N_{ef} were equal to zero for most sampling locations, indicating small founder populations. For *E. coruscans* and *E. sp.*, estimates of current N_{ef} reached the maximum possible value in the ARLEQUIN analysis (which was 99 999) for most sampling locations, whereas this was true for only one location for *E. carbunculus* (Gardner in the Hawaiian Archipelago). The N_{ef} values in the rest of the locations for *E. carbunculus* ranged from 2095 to 41 284.

Discussion

Our surveys of 3 *Etelis* snappers revealed shallow mtDNA coalescence and levels of genetic diversity that are well within the range of shallow coastal fishes (Figure 2, Tables 5–7). Pyle et al. (2019) suggested that populations below the level of glacial sea-level changes (~100 m) might be older and more stable than populations in shallow waters that are displaced or extirpated on a scale of 10^5 years. Older, more stable populations are expected to maintain higher levels of genetic diversity (Kimura 1983). Our data do not support this "older more stable" theme for deepwater fishes. Shallow mtDNA coalescences seem to be a ubiquitous feature in marine fishes, and one possible explanation is highly unstable populations with frequent bottlenecks (Grant and Bowen 1998), a plausible explanation for fauna under the influence of glacial sea-level fluctuations. However, the fact that we observe the same shallow coalescence in deepwater snappers that occur below the glacial sea-level fluctuations indicates the need for alternate explanations for this widespread observation. Prominent among them is the *r*-selected strategy of most marine fishes, wherein hundreds or thousands of eggs are produced but few survive to reproductive maturity. This would yield a small effective population size (N_e), which is the harmonic mean of reproducing individuals contributing to the next generation (Wright 1931). A harmonic mean is strongly affected by periods of low reproductive success and large fluctuations in N_e, resulting in an effective population size that is considerably less than the arithmetic mean size of each generation (Avise 2004; Hartl and Clark 2006). Sweepstakes reproduction would further reduce mtDNA diversity, wherein a small number of females (by chance) place progeny in optimal physical and environmental conditions for survival (Hedgecock and Pudovkin 2011). The *r*-selected strategy, combined with sweepstakes wherein a few females produce most of the next generation, could explain the shallow mtDNA coalescence in marine fishes, without having to invoke glacial population bottlenecks.

Our findings also revealed low population structure overall for all 3 *Etelis* species, with signals of isolation at the ends of the Indo-Pacific distributional range in Hawai'i and the western Indian Ocean. For *E. sp.*, mtDNA pairwise F_{ST} comparisons consistently showed isolation of Seychelles, our only sampling location from the western Indian Ocean, as well as isolation of Tonga in the South Pacific, located between Australia and French Polynesia (Table 4).

Table 5. Tajima's *D*, Fu's F_S, and mismatch parameter estimates for *Etelis coruscans*

Location	Tajima's *D*	Fu's F_S	τ (years)	Θ_0 ($N_{ft=0}$)	Θ_1 ($N_{ft=1}$)
Seychelles	−1.73*	−7.17*	1.9 (193 878)	0 (0)	11.95859 (122 026)
Ningaloo	−1.39	−3.56*	1.2 (122 449)	0 (0)	∞ (NA)
Guam	−2.13*	−15.95*	1.2 (122 449)	0 (0)	∞ (NA)
New Caledonia	−1.77*	−7.83*	1.1 (112 245)	0 (0)	∞ (NA)
Fiji	−1.63*	−9.13*	1.3 (132 653)	0 (0)	∞ (NA)
Tonga	−1.76*	−6.23*	1.1 (112 245)	0 (0)	∞ (NA)
Sāmoa	−1.14	−0.88*	1 (102 041)	0 (0)	∞ (NA)
Hawai'i: Raita	−1.83*	−6.55*	1.2 (122 449)	0 (0)	∞ (NA)
Hawai'i: Gardner	−2.11*	−23.08*	1.4 (142 857)	0.00176 (18)	∞ (NA)
Hawai'i: Rogatien	−1.83*	−7.48*	1.8 (183 673)	0 (0)	∞ (NA)
Hawai'i: Brooks	−1.78*	−7.29*	1.1 (112 245)	0 (0)	∞ (NA)
Hawai'i: Other	−2.32*	−28.59*	1.3 (132 653)	0 (0)	∞ (NA)

Shading and asterisks indicate $P < 0.05$. τ(years): coalescent time; Θ_0 ($N_{ft=0}$): initial female effective population size; Θ_1($N_{ft=1}$): post-expansion female effective population size. Some estimates of Θ_1 yielded the maximum allowable value (99 999, here indicated by ∞), so that calculation of $N_{ft=1}$ was not possible (NA).

