USING SINGLE NUCLEOTIDE POLYMORPHISMS TO RESOLVE THE ORIGINS AND POPULATION STRUCTURE OF DEEPWATER *ETELIS* SNAPPERS IN THE NORTH PACIFIC OCEAN

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULLFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTERS OF SCIENCE

IN

ZOOLOGY (ECOLOGY, EVOLUTION AND CONSERVATION BIOLOGY)

DECEMBER 2022

BY

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Keywords: Hawaii bottomfish, Lutjanidae, Etelis, phylogeography, population structure, single nucleotides polymorphisms

ACKNOWLEDGMENTS

I would like to thank Brian Bowen, Rosana Zenil-Ferguson, and Jeffrey Drazen for their mentorship, guidance, and tutelage. Thank you all for being patient and giving me your time and effort throughout the course of my research.

Mahalo to the fishers in the Hawaiian bottomfish fishery for their assistance in sample collection. For collecting and curating specimens, I thank Kimberly Andrews, Gordon Grau, Christopher Kelley, and Virginia Moriwake. For logistic support and intellectual contributions, I thank Edward DeMartini, Robert Humphreys, Sam Pooley, Michael Seki, and Robert Moffitt at the NOAA Pacific Islands Fisheries Science Center, Randall Kosaki at the Papahānaumokuākea Marine National Monument, and the Hawai'i State Division of Aquatic Resources. Thanks to Texas A&M Core Facility for sequencing services.

In addition, I would like to express my gratitude and appreciation to members of the ToBo Lab at the Hawai'i Institute of Marine Biology. I am especially thankful for Chris Suchocki, Derek Kraft, Sean Canfield, Richard Coleman, and Eric Crandall for your guidance on data analysis and bioinformatics. Thanks to Leah Shizuru, Taylor Ely, ʻAleʻalani Dudoit, and Cassie Ka'apu-Lyons for your endless support and encouragement on this journey.

Lastly, words cannot express my gratitude to Joshua Copus. Thank you for all that you have done for me. I am forever grateful for your mentorship and friendship.

ABSTRACT

Deepwater *Etelis* snappers economically and culturally support fisheries in Hawai'i and throughout the Indo-Pacific. In Hawai'i, *Etelis coruscans* ("onaga") and *Etelis carbunculus* ("ehu") are the most abundantly harvested in the Deep 7 Bottomfish Complex, therefore it is important to understand genetic connectivity to make proper management implementations. In addition, understanding their origins will provide further information on how to ensure sustainable stocks within Hawai'i waters. Previous studies have shown that Johnston Atoll is the gateway for marine species to colonize the Hawaiian Archipelago. An alternative route is that marine species can colonize from the west, essentially Japan. To resolve population structure and the origin of the Hawaiian cohorts, we used single nucleotide polymorphisms (SNPs) to assess *E. coruscans* (N = 59) and *E. carbunculus* (N = 55), sampled from Japan, Johnston Atoll (nearest habitat south of Hawai'i), the Main Hawaiian Islands (MHI), and the Northwestern Hawaiian Islands (NWHI). Johnston Atoll samples were excluded from *E. carbunculus*. For both species, Japan was significantly differentiated with pairwise F_{ST} values for MHI and NWHI, and there was non-significant F_{ST} values between MHI and NWHI. *Etelis coruscans* showed no significant F_{ST} values between Johnston and MHI/NWHI. STRUCTURE plot of *Etelis coruscans* showed no genetic clustering, indicating larval exchange from both locations, Japan and Johnston Atoll. STRUCTURE plot of *E. carbunculus* showed clear population distinction between Japan and Hawaiian Islands, therefore we can tentatively suggest larval exchange between Johnston Atoll and Hawaiian population. To explore this idea further, future studies should focus sampling effort on Johnston to accurately make this suggestion. Management implications and strategies are needed to ensure long term sustainability of these populations of deepwater *Etelis* snappers. The indeterminate origin of the Hawaiian population may indicate that gene genealogies (i.e. phylogeography) are more appropriate than allele frequencies (SNPs) in resolving colonization routes.

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INTRODUCTION

The Hawaiian Archipelago lies about 4100 km from the nearest continent (North America) and 800 – 1700 km from the nearest emergent lands (Johnston and Palmyra Atolls). It is the most isolated landmass in the world. Despite being so remote, the archipelago is home to a wide diversity of marine fauna and a hotspot of endemic species. Due to the volcanic origins of this archipelago, the Hawaiian fauna either colonized from elsewhere or descended from such colonists. Hence the origins of Hawaiian flora and fauna, both above and below the waterline, constitutes an enduring biogeographic enigma.

The Hawaiian Islands have been regarded as an evolutionary graveyard for marine organisms, hosting colonists that may turn into endemics, but with no further evolutionary radiations (Bowen et al. 2013). However, studies have shown that marine species radiations can occur in Hawai'i (Bird et al. 2011; Bowen et al. 2020) and native species can colonize out of Hawai'i (Eble et al. 2011; Bowen et al. 2013). Understanding the origins of marine fishes will help reveal the source of Hawaiian marine biodiversity and enable proper management strategies to preserve these biodiversity gateways. Craig et al. (2010) investigated genetic connectivity and colonization routes for Hawai'i endemic butterflyfishes, showing several pathways to colonize the Hawaiian Archipelago.

For most marine fishes and invertebrates, colonization of Hawai'i occurs through the pelagic larval phase. During this phase, long-distance dispersal can shape the genetic connectivity among locations (Faillettaz et al. 2018). The length of the pelagic life stage of reef fish is variable with damselfishes (Pomacentridae) lasting as little as a week, while moray eels (Muraenidae) can extend this phase for more than 60 weeks (Leis & McCormack 2002). Those with a longer pelagic larval duration (PLD) may have the potential to establish and maintain more distant populations via currents and gyres (Lester & Ruttenberg 2005). However, pelagic larval duration is not the sole determination of dispersal potential. In a survey of 35 reef-associated species across the Hawaiian archipelago, Selkoe et al. (2014) could attribute at most 50% of variance in population structure (a genetic measure of dispersal) to pelagic larval duration.

Several studies have shown evidence that Johnston Atoll is a gateway for marine species colonization into the Hawaiian Archipelago (e.g. LeRay et al. 2010). Because Johnston Atoll lies between the Line Islands and the Hawaiian Islands, Kobayashi (2006) suggests that reef fishes with a PLD of 40 – 50 days can colonize Hawai'i via this Atoll. Much marine fauna is found only in the Hawaiian Archipelago and areas in the south Pacific, indicating a connection between Johnston Atoll and Hawaii (Mundy 2005). Larval transport is facilitated from Johnston Atoll to the Hawaiian Islands by the subtropical countercurrent and the Hawaiian Lee countercurrent (HLCC) (Fig. 1) (Kobayashi 2006). The dynamics of the HLCC are influenced by Ekman pumping patterns, creating anticyclonic and cyclonic eddies that circulate to the north and south (Xie et al. 2001). For example, based on the distribution and abundance of corals of the genus *Acropora*, with a PLD of about 91 days, these species likely arrived in Hawai'i from Johnston Atoll (Harrison et al. 1984).

