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Stock Composition Of Striped Marlin (Kajikia Audax) In The Central North Pacific Ocean Inferred By Analyses Of Genome-Wide Molecular Markers

Jackson Martinez
William & Mary - Virginia Institute of Marine Science, jacksonmartinez91@gmail.com

Stock Composition of Striped Marlin (*Kajikia audax)* in the Central North Pacific Ocean Inferred by Analyses of Genome-Wide Molecular Markers

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Jackson L. Martinez

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Jan R. McDowell, Ph.D.
Committee Chair / Advisor

John E. Graves, Ph.D
Committee Co-chair / Co-advisor

Eric J. Hilton, Ph.D.

Mark J. Brush, Ph.D.

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Abstract

Relative to many highly migratory fishes, Striped Marlin, *Kajikia audax*, exhibit considerable stock structure. At least four genetically distinct stocks of Striped Marlin have been delineated in the Pacific and Indian oceans, although stock composition in the central North Pacific (CNP) remains unclear and the presence of an additional stock in the North Pacific has been suggested in two recent studies. The goals of this research were to clarify the number of Striped Marlin stocks in the North Pacific and utilize temporal sampling to better understand the stock dynamics of Striped Marlin exploited by the Hawaii-based pelagic longline fishery (HBPLLF). Fishery observers collected 417 samples of Striped Marlin from the HBPLLF from 2019-2020. Of these, 85 samples underwent genotyping-by-sequencing using DArTSeq™ and the data were co-analyzed with an existing single nucleotide polymorphism (SNP) dataset for 256 individuals of Striped Marlin collected from throughout the species' range and reported in a previous study. Three of 12 Striped Marlin previously reported to comprise a putative second stock in the North Pacific and all with high observed heterozygosities were also re-sequenced to test the hypothesis that sample contamination resulted in the identification of a spurious stock. After re-sequencing, the observed heterozygosity of each of the three individuals was reduced by approximately 50%, confirming contamination and the original sequences for the 12 individuals comprising the putative second stock were removed from the dataset. Clustering analyses of the resulting dataset strongly supported a single North Pacific stock; the three re-sequenced individuals clustered into previously described stocks. The 73 (post-quality filtering) Striped Marlin sampled from the HBPLLF clustered into either the North Pacific (NPO; Japan, Taiwan, Hawaii, and California sample locations) or Oceania (New Zealand, western Australia, and eastern Australia sample locations) stocks, indicating mixing of the two stocks in the CNP. A panel of 48 SNPs with the highest power to discriminate between the two stocks was developed and 32 of these loci were used to genotype and assign an additional 325 Striped Marlin collected from the HBPLLF to stock of origin. Overall, 305 of these fish were assigned to stock of origin with high (> 90%) confidence and combined with DarTSeq-based assignments of the original 73 fish. Both stocks were present throughout the sampling period (NPO: 41.3%; Oceania: 58.7%). Temporal changes in stock composition were identified, with NPO fish dominant during the winter and spring, and Oceania fish dominant during the summer and fall. Although the HBPLLF is known to exploit mostly sub-adult Striped Marlin, 13 (3.1%) samples were found to be in an active spawning condition at the time of capture based on visual inspection. Of these, 10 assigned to NPO and two assigned to Oceania (the 13th fish assigned into Oceania but scores were below 90%). Factors that may influence the stock composition of Striped Marlin in the HBPLLF, including stock-specific movements to different spawning grounds and alternate feeding areas, as well as seasonally displaced recruitment to the HBPLLF, are discussed.

Stock Composition of Striped Marlin (*Kajikia audax)* in the Central North Pacific Ocean Inferred by Analyses of Genome-Wide Molecular Markers

Introduction

Large marine fishes such as billfishes (Istiophoridae) and tunas (Scombridae) inhabit the pelagic environment and encounter few physical barriers to migration and dispersal(Graves 1998; Waples 1998, Ward et al. 1994). The highly migratory nature of these fishes, coupled with the potential for extensive passive larval dispersal, can facilitate high levels of intraspecific gene flow, and as a result, genetic differences among populations may be slow to accumulate. Even so, many large pelagic fishes have been found to exhibit low, but statistically significant, genetic structuring between populations in different oceans, and in some cases, within oceans (general F_{ST} values below 0.05).