Table 6. Tajima's *D*, Fu's F_S, and mismatch parameter estimates for *Etelis carbunculus*

Location	Tajima's *D*	Fu's F_S	τ (years)	Θ_0 ($N_{ft=0}$)	Θ_1 ($N_{ft=1}$)
Guam	−1.36	−5.04*	3 (344 037)	0 (0)	0.52559 (6027)
N. Caledonia	−1.88*	−3.82*	3 (344 037)	0 (0)	3.6 (41 284)
Wallis & Futuna	−1.86*	−0.57	3 (344 037)	0 (0)	0.18511 (2123)
Fiji	−1.75*	−5.77*	3 (344 037)	0 (0)	0.53535 (6139)
Tonga	−1.68*	−2.95*	3 (344 037)	0 (0)	0.18267 (2095)
Sāmoa	−1.32	−4.78*	0.5 (57 339)	0 (0)	2.2623 (25 944)
Hawai'i: Gardner	−1.39	−3.18*	0.7 (80 275)	0 (0)	∞ (NA)
Hawai'i: Rogatien	−1.73*	−3.44*	3 (344 037)	0 (0)	0.24248 (2781)
Hawai'i: Other	−2.23*	<−30*	3 (344 037)	0 (0)	0.2791 (3201)

Shading and asterisks indicate $P < 0.05$. τ(years): coalescent time; Θ_0 ($N_{ft=0}$): initial female effective population size; Θ_1($N_{ft=1}$): post-expansion female effective population size. Some estimates of Θ_1 yielded the maximum allowable value (99 999, here indicated by ∞), so that calculation of $N_{ft=1}$ was not possible (NA).

Table 7. Tajima's *D*, Fu's F_S, and mismatch parameter estimates for *Etelis sp.*

Location	Tajima's *D*	Fu's F_S	τ(years)	Θ_0 ($N_{ft=0}$)	Θ_1 ($N_{ft=1}$)
Seychelles	−0.91	−3.05	1.6 (183 486)	0 (0)	32.59063 (373 746)
Ashmore Reef	−1.22	−5.48	2.2 (252 294)	0.00352 (40)	∞ (NA)
Scott Reef	−1.71	−10.85	1.8 (206 422)	0.00176 (20)	∞ (NA)
Clerke Reef	−1.32	−7.68	1.8 (206 422)	0 (0)	∞ (NA)
Imperieuse Reef	−1.60	−10.25	1.5 (172 018)	0 (0)	∞ (NA)
Gascoyne	−1.21	−5.23	1.6 (183 486)	0 (0)	∞ (NA)
Coral Bay	−1.55	−10.19	1.7 (194 954)	0 (0)	∞ (NA)
Perth	−1.55	−7.30	2.2 (252 294)	0 (0)	∞ (NA)
New Caledonia	−1.83	−23.05	1.7 (194 954)	0 (0)	∞ (NA)
Wallis & Futuna	−1.66	−9.68	1.8 (206 422)	0 (0)	∞ (NA)
Fiji	−1.56	−11.31	1.9 (217 890)	0 (0)	∞ (NA)
Tonga	0.76	0.23	4.2 (481 651)	0.00352 (40)	26.54297 (304 392)
Sāmoa	−1.51	−5.16	1.3 (149 083)	0 (0)	∞ (NA)

Shading and asterisks indicate $P < 0.05$. τ(years): coalescent time; Θ_0 ($N_{ft=0}$): initial female effective population size; Θ_1($N_{ft=1}$): post-expansion female effective population size. Some estimates of Θ_1 yielded the maximum allowable value (99 999, here indicated by ∞), so that calculation of $N_{ft=1}$ was not possible (NA).

It would be informative to conduct more detailed sampling of the Oceania region around Tonga, as this probably represents the eastern fringe of the range for *E. sp*. The other member of the cryptic species pair, *E. carbunculus*, shows isolation of Hawai'i, at least from some locations, as well as genetic divergence between Tonga and Fiji (Table 3). *Etelis coruscans*, distributed from the central Pacific to eastern Africa, has isolated populations at the edges of its range in the Seychelles and Hawai'i (Table 2).