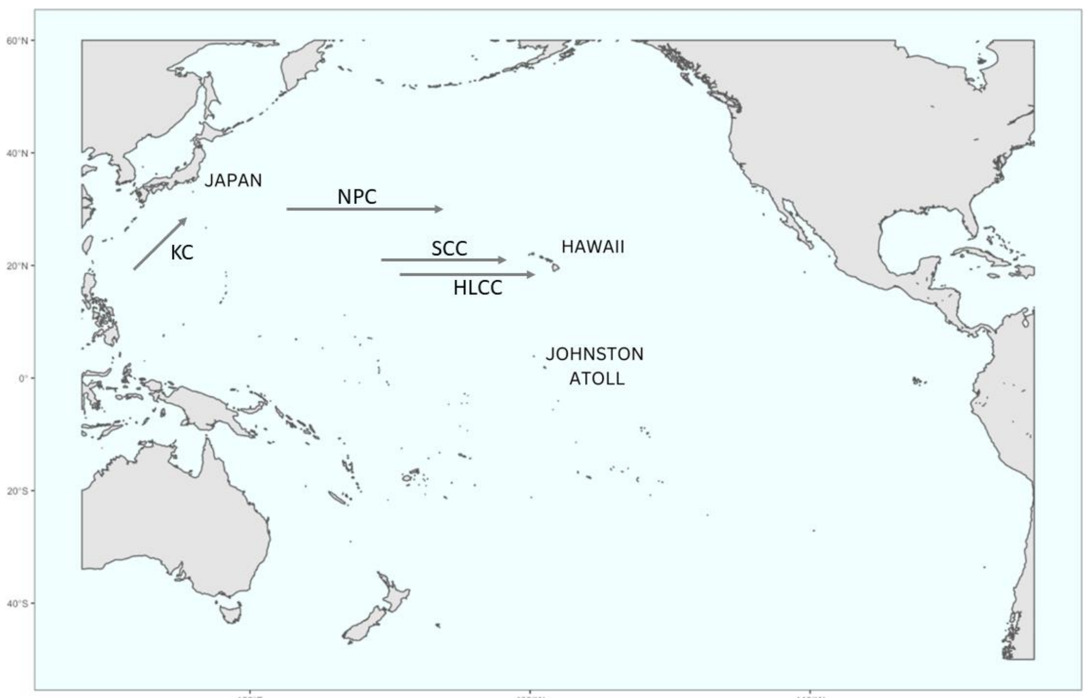

Figure 2. Map of Indo-Pacific Ocean with general patterns of ocean currents. Labeled locations show area of study and arrows indicate the direction of the currents' flow. Abbreviation for currents: KC=Kuroshio Current, NPC= North Pacific Current, SCC=Subtropical Countercurrent, HLCC=Hawaiian Lee Countercurrent.

There is also evidence that marine species can colonize Hawai'i from the west, essentially Japan, 6700 km to the west. The Kuroshio current, originating in the Northwest

Pacific, feeds into the North Pacific Current that flows in an easterly direction at latitudes above the Hawaiian Islands (Fig. 1). This is the suspected route for West Pacific fishes to colonize the Northwest Hawaiian Islands, including the Japanese angelfish (C*entropyge interrupta*) and the blotch-eye squirrelfish (*Myripristis murdan*) (Randall 2007). Juvenile sea turtles are routinely transported from Japan, via the Kuroshio Current and North Pacific Current, to waters north of Hawai'i (Bowen et al. 1995).

Bottomfish fishing is economically and culturally important to the Hawaiian Islands (Haight et al. 1993). Fisherman target snappers and groupers, but the most prized fish are the ones in the Deep 7 Bottomfish Complex. This complex in Hawai'i is comprised of six snappers (Lutjanidae) and one grouper species (Epinephelidae). The snappers *Etelis coruscans* ("onaga") and *Etelis carbunculus* ("ehu") are the most abundantly harvested (Haight et al. 1993; Misa et al. 2013). Both are widely distributed throughout the Indo-Pacific Ocean, residing at submesophotic depths of 100 – 400 meters (Gomez et al 2015; Langseth et al. 2018). *Etelis* snappers have a PLD of approximately 40 days and larvae are found beyond the continental shelf, inhabiting deep slopes and seamounts (Leis & Lee 1994; D'Alessandro et al. 2010).

Due to their moderately slow growth, high longevity, and low natural mortality, deepwater snappers may be susceptible to over-exploitation, indicating the need for informed management plans that incorporate natural history and population structure (Williams et al. 2017; Andrews et al. 2012). In 1998, the National Marine Fisheries Service determined that *E. coruscans and E. carbunculus* were approaching a low spawning potential ratio in the Hawaiian Islands (Misa et al 2013). A 2004 assessment indicated that *E. coruscans and E. carbunculus* were of greatest concern due to excessive fishing (Moffit et al. 2006; Nichols 2019). In response, the state of Hawaii's Department of Land and Natural Resources created bottomfish restricted fishing areas (BRFAs), prohibiting fishing in certain regions. Without a complete understanding of the spatial scale of populations and connectivity patterns, it will not be possible to accurately identify populations that are in the process of being depleted and in need of protection (Misa et al. 2013). Undermanaged or improperly managed fisheries can lead to a local decrease in population size and productivity, thereby reducing genetic diversity and altering connectivity patterns (Reiss et al. 2009). Understanding genetic connectivity will advance the ecological framework for conservation and management. Additionally, a range-wide survey of the target species can provide insight into the evolutionary mechanisms that are promoting or inhibiting diversity in submesophotic environments.

A recent study surveyed *Etelis* snappers across the Indo-Pacific Ocean, using mitochondrial sequences and 9 -11 microsatellite loci, observed low population structure, indicating high connectivity (Andrews et al. 2020). A survey of another deepwater Indo-Pacific snapper, *Pristipomoides filamentosus*, using similar methods revealed no population structure across the Pacific Ocean except the isolated Hawaiian Archipelago (Gaither et al. 2011). An assessment of population structure for deepwater snappers has not been conducted using single nucleotide polymorphisms (SNPs). SNPs are a powerful tool to elucidate population structure (D'aloia et al. 2020). Compared to a few microsatellite loci or mitochondrial DNA (mtDNA), a genome-wide scan of thousands of SNPs can provide higher resolution of genetic diversity and fine scale population structure (Carreras et al. 2017; Sherman et al. 2020). For example, Kraft et al. (2020) detected population structure in a shark that was not resolved in a previous mtDNA survey. Gaither et al. (2015) used SNPs to show signals of selection and genetic drift in Orangeband surgeonfish, *Acanthurus olivaceus*, that associated with populations diverging due to geographic isolation and habitat differences, a pattern not observed using mtDNA.

The primary purpose of this study was to investigate the genetic structure of the Hawaiian populations of ehu and onaga, and resolve routes of marine colonization into the Hawaiian Islands. Previous studies have relied on phylogenetic means to find the closest relative to endemic Hawaiian organisms (Craig et al. 2010; Leray et al. 2010; Hodge et al. 2014). Here we push this investigation in two novel directions: examining patterns of gene flow within two species, and using SNPs instead of microsatellite loci and mitochondrial DNA to compare Hawaiian populations to the two known sources of colonists, West Pacific and South Pacific. We also aim to inform management strategies to ensure the long-term sustainability of Hawaiian Eteline snapper fisheries.