There are many ways in which to define a stock, with previous attempts resulting in a continuum of context-specific definitions (Skillman 1989; Carvalho and Hauser 1994; Waples and Gaggiotti 2006; Kerr et al. 2017). Broadly, a stock can be defined as an intraspecific group that is self-sustaining and retains genetic, demographic, and spatial integrity (Ihssen et al. 1981; Waples and Gaggiotti 2006). In this thesis, a stock will be defined as an evolutionary unit that has limited genetic connectivity with other intraspecific groupings. A thorough understanding of a species' stock structure is crucial for sustainable management and to prevent the loss of unique genetic variation (Graves 1998; Ward 2000).

A variety of methods have been developed to identify stocks and to estimate connectivity among such units, each with their own strengths and weaknesses (Skillman 1989; Cadrin et al. 2014). These methods include analyses of morphometric and meristic characters, chemical composition of hard parts (e.g., otoliths and vertebral elements), life

history characters, and molecular markers. Over the years, all of these methods have been used to investigate stock structure in pelagic fishes.

Some of the earliest methods to investigate stock structure in pelagic fishes included analyses of meristic and morphometric characters. These studies compared morphological differences among fish from different sample locations and significant differences were considered to be indicative of a lack of gene flow. For example, regional morphological differences in collections of Yellowfin Tuna (Schaefer 1955), Striped Marlin, and Sailfish (Wares and Sakagawa 1972) have been identified, suggesting potential stock structure. Analyses of life history characters, as well as analyses of the temporal patterning and distribution of fishery catches, have also been used to suggest spatial structuring based on regional differences. Schaefer (1998) and Bayliff (1988) identified regional differences in lengths at 50% maturity and growth rates for Pacific Yellowfin Tuna, and the occurrence of multiple geographically separated areas with concurrent high catches of Black Marlin suggested the presence of more than one stock in the Pacific (Shomura 1980; Skillman 1989). More recently, analyses of trace elements and stable isotopes that are deposited in otoliths and vertebrae have been used to investigate stock structure by establishing stock-specific chemical signatures to which fish of unknown origin are classified. For example, Yellowfin and Bigeye tunas sampled from the western equatorial Pacific were found to originate from local production with little contribution from fish from the central equatorial Pacific (Rooker et al. 2016). Similarly, adult Swordfish sampled from foraging grounds in Hawaii, California, and Mexico were found to originate from a single nursery area in the central equatorial North Pacific (Wells et al. 2021).

Since the 1960s, a variety of molecular markers have been analyzed to investigate stock structure in pelagic fishes. Early genetic techniques surveyed variation within nuclear DNA (nDNA) indirectly by studying proteins. Known as allozyme analysis, variation in protein charge or major changes in protein shape reflecting DNA changes among individuals, was surveyed using electrophoresis to characterize allelic differences at polymorphic loci among sample collections (Buonaccorsi et al. 1999; Ward 2000). While allozyme analysis did not reveal high amounts of variation, it proved useful for investigating intraspecific stock structuring in several tunas and billfishes including Yellowfin Tuna (Sharp and Dizon 1979; Ward et al. 1994), Skipjack Tuna (Fujino and Kang 1968), and Striped Marlin (Morgan 1992).

In the late 1980s, surveys of variation within mitochondrial DNA (mtDNA) revealed greater levels of genetic variation and stock structuring than allozyme analysis. Early studies of mtDNA, a haploid, non-recombining genome that is maternally inherited, employed restriction fragment length polymorphism (RFLP) analysis to reveal significant genetic differences between collections of blue marlin and sailfish from the Atlantic and Pacific oceans (Graves and McDowell 1995). The development of the polymerase chain reaction (PCR; Saiki et al. 1988) allowed for the amplification of specific regions of mtDNA for RFLP analysis as well as direct nucleotide sequence analysis (Sanger et al. 1977). These approaches achieved a greater resolution of stock structure for several pelagic fishes including Swordfish (Alvarado Bremer et al. 1995, 1996), Bigeye Tuna (Alvarado Bremer 1998), and Sailfish (McDowell 2002).