The Hawaiian Archipelago is consistently isolated in population genetic surveys of both shallow and deepwater fishes. The prevailing westerly currents around the archipelago presumably restrict colonization from the West Pacific. For the 2 snappers that occur in Hawai'i, almost no population structure is detected within the 2000 km archipelago. However, both *E. carbunculus* and *E. coruscans* had several significant pairwise comparisons (F_{ST} values) and elevated genetic diversity around the middle of the archipelago (Raita

Banks to French Frigate Shoals), indicating that this region may receive propagules from Johnston Atoll to the south (Andrews et al. 2014b, Bowen 2016).

Our results are consistent with those of Loeun et al. (2014), who reported no population structure in *E. carbunculus* and *E. coruscans* on a scale of hundreds of km around New Caledonia for mtDNA control region sequences. This stands in sharp contrast to the finding of population structure in 3 shallow reef fishes within the New Caledonia lagoon (Planes et al. 1998). Loeun et al. (2014) noted that *E. carbunculus* in New Caledonia included 2 highly divergent mtDNA lineages, indicating that they sampled both members of the cryptic species pair *E. carbunculus* and *E. sp*.

Eteline larvae are larger, more oceanic (Leis 1987), have a deeper depth distribution (0–100 m for *Etelis oculatus*; D'Alessandro et al. 2010), and stay in the water column longer than shallow water snappers (36 days compared to 26 days in a Caribbean study; D'Alessandro et al. 2010). This may translate into a greater dispersal and connectivity. However, previous studies have found weak connections between pelagic larval duration and genetic connectivity (Bay et al. 2006, Faurby and Barber 2012, Liggins et al. 2015). In a multi-species survey of genetic connectivity in the Hawaiian Archipelago, Selkoe et al. (2014) found that pelagic larval duration could account for about half (R^2 = 0.50) of the variance in population structure.

It is possible that post-settlement (juvenile and adult) *Etelis* snappers are more vagile than their shallow-water counterparts. Based on sonic tagging, Okuyama et al. (2019) found that *E. coruscans* is not site philopatric like shallow water snappers, and is capable of moving several km per day. We conclude that in the more pelagic *E. coruscans*, adult mobility may contribute to the lowest level of population structure observed in this study (range-wide mtDNA Φ_{ST} = 0.010 vs. Φ_{ST} = 0.021 and Φ_{ST} = 0.018). However, since this dearth of population structure extends to the more demersal *E. carbunculus* (and presumably more demersal *E. sp*.), as well as other deepwater snappers (see below), it seems likely that extended larval dispersal is the more important factor in the dispersion and connectivity of Eteline snappers.

Other Deepwater Species

The pattern of low population structure extends to the few previous studies of deepwater snappers. *Pristipomoides filamentosis* has an Indo-Pacific distribution similar to *E. coruscans*, and is found between 100 and 400 m depth on continental shelves and islands across the tropical Indo-Pacific. Gaither et al. (2011) observed no population structure across most of the range (Central Pacific to Western Indian Ocean), with the exception of Hawai'i (mtDNA Φ_{ST} = 0.029, microsatellite F_{ST} = 0.029). However, this species has an extended pelagic larval stage estimated at 60–120 days (Leis and Lee 1994), compared to ~36 days for *Etelis* snappers, which could account for the lack of population structure across 14 000 km. It is notable that this species shows no genetic break at the IPB between the Indian and Pacific Oceans (see below).

For the deepwater snapper *Pristipomoides zonatus* (depth range 125–275), Kennington et al. (2017) reported very low but significant population structure (using mtDNA and 6 microsatellites) with F_{CT} = 0.009 between the Indian and Pacific Oceans, but no structure within oceans, even among locations separated by >2000 km. Hence this species shows a break at the IPB, which is not evident in other deepwater snappers. In contrast, *Pristipomoides multidens* (depth range 125–275 m) had population structure (F_{ST} = 0.17) over a span of ~500 km in the Coral Triangle (between the Philippines, Malay Peninsula, and New Guinea) based on mtDNA control region sequences (Ovenden et al. 2004), but genetic homogeneity across most of northern Australia (Ovenden et al. 2002).