METHODS

Specimen collection and DNA extraction

A total of 59 fin clips for *E. coruscans* and 55 fin clips for *E. carbunculus* were sampled from commercial fishermen and scientific missions at four locations: Japan, Johnston Atoll, the

Main Hawaiian Islands (MHI), and the Northwestern Hawaiian Islands (MWHI) (Fig. 2). These are subsamples of the specimens used for mtDNA and microsatellite studies, and more details about collections are available in Andrews et al. (2014; 2020). Fin clips were preserved in 20% salt-saturated DMSO or 95% ethanol and stored at room temperature. DNA was extracted using Qiagen DNeasy Blood & Tissue Kit (Qiagen, Mississauga, ON, Canada) following the manufacturer protocols. DNA integrity was assessed using gel electrophoresis and imaged using Gel Doc E-Z System (Bio Rad, Hercules, California, USA). Quality DNA was quantified using AccuClear Ultra high sensitivity dsDNA quantification kit.

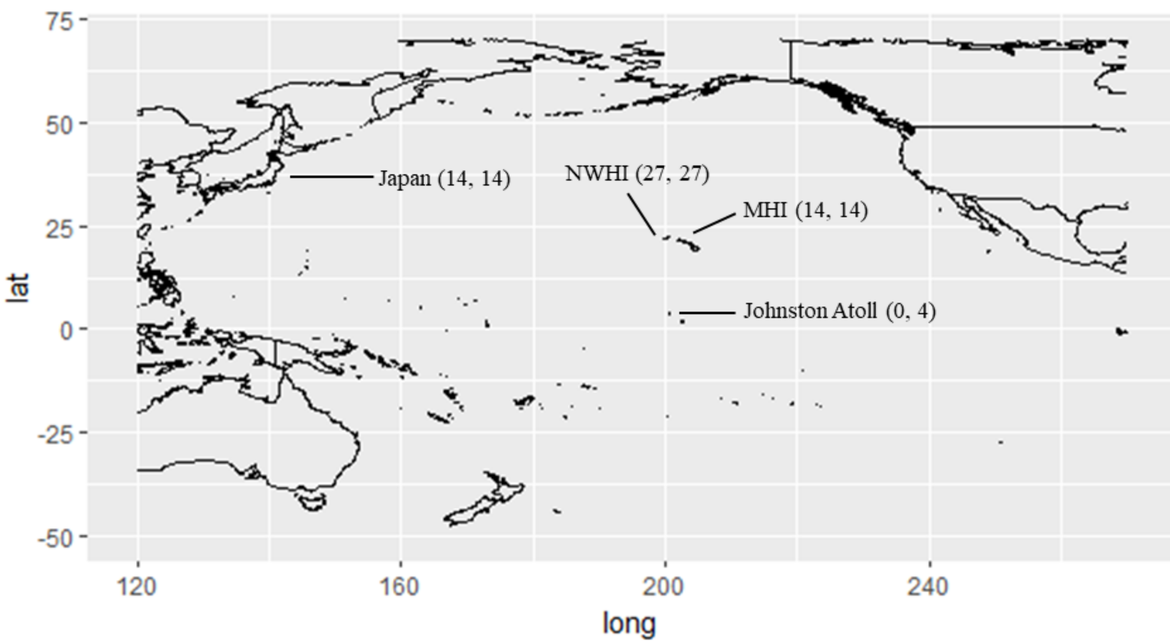

Figure 3. Location of sample collection. The four populations are Japan, Northwestern Hawaiian Islands (NWHI), Main Hawaiian Islands (MHI), and Johnston Atoll. Sample sizes of each species are listed in parenthesis including *Etelis carbunculus* and *Etelis coruscans* respectively.

Library preparation and sequencing

Individual library preparations followed a double-digest restriction-site associated DNA (ddRAD) library preparation protocol (Toonen et al. 2013; Knapp et al. 2016; Peterson et al. 2012). Samples were digested with restriction enzymes *Mspl* and E*cori* (New England Biolabs, Ipswich, MA, USA), followed by ligation of adaptors. After digestion and ligation, PCR was performed using dual-indexed primers. Fragments between 425-525 bp were selected and individual libraries were sequenced on an Illumina HiSeq® 4000 (150 paired-end reads, performed by the Texas A&M Core Facility). Using *process_radtags* from Stacks (Catchen et al. 2013), barcodes from the adaptor were used to demultiplex sequenced data.

Genotyping

Denovo_map.pl pipeline through Stacks was used to create a catalogue of all loci in the dataset where loci are matched up across each sample according to their sequence similarity and call SNPs within individuals. For both species, settings were set at 5 reads per stacks, 4 mismatches allowed between stacks within individuals, and 4 mismatches allowed between stacks between individuals. Two population filtering options included only keeping loci that appeared in 80% of individuals in all populations and only keeping loci that appeared in 100% of individuals in all populations. Data was stringent by setting the p-value cutoff at 0.05 for Hardy-Weinberg Equilibrium. Non-variant loci and loci with only a single minor allele were removed. SNPr packages in *RStudio* (Team, 2021) were used to further evaluate and filter the SNPs.

Population genetic analysis

ARLEQUIN v.3.5 (Excoffier & Lischer, 2016) was used to calculate pairwise F_{ST} values to assess genetic structure between each location. F_{ST} values measures the differences in allele frequency between populations. A F_{ST} value of 0 indicates connectivity and gene flow, exhibiting no genetic structure, whereas a F_{ST} value of 1 indicates low connectivity and low gene flow, hence presence of genetic structure. STRUCTURE v.2.3.4 (Pritchard et al. 2000) was utilized to further identify genetically distinct populations. This program groups individuals based on how genetically similar they are into separate populations. The STRUCTURE simulation was run for 500,000 generations with the first 100,000 discarded as burn-in and K=1-6 genetic clusters with 10 repetitions for each K value. STRUCTURE HARVESTER v.0.6.93 (Earl & Vonholdt, 2012) was used to visualize structure output, implementing the Evanno method to determine the best K value. The Evanno method calculates the best K value that fits the dataset best. STRUCTURE PLOT v.2.0 (Ramasamy et al. 2014) and CLUMPAK (Kopelman et al. 2015) was used to aesthetically edit the plot.

Demographic history

Coalescence methods can infer the origins of Hawaiian deepwater snappers. Understanding the effective population size of each species can be useful for management of highly fished populations and can possibly detect changes in population sizes. MIGRATE 5.0.4

(Beerli 2006) was used to estimate past migration rates and infer the direction of gene flow. Parameters and workflow used for the models can be found on GitHub: https://ericcrandall.github.io/Etelis_migrate/Etelis_migrate.html. Models tested were as follows: (a) panmixia with high levels of dispersal (proportion of migrants (m) > 0.1) the sampled populations; (b) an n-island model with populations same size and all exchange migrants (c) divergence (d) divergence with gene flow (e) pure gene flow and (f) full model with pure gene flow. For *E. coruscans*, models (c), (d), and (e) had additional modifications to three different migration directions, Johnston to MHI to NWHI, Johnston to NWHI to MHI, and Japan to NWHI and MHI. For *E. carbunculus*, models (c), (d), and (e) also had additional modifications to two different migration directions, Johnston to MHI to NWHI and Johnston to NWHI to MHI. In total, 12 metapopulation models were created for *E. coruscans* and 9 metapopulations were created for *E. carbunculus*. Migration prior is increased to have a maximum of 100,000,000 and mean of 10,000. In addition, on average 1 out of every 100,000 individuals will send a migrant. 10 replicates of 3 replicates were completed for each model. Bezier corrected marginal likelihood was calculated for each model and compared and ranked amongst the different models (Beerli and Palczewski (2010).