The 1990s saw an increase in genetic investigations of nuclear DNA (nDNA) using PCR and sequencing technologies. These studies resulted in the detection of an

increased number of polymorphic loci available for analysis, and the investigations often included analyses of mtDNA, as well. One class of nuclear markers investigated was single copy nuclear DNA (scnDNA), non-repetitive regions in the nuclear genome that may consist of both coding and non-coding regions (Karl and Avise 1993). A comparison of the levels of genetic diversity within and divergence between Atlantic and Pacific Blue Marlin revealed by various molecular markers demonstrated lower levels of divergence and variation with analyses of scnDNA and allozymes compared to those of mtDNA (Buonaccorsi et al. 1999).

In the late 20th century, the discovery of nuclear microsatellite DNA markers provided greater power to investigate stock structure, largely due to their relatively rapid evolutionary rates. Microsatellites are tandem repeats of one to six base pair motifs and are widely distributed throughout the nuclear genome. The increased variability of these markers is thought to be a result of slipped-strand mispairing during DNA replication (Tautz 1989; Fischer et al. 2007), which can result in the generation of many different allelic states at a single microsatellite locus. Although the use of microsatellites increased the ability to detect stock structure, studies analyzing microsatellites have limitations. Marker development is costly, time-consuming, and the markers are often taxa-specific. Additionally, the presence of null alleles, mutations at primer binding sites that prevent the amplification of a microsatellite allele, frequently occur. Despite these limitations, microsatellites became a molecular marker of choice for many genetic investigations, some of which have revealed statistically significant stock structure within large pelagic fishes including Sailfish (McDowell 2002), Bluefin Tuna (Carlsson et al. 2004, 2006), and Black Marlin (Williams et al. 2016).

Recent advances in molecular techniques, specifically next-generation sequencing (NGS) approaches that allow genetic variation to be surveyed at literally thousands of nuclear loci, have greatly increased the power to detect and resolve genetic stock structure for many species (Baird et al. 2008; Narum et al. 2013; Hohenlohe et al. 2020). These advances allow for the amplification and subsequent sequencing of millions of base pairs of DNA in parallel (Levy et al. 2016). The advent of high-throughput NGS approaches has facilitated the development of genotyping-by-sequencing (GBS) technology, combining restriction enzymes and NGS techniques to discover thousands of variable genetic markers known as single nucleotide polymorphisms (SNPs; Elshire et al. 2011). SNPs are single base-pair mutations that occur at high frequencies (generally every 200-500 base pairs) throughout the genome, thereby providing high-resolution surveys of genetic variation at the DNA sequence level (Brumfield et al. 2003). To date, a limited number of studies have utilized GBS methods to characterize the stock structure of large pelagic fishes including Yellowfin Tuna (Grewe et al. 2015; Pecoraro et al. 2018), Bluefin Tuna (Puncher et al. 2018), Striped Marlin (Mamoozadeh et al. 2020), and Albacore (Vaux et al. 2021).

Among large pelagic fishes, one species that has been shown to exhibit relatively high levels of stock structuring based on the analyses of a variety of molecular markers is the Striped Marlin, *Kajikia audax*. Over the past 30 years, molecular genetic techniques ranging from allozyme analysis to next-generation-sequencing have reported significant stock structuring of Striped Marlin throughout its range (Graves and McDowell 2015). However, there remains uncertainty about the stock structure of Striped Marlin in the

central North Pacific. The goal of this thesis is to better understand stock composition in this region.

To introduce the problems surrounding the stock structure of Striped Marlin, I will first present a brief overview of the biology and fisheries of this species. Striped Marlin are found at latitudes between 45°N and 45°S in the tropical and temperate waters of the Pacific and Indian oceans, and are considered to have the greatest latitudinal range of the istiophorid species (Nakamura 1985; Collette and Graves 2019). Although they are an Indo-Pacific species, Striped Marlin occasionally stray into waters on the Atlantic side of the Cape of Good Hope (Nakamura 1985; Talbot and Penrith 1962). Based on Japanese longline catch data, higher densities of Striped Marlin in the Pacific occur in a horseshoe-shaped distribution with the base of the horseshoe centered across the western coast of Central America and each arm extending across the North and South Pacific, respectively (Nakamura 1985).