Other coastal deepwater fishes show little to no population structure across entire species ranges. *Caulolatilus microps* (Blueline Tilefish, family Malacanthidae) is distributed along the East Coast of North America from Virginia (United States) to Campeche (Mexico) at a depth of 75–250 m. McDowell and Brightman (2018) observed no population structure across the species range, based on mtDNA control region sequences and 25 microsatellite loci. Similarly, Bentley et al. (2014) reported no genetic differentiation across the Indo-West Pacific region for the reef-associated *Gymnosarda unicolor* (dogtooth tuna, depth range 10–300 m), based on 13 microsatellite loci and the mtDNA cytochrome c oxidase subunit 1 (COI).

Deepwater sharks also show extensive dispersal. *Centrophorus squamosus* (Leafscale Gulper) is a squaloid shark that occurs at depths of 300–1500 m from the eastern Atlantic to the western Pacific. Veríssimo et al. (2012) report no population structure across this range based on 6 microsatellite loci, although mtDNA data indicated structure due to female philopatry. *Centroscymnus coelolepis* (Portuguese dogfish), is another deepwater squaloid that occurs at depths of 500–1700 m in the eastern Atlantic. Veríssimo et al. (2011) reported no population structure in this species based on 8 microsatellite loci and mtDNA control region sequences, across a sampling range that extended from Ireland to South Africa, including the Azores on the mid-Atlantic Ridge.

Indo-Pacific Barrier

Among the most prominent marine phylogeographic boundaries in the Indo-Pacific is the IPB, a terrestrial barricade between Indian and Pacific basins that arises during low sea-level stands. Many shallow-water fishes show a pronounced genetic partition here (Gaither and Rocha 2013, Bowen et al. 2016). In contrast, none of the 3 species surveyed herein show this partition. Perhaps the split between the cryptic species pair *E. carbunculus* and *E. sp*. (at about 5 Ma; Andrews et al. 2016) was initiated by this barrier. However, modern glacial cycles began much later, around 2.5 Ma, so it is not clear that a barrier was operating when the species bifurcation occurred. The deepwater snapper *P. zonatus* has a very shallow genetic partition between Indian and Pacific Ocean samples (Kennington et al. 2017), but the congeneric *P. filamentosis* shows no evidence of a partition at the IPB. Since a terrestrial barrier would presumably apply uniformly to fishes both shallow and deep, we surmise that the lack of genetic partitioning across the IPB for deepwater snappers results from dispersal after the barrier dropped (on a glacial cycle of ~100 000 years).

Species Delineation

Species delineation is a fundamental premise for accurate science and effective management and conservation, especially when the study organism is subject to harvest. Species delineation has been particularly challenging for *E. carbunculus*, which was recently found to be comprised of a pair of cryptic species with overlapping geographic distributions (i.e., *E. carbunculus* and *E. sp*., Andrews et al. 2016). The cryptic species pair was proposed based on a range-wide survey using mtDNA cyt*b* and nuclear intron sequences and 2 morphological characters found to be species-diagnostic (opercular spine shape and presence/absence of black coloration on the upper-caudal fin tip) (Andrews et al. 2016; also see Loeun et al. 2014).

However, a subsequent study investigating a wider range of morphological characters for *E. carbunculus* reported variation potentially indicative of a species swarm of at least 7 potential species (Randall et al. 2019). Our results here do not support a species swarm, but instead indicate minimal population genetic structure across the Indo-Pacific within both *E. carbunculus* and *E. sp*. Therefore, these results support the presence of just one cryptic species pair as proposed by Andrews et al. (2016), and also indicate that the morphological variation within *E. carbunculus* and *E. sp*. observed by Randall et al. (2019) occurs despite the presence of extensive gene flow, indicating phenotypic plasticity or local selection.

Our results clarify the species delineation that is critical for effective management of these important food fish. Previous efforts reveal the problems that arise when taxonomy is misaligned. It is possible that regional differences in otolith structure reported by Smith (1992) were differences between *E. carbunculus* (sampled in Hawai'i, French Polynesia, and Northern Mariana Islands) and *E. sp*. (sampled in Fiji and Tonga), given that Wakefield et al. (2014) demonstrated that otoliths of these 2 species are morphometrically distinguishable. Likewise, Smith and Kostlan (1991) reported regional differences in age and growth that would be confounded by sampling both species (Williams et al. 2017; Wakefield et al. 2020).