RESULTS

Individuals of the two species, *E. carbunculus* and *E. coruscans*, were analyzed separately. *Etelis carbunculus* data from Johnston Atoll were excluded due to contamination of specimen tubes; data for all other populations (Japan, NWHI, and MHI) were included. *E. coruscans* samples were unaffected and data for all four populations (Japan, Johnston Atoll, NWHI, and MHI) were used. Following calling and filtering SNPs, we were able to retain 440 loci and 59 individuals for *E. coruscans,* and 1,650 loci and 55 individuals for *E. carbunculus.*

Pairwise F_{ST} values indicated the Japan population of *E. coruscans* was significantly distinct from the populations in the Main Hawaiian Islands (MHI) and Northwestern Hawaiian Islands (NWHI), with significant values at 0.0101 and 0.0102 ($P < 0.05$) (Table 1). Johnston Atoll was not significantly differentiated from any other population, including the Hawaiian Islands. Pairwise F_{ST} comparisons between NWHI and MHI were not significant. Based on F_{ST} values, NWHI is more closely related to Japan than MHI.

Table 1. Matrix of pairwise F_{ST} values for four populations of *Etelis coruscans*. Four populations consist of Japan, Johnston Atoll, Main Hawaiian Islands (MHI), and Northwestern Hawaiian Islands (NWHI). Numbers bolded indicate significance at P<0.05.

	Japan	Johnston Atoll	MHI	NWHI
Japan	--			
Johnston Atoll	-0.0076	--		
MHI	**0.0101**	-0.0087	--	
NWHI	**0.0102**	-0.0107	0.0003	--

Pairwise F_{ST} values were significantly differentiated between Japan and the Hawaiian Islands with significant values at 0.0269 for MHI and 0.0299 for NWHI ($P < 0.05$) (Table 2). The NWHI and MHI did not show a significance difference. F_{ST} values indicate that Japan is more closely related to NWHI than MHI for *E. carbunculus*.

Table 2. Matrix of pairwise F_{ST} values for three populations of *Etelis carbunculus*. Three populations consist of Japan, Main Hawaiian Islands (MHI), and Northwestern Hawaiian Islands (NWHI). Johnston Atoll was excluded. Bolded numbers indicate significance at p<0.05.

	Japan	MHI	NWHI
Japan	--		
MHI	**0.0269**	--	
NWHI	**0.0299**	0.0026	--

We calculated the K values to determine the maximum number of clusters based on the loci to determine population structure using the program STRUCTURE HARVESTER v.0.6.93. The optimal K value for *E. coruscans* was 3. *Etelis coruscans* revealed no genetic clustering or support for both species. Population structure identified by F_{ST} values could potentially be too low to be detected with STRUCTURE, which segregates specimens into groups that optimize Hardy-Weinberg equilibrium. When allele frequencies are very similar among samples, STRUCTURE may fail to detect the finest scale of population structure. Groups represented by blue within the analysis are located among all sampling sites for K=3, whereas the orange groups are found at Japan, Johnston, and MHI. Purple groups are found at Johnston Atoll and NWHI (K=3; Fig. 3A). The optimal K value for *E. carbunculus* was 2. STRUCTURE revealed two distinct population groups (K=2, Fig. 3B), one associated with Japan, and the other corresponded to MHI and NWHI.

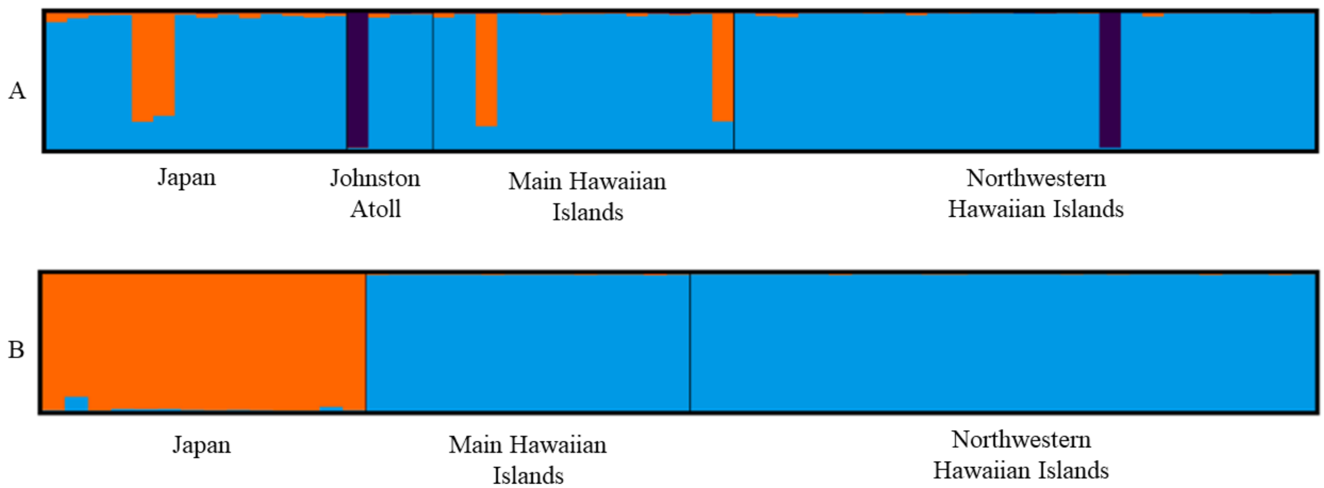

Figure 3. STRUCTURE bar plots for both species. Individuals are represented by a single column segregated into *K* colored segments, with different colors indicating groupings that conform to Hardy-Weinberg equilibrium. (A) STRUCTURE bar plot (K=3) *for* four populations of *E. coruscans* with 440 loci. (B) STRUCTURE bar plot (K=2) for three populations of *E. carbunculus* with 1,650 loci.

MIGRATE-N analysis determined the best population model and ranked them in order according to their marginal likelihood and calculated Bayes factors. The top model for *E. coruscans* species is full equilibrium model with a high model probability at 1 (Table 3). This states that the model has 4 distinct populations exchanging migrants at some rate throughout all locations. Migrants per generation were calculated for each location, varying between 3-4 (Table 4). Most migrants are coming from Japan to NWHI, Johnston to NWHI, and MHI to NWHI (Table 4). Migration into Johnston is low with approximately 0 migrants per generation (Table 4). MIGRATE-N didn't find much evidence of recent divergence, suggesting that it has been many thousands of generations since the Hawaiian population diverged from the Indo-Pacific. For *E. carbunculus*, we found that the top model is panmixia (Table 5). This means we see that all individuals are potential partners and there are no mating restrictions. MIGRATE-N indicated that snappers are entering Hawaiian Islands from the West Pacific and South Pacific for both *E. carbunculus* and *E. coruscans*.