Striped Marlin, like all istiophorid billfishes, feature elongated bodies, a spear-like bill, and a dorsal fin that extends along much of the dorsal margin of the body. Features that distinguish Striped Marlin from other istiophorids include pointed first anal, first dorsal, and pectoral fins, with the height of the first dorsal exceeding the body depth. Known for their vibrant coloration, Striped Marlin possess about 15 vertical cobalt blue stripes flanking their blue-black and silvery white dorsal and ventral surfaces, respectively (Collette and Graves 2019). Very similar in appearance to Striped Marlin is its sister species, the white marlin, *Kajikia albida*, which is found in the Atlantic Ocean and features rounded dorsal and anal fins.

Analysis of hard parts (otoliths and fin spines) to age Striped Marlin suggest a maximum life span of approximately 10 years for the species. Studies of daily otolith rings demonstrate that Striped Marlin exhibit some of the fastest growth rates among bony fishes (Bromhead et al. 2003; Melo-Barrera et al. 2003; Kopf et al. 2011), with estimated daily growth rates of 3.1 mm per day during the first six months of life and 1.5 mm per day after 12 months (Kopf et al. 2011). Striped Marlin reach 45% of their asymptotic length in the first year and females generally attain greater sizes than males (Melo-Barrera et al. 2003; Kopf et al. 2011). Striped Marlin in the western South Pacific have been found to achieve the fastest reported growth rates and largest maximum sizes for the species (Kopf et al. 2005; Sun et al. 2011; Fitchett 2019). Not surprisingly, this region is where many world-record Striped Marlin have been captured, with the current world record of 494 lbs. taken off Tutukaka, New Zealand in 1986 (IGFA; International Game Fish Association).

Found primarily within epipelagic waters, Striped Marlin inhabit a wide range of surface temperatures (15-31°C) (Nakamura 1985; Collette and Graves 2019). Electronic tagging approaches have been used to characterize habitat use and vertical movement patterns (e.g., Lam et al. 2015; Domeier 2006). Results indicate that Striped Marlin frequent the mixed layer and generally prefer water temperatures above 20°C (Sippel et al. 2007; Lam et al. 2015; Rohner et al. 2020). Lam et al. (2015) used pop-up satellite archival tags (PSATs) to investigate the depth and temperature distribution of Striped Marlin in multiple regions of the Pacific Ocean, including Australia, New Zealand, Hawaii, Southern California, Baja California, Costa Rica, Panama, and Ecuador. Tagged

fish were found to spend the majority of their time at depths less than 10 m and within 8°C of sea surface temperature, however, deep dives to 532 m and 8.6°C were observed.

Similar to other large pelagic fishes, Striped Marlin are apex predators that opportunistically feed on pelagic fishes and squids throughout the upper 200 meters of the water column (Nakamura 1985; Torres-Rojas et al. 2013; Loor-Andrade et al. 2017). Shimose et al. (2010) reported that Striped Marlin in the western North Pacific feed predominantly on molids, ostraciids, and scombrids in the open-ocean area, shifting to tetraodontids and scombrids in the near-shore waters. In the eastern North Pacific, Striped Marlin have been found to consume approximately 2 kg per day from a variety of prey items including chub mackerel, California pilchard, jumbo squid, northern anchovy, and Pacific saury (Morrow 1952; Eldridge and Wares 1974; Abitia-Cardenas et al. 2011).

Conventional and electronic tagging studies suggest that Striped Marlin are less vagile than other istiophorid billfishes, such as the black marlin and blue marlin, which have well-documented trans-Pacific and, in the case of blue marlin, inter-oceanic movements (Squire and Suzuki 1990; Ortiz et al. 2003; Graves and McDowell 2015). Results of conventional (dart) tagging efforts reviewed by Ortiz et al. (2003) indicate that Striped Marlin at liberty for up to 2.5 years displayed limited dispersal relative to most other billfishes, and a lack of cyclical annual movements, as reported for white marlin (Ortiz et al. 2003; Loose 2014). No trans-Pacific movements have been reported, and unlike other istiophorid billfishes, over 90% of Striped Marlin tag recoveries have been for individuals at-large for less than one year (Ortiz et al. 2003).