Management Implications

The genetic results reported herein indicate that populations of *E. carbunculus*, *E. coruscans*, and *E. sp*. display limited differentiation across large areas. This indicates that widely-separated habitats are linked by larval connectivity, with restrictions to gene flow mainly limited to locations at the edge of the species ranges. Adult connectivity is less likely to contribute to the lack of genetic differentiation across large areas, as these *Etelis* species have not been reported to traverse large distances as adults and are considered to be somewhat resident over limited areas, such as seamounts. However, high genetic connectivity as measured with population genetics does not mean that depleted fisheries will be quickly replenished by immigrants, because local retention is probably a much greater source of larvae than dispersal from long distances. As such, the management of these species could be made more effective by delineating operational management units on smaller spatial scales. It is likely that several management units are present within countries or territories, or that a country or territory is of itself a management unit. As such, management unit-specific stock assessments and corresponding administrative arrangements need to be considered by fisheries managers. Each country and/or territory and their associated management units should seek to maintain an adequate total level of spawning biomass and avoid depletion events. This strategy seeks to ensure a robust approach to fisheries management, assuming that local stocks are likely to be reliant on self-recruitment to a large degree, especially in isolated areas. Our findings indicate that if individual management units are overfished, they are likely to receive some level of recruitment from elsewhere that may assist in rebuilding the spawning biomass of these species. However, this level is likely to be substantially lower than local stock recruitment.

Summary

Our range-wide population genetic study of 3 deepwater snappers found Pleistocene mtDNA coalescence times similar to those of shallow fishes, indicating similar demographic histories for deep and shallow water fishes despite their habitat differences. However, we found weaker population structure for the deepwater snappers than their shallow-water counterparts, with minimal differentiation across the Indo-Pacific for all 3 species. The conclusion of low population structure across these vast geographic ranges seems to apply to most of the fishes that exist in deep waters at the edge of the coastal shelf. It remains to be determined whether this is caused by extensive larval dispersal, broader habitat mosaics, or movement by juveniles and/or adults. We favor the first explanation, based on the finding that Eteline larvae have a longer pelagic duration and more oceanic habitat than the shallow water members of the Lutjanidae, likely facilitating greater oceanic dispersal. Based on the studies available to date, deepwater fishes exhibit population structure on a geographic scale more akin to pelagic fishes than shallow-water coastal fishes.

Supplementary Material

Supplementary material is available at *Journal of Heredity* online.

Figure S1. Bayesian clustering analysis results obtained with the program STRUCTURE 2.3.3 (Pritchard et al. 2000) for *Etelis coruscans*. Ln probability of the data (a) without and (b) with using sampling location as a prior. Ancestry proportions for K=2, K=3, and K=4 (c) without and (d) with using sampling location as a prior.

Figure S2. Bayesian clustering analysis results obtained with the program STRUCTURE 2.3.3 (Pritchard et al. 2000) for *Etelis carbunculus*. Ln probability of the data (a) without and (b) with using sampling location as a prior. Ancestry proportions for K=2, K=3, and K=4 (c) without and (d) with using sampling location as a prior.

Table S1. Specimen ID, sampling location, and microsatellite allele lengths (bp) for *Etelis coruscans*. Missing data encoded by "0." Hawaiian Archipelago data are from Andrews et al. 2014b.

Table S2. Specimen ID, sampling location, and microsatellite allele lengths (bp) for *Etelis carbunculus*. Missing data encoded by "0." Hawaiian Archipelago data are from Andrews et al. 2014b.

Table S3. Genetic diversity for *Etelis coruscans* for cyt*b* and microsatellites. h, haplotype diversity; π, nucleotide diversity; A_R, allele richness; H_o, observed heterozygosity; H_e, expected heterozygosity. Diversity values are only calculated for $n \geq 10$.

Table S4. Genetic diversity for *Etelis carbunculus* for cyt*b* and microsatellites. h, haplotype diversity; π, nucleotide diversity; A_R, allele richness; H_o, observed heterozygosity; H_e, expected heterozygosity. Diversity values are only calculated for $n \geq 10$.

Table S5. Genetic diversity for *Etelis sp*. for cyt*b*. h, haplotype diversity; π, nucleotide diversity.

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Data Availability

Mitochondrial DNA sequences generated for this study have been deposited in GenBank (accession numbers MT814889–MT815254), and microsatellite genotypes for all samples used in this study are included in Supplementary Tables S1 and S2. In addition, the following data have been submitted to Dryad (https://doi.org/10.5061/dryad.2z34tmpjm): Fasta files for each species with mitochondrial DNA sequences for each sample used in this study; Arlequin infiles for each species with mitochondrial sequence data for each sample used in this analysis; a text file for each species with microsatellite genotypes for each sample used in this study.

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