Table 3. Model marginal likelihoods for *Etelis coruscans*. Model probability shows the best model at 100% which is considered as full equilibrium model.

MODEL	BEZIER.CORRECTED	LOG BASED FACTOR	CHOICE	MODEL PROBABILITY
divergence_geneflow_1	-276833.2	-17689.624	6	0
divergence_geneflow_2	-276590.2	-17203.492	5	0
divergence_geneflow_3	-273066.6	-10156.304	3	0
divergence_only_1	-283277.7	-30578.460	12	0
divergence_only_2	-282996.4	-30015.984	11	0
divergence_only_3	-280567.1	-25157.378	9	0
full	-267988.4	0.000	1	1
geneflow_only_1	-277466.4	-18955.892	8	0
geneflow_only_2	-277325.4	-18673.954	7	0
geneflow_only_3	-274059.8	-12142.666	4	0
n-island	-282650.8	-29324.732	10	0
panmixia	-269004.4	-2031.868	2	0

Table 4. Number of migrants per generation from each parameter location for *Etelis coruscans*. Based on the full equilibrium model, we were able to calculate the migrants per generation. Most locations had about 3-4 generations. Migration into Johnston Atoll is low.

MODEL	BEZIER.CORRECTED	LOG BASED FACTOR	CHOICE	MODEL PROBABILITY
divergence_geneflow_1	-525371.9	-8255.810	4	0
divergence_geneflow_2	-524648.4	-6808.766	3	0
divergence_only_1	-531037.2	-19586.320	8	0
divergence_only_2	-530232.1	-17976.168	7	0
geneflow_only_1	-527826.4	-13164.674	6	0
geneflow_only_2	-527064.4	-11640.702	5	0
geneflow_only_full	-522629.8	-2771.548	2	0
n-island	-538937.9	-35387.814	9	0
panmixia	-521244.0	0.000	1	1

Table 5. Model marginal likelihoods for *Etelis carbunculus*. Model probability shows the best model at 100% which is considered as panmixia. Bezier corrected was used for large datasets and large population models because it requires less time than Markov chain Monte Carlo.

PARAMETER	MIGRANTS/GENERATION	STANDARD DEVIATION
Johnston Atoll to Japan	3.233525	1.967809
MHI to Japan	3.518839	2.173615
NWHI to Japan	3.600927	2.263313
Japan to Johnston Atoll	0.331339	0.298118
MHI to Johnston Atoll	0.377493	0.300651
NWHI to Johnston Atoll	0.347264	0.301059
Japan to MHI	3.496756	2.147613
Johnston Atoll to MHI	3.342534	2.049211
NWHI to MHI	3.42852	2.141808
Japan to NWHI	4.11469	2.553976
Johnston Atoll to NWHI	3.741773	2.277974
MHI to NWHI	3.879294	2.401615

DISCUSSION

Deepwater snappers make up an important component of local fisheries in Hawai'i and across the Indo-Pacific (Newman et al. 2016). Understanding genetic connectivity is crucial to make proper management strategies. Previous studies have used mtDNA sequences and microsatellite loci to examine genetic connectivity in *Etelis* snappers (Gaither et al. 2011; Andrews et al. 2020). This study is among the first applications of SNPs to characterize the population structure of submesophotic deepwater fish across regions of the Indo-Pacific Ocean. In addition, resolving the origins of Hawaiian populations of deepwater snappers between potential source populations, either from Johnston Atoll or Japan, will enhance prospects for sustainable stocks within Hawaiian waters.

Genetic connectivity with Japan and Johnston Atoll

In my survey of deepwater *Etelis* species in the North Pacific, the only significant genetic differentiation was between Japan and the Hawaiian Islands, with no population structure detected between the inhabited high islands of the MHI and the low islands and atolls of the NWHI. The latter finding is concordant with a previous survey of the Hawaiian Islands for both species, using mtDNA and 11 microsatellite loci (Andrews et al. 2014). If stock structure exists, it is below the level detectable with SNPs as well. Future studies should increase sample sizes in order to detect stock structure using SNPs.

For *E. coruscans*, the finding of no structure between Johnston Atoll and MHI/NWHI is concordant with the observation of possible gene flow between Johnston and the Hawaiian archipelago (Andrews et al. 2014; Coleman & Bowen 2022). Johnston Atoll, located in the central Pacific Ocean and over 800 km south of the Hawaiian Islands, shares a high faunal similarity with Hawai'i (Kosaki et al. 1991; Lobel 2003; Randall 2007). Because of this affinity, scientists have previously suggested that Johnston Atoll is a stepping-stone for Indo-Pacific biodiversity to colonize into the northwestern Hawaiian Islands (Gosline 1955; Bowen 2016). Previous studies have shown this reoccurring pattern of Johnston Atoll acting as source of propagules for the Hawaiian Archipelago (Leray et al. 2010; Rivera et al. 2011; Coleman & Bowen 2022). Biophysical models provide additional evidence of larval transport between Johnston Atoll and the Hawaiian Archipelago via the eddies from the eastward-flowing subtropical countercurrent and the Hawaiian Lee countercurrent (Kobayashi 2006).

Japan can be another source of propagules. Because Japan and Hawaii share some fish fauna that do not occur elsewhere in the central Pacific, there are strong indications that larvae can disperse from Japan into the Northwestern atolls and islands of Hawai'i through the Kuroshio Current and the North Pacific Current. Two endemic butterflyfish species of Hawai'i, *C. fremblii* and *C. miliaris*, have closest relatives in the West Pacific indicating colonization through the North Pacific Current (Craig et al. 2010). Likewise, the Japanese Angelfish *Centropyge interrupta* occurs in Hawai'i only at the closest point to Japan, the far northwestern islands of Midway and Kure (Randall 2007).

In addition, we would expect to find structure between Japan and Johnston for *E. coruscans*, however, F_{ST} values indicated no significance between them (Table 1). The North Equatorial Current flows, moving at such a rapid pace from east to west, turns northward and intersects the Kuroshio current, potentially promoting larvae movement from Johnston to Japan. Another possible reason for this non-significant differentiation could be due to the low sample size of Johnston with only 4 individuals therefore lacking statistical power.

Factors guiding dispersal

Larval behavior may be the most important factor in guiding marine dispersal, specifically species with a pelagic larval phase. Species with a PLD greater than 40 days can make the journey from Johnston Atoll to the Hawaiian Archipelago (Kobayashi et al. 2006). The Hawaiian grouper, *Epinephelus quernus*, with a PLD of 35-45 days, may have colonized the Hawaiian Archipelago through Johnston Atoll (Rivera et al. 2011). The Eteline snappers have a PLD greater than 40 days, allowing them to make this journey. However, previous studies have found that genetic connectivity is not driven solely by PLD, and that PLD accounts for at most 50% of the variance in populations structure (Selkoe et al. 2014). Recent studies have suggested that movement of juveniles and adults Eteline snappers can also contribute to genetic connectivity (Okuyama 2019).