Electronic tagging approaches are useful for demonstrating large-scale horizontal movements; however, meaningful inferences of site fidelity or annual movements are

limited by a lack of tag deployments exceeding one year. Nonetheless, studies using satellite tags have shown that Striped Marlin in several locations exhibit regional site fidelity and/or limited dispersal (Domeier 2006; Holdsworth et al. 2009; Rohner et al. 2020). In the Pacific, tagged Striped Marlin were found to remain within a 2000 km radius of the tagging site during times at liberty of up to 9 months (Domeier 2006), and a recent study conducted in the Indian Ocean reported that Striped Marlin tagged off the Kenyan coast remained in the western Indian region for periods up to 183 days (Rohner et al. 2020). The first study to implant internal archival tags in billfish was conducted on Striped Marlin off Baja California, Mexico. Unfortunately, the tags failed to collect data after a few weeks, but fish carrying the implanted tags were recaptured in the eastern North Pacific after times at liberty ranging from 1.1-7.7 years (Domeier et al. 2018), a finding that supports the notion that Striped Marlin are not as migratory and have greater site fidelity than other istiophorids.

Striped Marlin spawning activity has been identified based on the presence of actively spawning ("running ripe") adults or larvae and is characterized by protracted spawning seasons and large reproductive output (Nakamura 1985; Collette and Graves 2019). Striped Marlin may undergo seasonal migrations to sub-tropical areas prior to spawning (Domeier 2006; Kopf et al. 2012). Reproductive activity appears to occur across a broad latitudinal band throughout their range, not unlike yellowfin tuna and bigeye tunas (Kopf et al. 2012). However, with relatively low population biomass compared to those of many tunas, spawning in Striped Marlin may be more spatially and temporally restricted, facilitating the development of multiple spawning events

throughout their range. Fidelity to a spawning area may promote the elevated stock structuring reported for this species.

Maximum larval abundance for Striped Marlin occurs in the early summer months throughout the Indo-Pacific (Nakamura 1985). With a lower temperature limit of 24°C for Striped Marlin larvae, spawning occurs in the western North Pacific and areas around Taiwan from April to August (Ueyanagi 1962; Squire and Suzuki 1990; Chang et al. 2018), in the central North Pacific from May to July (Hyde et al. 2006; Humphreys and Brodziak 2019), in the eastern central Pacific from May to December (Kume and Joseph 1969; Gonzales-Armas et al. 2006), and in the western South Pacific from October to January (Kopf et al. 2012). Spawning has also been found to occur in the eastern Indian Ocean in October and November, and the western Indian Ocean in December and January (Pillai and Ueyanagi 1978; Nakamura 1985).

Striped Marlin are highly fecund, with indeterminate batch spawning and asynchronous oocyte development (Kopf et al. 2012; Chang et al. 2018). Batch fecundity has been found to range from 2.2-4.1 million oocytes in females ranging from 223 to 269 cm lower-jaw-fork-length (LJFL), with an estimated annual fecundity between 90-281 million oocytes for an average 109 kg female (Kopf et al. 2012). Similarly, Chang et al. (2018) reported individual batch fecundities of 2.4-6.4 million oocytes with individual annual fecundities between 98.9 and 266.1 million oocytes per spawning season.

Striped Marlin have been found to exhibit regional differences in life history characters, including size at maturity. In the central North and eastern North Pacific, the size at 50% maturity for females is reported to be 160 cm eye-to-fork length (EFL) (Eldridge and Wares 1975; Humphreys and Brodziak 2019), while in the western North

and western South Pacific, the size at 50% maturity for females is 181 cm EFL (Kopf et al. 2012[1]; Chang et al. 2018). Generally, females reach maturity at greater lengths compared to males (Kopf et al. 2012).

Striped Marlin constitute a source of protein and a prized sport fish for many nations. Commonly caught in commercial, artisanal, and recreational fisheries, the majority of Striped Marlin are taken by pelagic longline fleets as non-target bycatch in commercial fisheries targeting tunas and swordfish. Historically, Japan has accounted for the majority of the reported Striped Marlin catch in the Pacific Ocean, with most of the catch taken in the central eastern and western North Pacific (Bromhead et al. 2003). Catches of Striped Marlin in the Pacific Ocean peaked at over 20,000 mt in the 1960s. Since that time, Pacific catches declined to approximately 13,000 mt in the late 1980s and to 7,000 mt by 2000. Reported catches of Striped Marlin in the Indian Ocean have historically been lower than those in the Pacific, with the majority of Striped Marlin catch taken by Taiwanese longliners. Catches in the Indian Ocean peaked at over 5000 mt in the 1960s and have decreased to as low as 2000 mt since then despite a general increase in effort (Bromhead et al. 2003). In both oceans, a lack of billfish identification to species and poor reporting (especially of artisanal landings) have hampered efforts to characterize Striped Marlin catches (Bromhead et al. 2003).

Striped Marlin are managed throughout their range by three regional fishery management organizations (RFMOs) with jurisdictions in the Pacific and Indian oceans. Four stocks are recognized and managed by these RFMOs. In the eastern Pacific, the

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1 Size at maturity for male and female Striped Marlin in the western South Pacific reported in Kopf et al. (2012) were converted from lower jaw-to-fork length to eye-to-fork length via the equation given in Sun et al. (2011); LJFL (cm) = 1.12 EFL + 7.33.

Inter-American Tropical Tuna Commission (IATTC) recognizes a single stock east of 150°W. The Western and Central Pacific Fisheries Commission (WCPFC) recognizes two Striped Marlin stocks west of 150°W with one in the western and central North Pacific and one in the western South Pacific. Striped Marlin in the Indian Ocean are managed as a single stock by the Indian Ocean Tuna Commission. In the eastern Pacific, the most recent stock assessment indicated that Striped Marlin are not overfished and overfishing is not occurring (IATTC 2019). Striped Marlin in the western and central North Pacific are considered overfished and subject to overfishing (WCPFC 2019a), and in the western South Pacific, the stock is likely to be overfished with the possibility of overfishing occurring (WCPFC 2019b). Lastly, Striped Marlin in the Indian Ocean are considered overfished with overfishing occurring (IOTC 2017).

The Striped Marlin stock boundaries defined by the RFMOs mentioned above do not necessarily correspond with the stock structure suggested by the available biological information. Stocks that are defined based on jurisdictional boundaries instead of biological information may result in overexploitation or regional depletion of the fishery resource (Cadrin et al. 2014; Kerr et al. 2017). The genetic stock structure of Striped Marlin has been investigated over the past three decades with a variety of molecular markers, revealing significant levels of structuring throughout their range.

An initial investigation into the genetic stock structure of Striped Marlin studied relatively low-resolution allozyme (protein) markers and suggested small but significant genetic differences among sample collections from Australia, Hawaii, Mexico, and Ecuador (Morgan 1992). A subsequent study employed RFLP analysis of mtDNA on many of the same samples analyzed by Morgan (1992) and demonstrated statistically

significant mtDNA heterogeneity among the four Pacific collections (Graves and McDowell 1994). These studies were among the first to identify significant levels of genetic stock structuring in a highly migratory species.

Additional investigations of Striped Marlin stock structure have utilized multiple marker classes and additional sample collections to resolve spatially distinct stocks in the Pacific. McDowell and Graves (2008) obtained samples from seven locations throughout the Pacific and analyzed genetic variation at five microsatellite loci and sequenced an 819 bp fragment of the mtDNA control region for 373 and 84 specimens, respectively. This study resolved four distinct stocks that correspond with areas of known spawning activity for Striped Marlin in the Pacific: western South Pacific (Australia), North Pacific (Japan, Taiwan, Hawaii, California), central east Pacific (Mexico), and eastern South Pacific (Ecuador). Subsequently, Purcell and Edmands (2011) analyzed genetic variation within Pacific Striped Marlin at twelve microsatellite loci for 1199 individuals and sequenced a 1000 bp fragment of the mtDNA control region for 451 individuals. Samples in this study were collected off Japan, Hawaii, Southern California, Mexico, Central America, Australia, and New Zealand. That study resolved three distinct stocks in the Pacific, generally agreeing with the results of McDowell and Graves (2008); a lack of specimens from South America prevented the verification of a stock in the eastern South Pacific. Depending on how the data were analyzed, Purcell and Edmands (2011) reported a putative fourth stock in the North Pacific comprised of only mature Hawaiian fish (n=312), while immature Hawaiian fish (n=227) clustered among the rest of the North Pacific sample collections (Japan, Taiwan, and California). It should be noted, however, that the classification of maturity for Hawaiian fish was based on lengths and weights at