Although the deepwater *Etelis* snappers live in similar habitats of deep slopes and seamounts, they inhabit different depths and have different specific habitat preferences that may affect population structure and larvae dispersal. Adult *E. coruscans* can be found 5 - 50 meters above the bottom, presumably foraging in the water column (Moore et al. 2016; Oyafuso et al. 2017). Adult *E. carbunculus* stay much closer to the bottom, showed preference for hard substrate with low slope (Misa et al. 2013). These habitat differences may account for the higher F_{ST} values in *E. carbunculus* (Table 2), as fish at deeper depths and closer to the bottom substrate can exhibit greater genetic structure than species living in the water column due to the lack of water movement and Ekman transport (Andrews et al. 2020). While many factors contribute to larval dispersal, the *Etelis* species examined here provide additional evidence that fishes in the water column are more dispersive than bottom-dwelling congeners. However, does this adult behavior correlate to genetic connectivity? We know that PLD plays an important factor in connectivity and populations can be linked through larval exchange. The real casual factors behind the differences between the two Eteline snappers' genetic connectivity are likely to relate to early life history details about eggs and larvae that are not well known for these Eteline snappers. Future studies need to focus on the early life history traits.

Colonization of Hawaiian deepwater snapper populations

Based on our results, for *Etelis carbunculus*, it seems like they are not colonizing from Japan, so we can tentatively conclude that it's coming from southern sources. Both STRUCTURE plot and F_{ST} values shows low connectivity between Japan and the Hawaiian

Islands. This is concordant with their postulated life history trait of being less dispersive due to their habitat preference. However, MIGRATE-N indicates that these snappers are coming from both locations, and they are all connected. MIGRATE-N is a complex program, and new models were recently introduced. We believe that this program has some bugs that it needs to work out and a few parameters need to be changed in order for this program to work correctly and consistently. On the other hand, *Etelis coruscans* showed different results. F_{ST} values indicate low gene flow between Japan and the Hawaiian Islands, but STRUCTURE plot showed no genetic structure. These analyses didn't match up due to the fact that F_{ST} values could be potentially too low for STRUCTURE program itself to detect. In addition, based on the migrants per generation, all populations are migrating at a similar rate. This model is not informative to base conclusions about the colonization of the Hawaiian snapper populations. Again, parameters in MIGRATE-N program needs to be adjusted.

SNPs for population structure or phylogeography

The virtues of SNP data relative to the few loci available in previous studies has been widely promulgated. Because SNPs are abundant and can vastly increase the number of loci sampled, providing more accurate and powerful detection of population structure (Zimmerman et al. 2020). Indeed, Kraft et al. (2020) detected population structure in silky sharks that was missed in a previous mtDNA study using the same specimens. Certainly, SNPS have greater power for detecting population structure. However, the foundation of phylogeography is knowing the relationships among alleles or haplotypes (Avise et al. 1987; Avise 2000), which SNP data does not convey. In reconstructing the history of colonization, it may be that fewer loci with complete sequence data will perform better than SNPs (Bowen et al. 2014).

Management implications

Since the 1950s, the *Etelis* spp. snappers continue to be the highest proportion of catch and have a high commercial value through to present day in Hawaii, Guam, Commonwealth of the Northern Mariana Islands, and American Samoa (WPRFMC 2005, Brodziak et al 2011; 2014). The establishment of Papahānaumokuākea Marine National Monument and Johnston as part of the Pacific Remote Islands Marine National Monument has resulted in a complete moratorium on fishing in these areas. However, the Main Hawaiian Islands are still exposed to high fishing pressures, prompting a need for genetic resolution of stocks (Leis et al. 2011).

Although there is connectivity between Johnston Atoll and the Hawaiian Islands, this does not necessarily mean that Johnston population has the ability to replenish the Hawaiian population of snappers. Migrants per generation varied between 3-4 for most locations except migration into Johnston was approximately zero for *E. coruscans*. Given that *Etelis* snappers have a generation time of about 5 years, this rate of migration is too low to impact fisheries forecasts. This is not enough individuals to impact recovery of the Hawaiian population if they were to be overfished. We cannot rely on distant populations to replenish the Hawaiian populations and management strategies are needed to ensure long term sustainability of these isolated population of deepwater *Etelis* snappers.

Future studies and conclusion

For future studies, it would be informative to include Johnston Atoll samples for *E. carbunculus*. Additional sampling at Johnston Atoll could potentially reveal more discoveries about species origins and population structure. Through our analysis, F_{ST} values and STRUCTURE plots show that *E. carbunculus* is less dispersive than *E. coruscans*. Because *E. carbunculus* as adults associate themselves closer to the bottom, we might potentially see additional genetic structure between Johnston Atoll and Japan compared to adults of *E. coruscans* who prefer the water column. Based on geographic distances, Johnston is closer to the Hawaiian Archipelago than Japan, acting as a potential gateway to colonization of Hawaiian Islands. Gaining a better understanding of life history traits such as spawning time, larval duration, habitats can also help explain genetic connectivity throughout the Pacific Ocean and create a stronger scientific foundation for managing these valuable marine resources.

REFERENCES:

Andrews, A. H., DeMartini, E. E., Brodziak, J., Nichols, R. S., & Humphreys, R. L. (2012). A long-lived life history for a tropical, deepwater snapper (Pristipomoides filamentosus): bomb radiocarbon and lead–radium dating as extensions of daily increment analyses in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(11), 1850-1869.

Andrews, K. R., Copus, J. M., Wilcox, C., Williams, A. J., Newman, S. J., Wakefield, C. B., & Bowen, B. W. (2020). Range-Wide Population Structure of 3 Deepwater Eteline Snappers Across the Indo-Pacific Basin. *Journal of Heredity*, *111*(5), 471–485. https://doi.org/10.1093/jhered/esaa029

Andrews, K. R., Moriwake, V. N., Wilcox, C., Grau, E. G., Kelley, C., Pyle, R. L., & Bowen, B. W. (2014). Phylogeographic Analyses of Submesophotic Snappers Etelis coruscans and Etelis "marshi" (Family Lutjanidae) Reveal Concordant Genetic Structure across the Hawaiian Archipelago. *PLoS ONE*, *9*(4), e91665. https://doi.org/10.1371/journal.pone.0091665

Avise, J. C. (2000). *Phylogeography: The History and Formation of Species*. Harvard University Press. https://doi.org/10.2307/j.ctv1nzfgj7

Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., Reeb, C. A., & Saunders, N. C. (1987). INTRASPECIFIC PHYLOGEOGRAPHY: The Mitochondrial DNA Bridge Between Population Genetics and Systematics. *Annual Review of Ecology and Systematics*, *18*(1), 489–522. https://doi.org/10.1146/annurev.es.18.110187.002421

Beerli, P. (2006). Comparison of Bayesian and maximum-likelihood inference of population genetic parameters. *Bioinformatics (Oxford, England)*, *22*(3), 341–345. https://doi.org/10.1093/bioinformatics/bti803

Beerli, P., & Palczewski, M. (2010). Unified framework to evaluate panmixia and migration direction among multiple sampling locations. *Genetics*, *185*(1), 313-326.

Bird, C. E., Holland, B. S., Bowen, B. W., & Toonen, R. J. (2011). Diversification of sympatric broadcast-spawning limpets (Cellana spp.) within the Hawaiian archipelago. *Molecular Ecology*, *20*(10), 2128-2141.