first maturity for Striped Marlin in the Coral Sea, which may not be accurate for fish in Hawaii. Additionally, the putative second central North Pacific stock was only evident after correcting the microsatellite allele frequencies for the presence of null alleles. The putative second North Pacific stock was detected only when the microsatellite data were corrected for the presence of null alleles (Purcell and Edmands 2011).

The existence of a second putative stock of Striped Marlin in the central North Pacific was also supported in a recent study by Mamoozadeh et al. (2020) that employed GBS methods (DarTSeq^{TM}) to discover genome-wide SNP markers from samples taken throughout the species' range, including collections from the Indian Ocean. Compared to the 5-12 nuclear microsatellite loci surveyed in the two previous studies, this investigation surveyed variation at 4,206 SNP loci from 245 individuals. The results supported the genetic structuring previously resolved within the Pacific Ocean and identified structure within the Indian Ocean. Through multivariate and Bayesian clustering simulations, Mamoozadeh et al. (2020) identified significant heterogeneity among samples collected from the North Pacific, with 53 individuals from Japan, Taiwan, Hawaii, and California clustering into a broadly distributed North Pacific stock (NPO; 15 from Hawaii) and an additional 12 samples clustering into a second North Pacific stock (NPO2; 6 from Hawaii, 6 from Japan). Unfortunately, length data to infer maturity were not available for fish sampled in this study, preventing direct comparison with the results of Purcell and Edmands (2011) for the central North Pacific. It was noted that the 12 individuals that comprised the putative NPO2 stock showed much higher heterozygosities than other individuals and the NPO2 stock showed the greatest genetic

differentiation to other stocks resolved in the study (F_{ST} = 0.0361-0.0819) vs. (F_{ST} = 0.0137-0.0614) raising concerns of possible sample contamination.

Both Purcell and Edmands (2011) and Mamoozadeh et al. (2020) suggested the presence of an additional putative stock of Striped Marlin in the central North Pacific, but there were technical issues with each study. As a result, there remains uncertainty regarding the stock structure in this region. The goals of this study were to clarify the number of Striped Marlin stocks in the North Pacific and utilize temporal sampling to better understand the stock dynamics of Striped Marlin exploited by the HBPLLF.

Objectives and Hypothesis

The primary objectives of this study were to resolve the genetic stock structure of Striped Marlin within the central North Pacific Ocean (CNP) and intensively study the stock composition of Striped Marlin caught in the Hawaii-based pelagic longline fishery (HBPLLF) over a 14-month period. The null hypotheses tested in this study were (1) Striped Marlin in the CNP comprise a single genetic stock, i.e., no additional genetic structure occurs within the region, and (2) the Hawaii-based pelagic longline fishery exploits a single genetic stock of Striped Marlin.

Materials and Methods

Experimental Design

To provide for a robust genetic analysis of Striped Marlin stock structure in the CNP, individuals of known size and reproductive condition were sampled from those caught in the HBPLLF throughout one year (Figure 1). A subset of those Striped Marlin,

as well as some of the samples that were identified as belonging to the NPO2 stock in Mamoozadeh et al. (2020), underwent DarTSeq™. The resulting sequence data were co-analyzed with those of Mamoozadeh et al. (2020) and aligned to a recently sequenced white marlin genome generated by the Fisheries Genetics Lab at VIMS. Clustering analyses were conducted on the co-analyzed dataset to investigate the presence of a second stock of Striped Marlin within the central North Pacific.