Bowen, B. W. (2016). The three domains of conservation genetics: case histories from Hawaiian waters. *Journal of Heredity*, *107*(4), 309-317.

Bowen, B. W., Abreu-Grobois, F. A., Balazs, G. H., Kamezaki, N., Limpus, C. J., & Ferl, R. J. (1995). Trans-Pacific migrations of the loggerhead turtle (Caretta caretta) demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(9), 3731–3734.

Bowen, B. W., Forsman, Z. H., Whitney, J. L., Faucci, A., Hoban, M., Canfield, S. J., Johnston, E.C., Coleman, R..R., Copus, J.M., Vicente, J., & Toonen, R. J. (2020). Species radiations in the sea: What the flock?. *Journal of Heredity*, *111*(1), 70-83.

Bowen, B., Rocha, L., Toonen, R., Karl, S., Gaither, M., Craig, M., Dibattista, J., Eble, J., Skillings, D., & Bird, C. (2013). Origins of tropical marine biodiversity. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2013.01.018

Bowen, B.W., Shanker, K., Yasuda, N., Malay, M.C.D., von der Heyden, S., Paulay, G., Rocha, L.A., Selkoe, K.A., Barber, P.H., Williams, S.T., Lessios, H.A., Crandall, E.D., Bernardi, G., Meyer, C.P., Carpenter, K.E., & Toonen, R.J. (2014). Phylogeography unplugged: comparative surveys in the genomic era. *Bulletin of Marine Science*, *90*(1), 13-46.

Brodziak, J. K. T., Ianelli, J. N., Lorenzen, K., & Methot, R. D. (2011). *Estimating natural mortality in stock assessment applications*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Brodziak, J. K. T., Yau, A., O'Malley, J., Andrews, A. H., Humphreys, R. L., DeMartini, E. E., Pan, M., Parke, M., & Fletcher, E. (2014). Stock assessment update for the main Hawaiian Islands Deep 7 bottomfish complex through 2013 with projected annual catch limits through 2016.

Carreras, C., Ordóñez, V., Zane, L., Kruschel, C., Nasto, I., Macpherson, E., & Pascual, M. (2017). Population genomics of an endemic Mediterranean fish: Differentiation by fine scale dispersal and adaptation. *Scientific Reports*, *7*, 43417. https://doi.org/10.1038/srep43417

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, *22*(11), 3124–3140. https://doi.org/10.1111/mec.12354

Coleman, R. R., & Bowen, B. W. (2022). Genomic assessment of an endemic Hawaiian surgeonfish, Acanthurus triostegus sandvicensis, reveals high levels of connectivity and fine-scale population structure. *Coral Reefs*, *41*(3), 687–697. https://doi.org/10.1007/s00338-022-02257-4

Craig, M. T., Eble, J. A., & Bowen, B. W. (2010). Origins, ages and population histories: comparative phylogeography of endemic Hawaiian butterflyfishes (genus Chaetodon). *Journal of Biogeography*, *37*(11), 2125-2136.

D'Alessandro, E. K., Sponaugle, S., & Serafy, J. E. (2010). Larval ecology of a suite of snappers (family: Lutjanidae) in the Straits of Florida, western Atlantic Ocean. *Marine Ecology Progress Series*, *410*, 159-175.

D'Aloia, C. C., Andrés, J. A., Bogdanowicz, S. M., McCune, A. R., Harrison, R. G., & Buston, P. M. (2020). Unraveling hierarchical genetic structure in a marine metapopulation: A comparison of three high-throughput genotyping approaches. *Molecular ecology*, *29*(12), 2189-2203.

Earl, D. A., & VonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation genetics resources*, *4*(2), 359-361.

Eble, J. A., Toonen, R. J., Sorenson, L., Basch, L. V., Papastamatiou, Y. P., & Bowen, B. W. (2011). Escaping paradise: Larval export from Hawaii in an Indo-Pacific reef fish, the Yellow Tang (Zebrasoma flavescens). *Marine Ecology Progress Series*, *428*, 245–258. https://doi.org/10.3354/meps09083

Excoffier, L., & Lischer, H. E. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular ecology resources*, *10*(3), 564-567.

Faillettaz, R., Paris, C. B., & Irisson, J. O. (2018). Larval fish swimming behavior alters dispersal patterns from marine protected areas in the North-Western Mediterranean Sea. *Frontiers in Marine Science*, *5*, 97.
fisheries of the western Pacific region, 2004 annual report. WPRFMC, Honolulu Hawaii.

Gaither, M. R., Bernal, M. A., Coleman, R. R., Bowen, B. W., Jones, S. A., Simison, W. B., & Rocha, L. A. (2015). Genomic signatures of geographic isolation and natural selection in coral reef fishes. *Molecular Ecology*, *24*(7), 1543-1557.

Gaither, M. R., Jones, S. A., Kelley, C., Newman, S. J., Sorenson, L., & Bowen, B. W. (2011). High Connectivity in the Deepwater Snapper Pristipomoides filamentosus (Lutjanidae) across the Indo-Pacific with Isolation of the Hawaiian Archipelago. *PLOS ONE*, *6*(12), e28913. https://doi.org/10.1371/journal.pone.0028913

Gomez, C., Williams, A. J., Nicol, S. J., Mellin, C., Loeun, K. L., & Bradshaw, C. J. A. (2015). Species Distribution Models of Tropical Deep-Sea Snappers. *PLOS ONE*, *10*(6), e0127395. https://doi.org/10.1371/journal.pone.0127395

Gosline, W. A. (1955). *The Inshore Fish Fauna of Johnston Island, a Central Pacific Atoll*. http://hdl.handle.net/10125/8911

Haight, W., Kobayashi, D., & Kawamoto, K. (1993). Biology and Management of Deepwater Snappers of the Hawaiian Archipelago. *Mar. Fish. Rev.*, *55*.

Harrison, P., Babcock, R., BULL, G., Oliver, J., Wallace, C., & Willis, B. (1984). Mass Spawning in Tropical Reef Corals. *Science (New York, N.Y.)*, *223*, 1186–1189. https://doi.org/10.1126/science.223.4641.1186

Hodge, J. R., Van Herwerden, L., & Bellwood, D. R. (2014). Temporal evolution of coral reef fishes: global patterns and disparity in isolated locations. *Journal of Biogeography*, *41*(11), 2115-2127.

Knapp, I. S. S., Puritz, J., Bird, C., Whitney, J., Sudek, M., Forsman, Z., & Toonen, R. (2016, December 13). *EzRAD- an accessible next-generation RAD sequencing protocol suitable for non-model organisms_v3.2*. Protocols.Io. https://www.protocols.io/view/ezrad-an-accessible-next-generation-rad-sequencing-e9pbh5n

Kobayashi, D. R. (2006). Colonization of the Hawaiian Archipelago via Johnston Atoll: A characterization of oceanographic transport corridors for pelagic larvae using computer simulation. *Coral Reefs*, *25*(3), 407–417. https://doi.org/10.1007/s00338-006-0118-5

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources*, *15*(5), 1179–1191. https://doi.org/10.1111/1755-0998.12387

Kosaki, R. K., Pyle, R. L., Randall, J. E., & Irons, D. K. (1991). New records of fishes from Johnston Atoll, with notes on biogeography. Lobel, P. S. (2003). *Marine Life of Johnston Atoll, Central Pacific Ocean*, (Not Indicated edition). Natural World Press.

Kraft, D. W., Conklin, E. E., Barba, E. W., Hutchinson, M., Toonen, R. J., Forsman, Z. H., & Bowen, B. W. (2020). Genomics versus mtDNA for resolving stock structure in the silky shark (Carcharhinus falciformis). *PeerJ*, *8*, e10186. https://doi.org/10.7717/peerj.10186

Langseth, B., Syslo, J., Yau, A., Kapur, M., & Brodziak, J. K. T. (2018). *Stock assessment for the main Hawaiian Islands Deep 7 bottomfish complex in 2018, with catch projections through 2022.* https://doi.org/10.7289/V5/TM-PIFSC-69

Leis, J. M., & Lee, K. (1994). Larval Development in the Lutjanid Subfamily Etelinae (Pisces): The Genera Aphareus, Aprion, Etelis and Pristipomoides. *Bulletin of Marine Science*, *55*(1), 46–125.

Leis, J. M., Van Herwerden, L., & Patterson, H. M. (2011). Estimating connectivity in marine fish populations: What works best? *Oceanography Marine Biology Annual Review*, *49*, 193-234.

Leis, J., & Mccormick, M. (2002). The Biology, Behavior, and Ecology of the Pelagic, Larval Stage of Coral Reef Fishes. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (pp. 171–199). https://doi.org/10.1016/B978-012615185-5/50011-6

Leray, M., Beldade, R., Holbrook, S. J., Schmitt, R. J., Planes, S., & Bernardi, G. (2010). Allopatric divergence and speciation in coral reef fish: The three-spot Dascyllus, Dascyllus trimaculatus, species complex. *Evolution: International Journal of Organic Evolution*, *64*(5), 1218-1230.

Lester, S. E., & Ruttenberg, B. I. (2005). The relationship between pelagic larval duration and range size in tropical reef fishes: A synthetic analysis. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1563), 585–591. https://doi.org/10.1098/rspb.2004.2985

Misa, W. F. X. E., Drazen, J. C., Kelley, C. D., & Moriwake, V. N. (2013). Establishing species–habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. *Fishery Bulletin*, *111*(4), 293–308. https://doi.org/10.7755/FB.111.4.1

Moffitt, R. B., Kobayashi, D. R., & DiNardo, G. T. (2006). *Status of the Hawaiian bottomfish stocks, 2004*. Pacific Islands Fisheries Science Center.

Moore, C., Drazen, J. C., Radford, B. T., Kelley, C., & Newman, S. J. (2016). Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. *Marine Policy*, *69*, 32–41. https://doi.org/10.1016/j.marpol.2016.03.021

Mundy, B. C. (2005). Checklist of the fishes of the Hawaiian Archipelago. *Bishop Mus. Bull. Zool.*, *6*, 1-704.

Newman, S. J., Williams, A. J., Wakefield, C. B., Nicol, S. J., Taylor, B. M., & O'Malley, J. M. (2016). Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. *Reviews in Fish Biology and Fisheries*, *26*(3), 537–562. https://doi.org/10.1007/s11160-016-9442-1

Nichols, R. S. (2019). Sex-specific growth and longevity of ehu, *Etelis carbunculus,* (Family Lutjanidae), within the Hawaiian Archipelago. http://hdl.handle.net/10125/63204

Okuyama, J., Shishidou, H., & Hayashibara, T. (2019). Post-release horizontal and vertical behavior and philopatry of deepwater longtail red snapper Etelis coruscans around a bank. *Fisheries Science*, *85*(2), 361–368. https://doi.org/10.1007/s12562-019-01287-2

Oyafuso, Zack. S., Drazen, J. C., Moore, C. H., & Franklin, E. C. (2017). Habitat-based species distribution modelling of the Hawaiian deepwater snapper-grouper complex. *Fisheries Research*, *195*, 19–27. https://doi.org/10.1016/j.fishres.2017.06.011

populations: What works best?. *Oceanography and Marine Biology*, 201-242

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945-959.

Ramasamy, R. K., Ramasamy, S., Bindroo, B. B., & Naik, V. G. (2014). STRUCTURE PLOT: a program for drawing elegant STRUCTURE bar plots in user friendly interface. *SpringerPlus*, *3*(1), 1-3.

Randall, J. E. (2007). Reef and shore fishes of the South Pacific. *University of Hawai'i Press, Honolulu*.

Reiss, H., Hoarau, G., Dickey-Collas, M., & Wolff, W. J. (2009). Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, *10*(4), 361-395.

Rivera, M. A. J., Andrews, K. R., Kobayashi, D. R., Wren, J. L. K., Kelley, C., Roderick, G. K., & Toonen, R. J. (2011). Genetic Analyses and Simulations of Larval Dispersal Reveal Distinct Populations and Directional Connectivity across the Range of the Hawaiian Grouper (*Epinephelus quernus*). *Journal of Marine Biology*, *2011*, 1–11. https://doi.org/10.1155/2011/765353

Selkoe, K. A., Gaggiotti, O. E., ToBo Laboratory, Bowen, B. W., & Toonen, R. J. (2014). Emergent patterns of population genetic structure for a coral reef community. *Molecular ecology*, *23*(12), 3064-3079.

Sherman, K. D., Paris, J. R., King, R. A., Moore, K. A., Dahlgren, C. P., Knowles, L. C., Kristine, S., Tyler, C.R., & Stevens, J.R. (2020). RAD-Seq analysis and in situ monitoring of Nassau Grouper reveal fine-scale population structure and origins of aggregating fish. *Frontiers in Marine Science*, 157.

Team, R. (2021). RStudio: integrated development environment for R [internet]. Boston, MA: RStudio, Inc.; 2016.

Toonen, R. J., Puritz, J. B., Forsman, Z. H., Whitney, J. L., Fernandez-Silva, I., Andrews, K. R., & Bird, C. E. (2013). ezRAD: A simplified method for genomic genotyping in non-model organisms. *PeerJ*, *1*, e203. https://doi.org/10.7717/peerj.203

Williams, A.J., Wakefield, C.B., Newman, S.J., Vourey,.E., Abascal, F.J., Halafihi, T., Kaltavara, J., and Nicol, S.J. (2017). Oceanic, latitudinal, and sex-specific variation in demography of a tropical deepwater snapper across the Indo-Pacific region. *Frontiers in Marine Science*, *4*, 382.

WPRFMC. (2005). Western Pacific regional fishery management council. Bottomfish and seamount groundfish

Xie, S. P., Liu, W. T., Liu, Q., & Nonaka, M. (2001). Far-reaching effects of the Hawaiian Islands on the Pacific ocean-atmosphere system. *Science*, *292*(5524), 2057-2060.

Zimmerman, S. J., Aldridge, C. L., & Oyler-McCance, S. J. (2020). An empirical comparison of population genetic analyses using microsatellite and SNP data for a species of conservation concern. *BMC Genomics*, *21*(1), 382. https://doi.org/10.1186/s12864-020-06783-9