Due to the costs associated with obtaining GBS data, it was not possible to sequence all of the Striped Marlin collected from the CNP over the year-long sample period. To provide for a more cost-effective genetic analysis that could be used to monitor the stock composition over time, the intent was to develop a panel of 48 SNPs that could be used in-house to rapidly assign Striped Marlin to their stock of origin. If the clustering analyses of the GBS data resolved two stocks within the central North Pacific (that is, if the existence of the putative NPO2 stock was verified), a SNP panel would be developed to discriminate between those stocks and then used to assign all temporal samples collected from the year-long sampling in the HBPLLF to their respective stock of origin. Subsequently, seasonal trends in fish size and spawning activity would be explored for each stock across the year-long sampling period. Alternatively, if the clustering analyses of the GBS data revealed a single stock within the CNP, a SNP panel would be developed to discriminate among the five Striped Marlin stocks that occur throughout the Indo-Pacific.

Sample Collection

Striped Marlin fin clips were collected by fisheries observers contracted by the National Marine Fisheries Service (NMFS) Pacific Islands Regional Office operating on vessels in the Hawaii-based pelagic longline fishery from September 2019 to October 2020 (Figure 1). Based on historical catch rates of Striped Marlin in this fishery and availability of observer time to process samples, the goal was to obtain sample sizes of approximately 50 Striped Marlin per month. Waples (1998) noted that a sample size of 50 individuals per location reduces random sampling error associated with low signal-to-noise ratios typical of genetic data.

Observers were provided with sampling kits that consisted of a sampling protocol, 1.5 ml vials pre-filled with a sarcosyl-urea preservative (Chapman et al. 2014), scissors, alcohol wipes, and gloves. Following the sampling protocol, observers collected a small (1 cm x 1 cm) fin clip tissue sample from the membrane between the first dorsal fin spines, submerged it in preservative in the vial, and labeled it with a specimen number and collection date. To avoid sample contamination, observers used alcohol wipes to sterilize their scissors between samples. In addition to fin clips, biological information was obtained for each specimen, including location and date of capture, fish length (EFL), sex, and spawning condition. Due to the concerns regarding confidentiality of fishing locations reported by commercial fishers operating in the HBPLLF, personnel at the NMFS Pacific Islands Regional Office aggregated catch locations into one of four spatial quadrants (Figure 1). To determine if the fish were in an active spawning condition, observers visually checked for the presence of enlarged ovaries in females or enlarged testes and the presence of milt in males, and also took a photograph of the fish and its gonads. For fish not in active spawning condition, maturity was assigned based on

the reported length in comparison to the length at 50% maturity for Striped Marlin in the CNP (160 cm EFL; Humphreys and Brodziak 2019). Once observers returned from deployments, samples and associated catch data underwent quality-control checks by NMFS personnel. Striped Marlin samples and catch data for individuals collected in 2019 (n=155) were shipped to VIMS in early 2020, and samples and catch data for individuals collected in 2020 (n=262) were shipped to VIMS in January 2021.

DNA Isolation

High molecular weight genomic DNA was isolated from all Striped Marlin fin clips using Puramag™ carboxylated magnetic beads (Molecular Cloning Laboratories (MCLAB), South San Francisco, CA). DNA quality was assessed via gel electrophoresis on a 1.5% agarose gel (1X TBE buffer, pH = 8) run at 90 V for approximately 45 minutes. Samples were run with a 1Kb plus DNA Ladder (Thermo Fisher Scientific, Waltham, MA) and visually inspected to determine the presence of high molecular weight DNA. DNA was quantified and concentrated to between 50 and 100 ng/μL for each sample. DNA quantity and purity were assessed using a NanoDrop™ 2000 Spectrophotometer (Thermo Fisher Scientific, Waltham, MA) or a Qubit 4.0 fluorometer (Thermo Fisher Scientific, Waltham, MA). DNA was considered sufficiently pure if the 260/280 ratio was between 1.6 and 1.8. Isolations that did not produce DNA of the necessary quality or quantity were re-isolated and re-evaluated as above.

DarTseq™ 1.0 Genotyping

A subset of 85 Striped Marlin collected during the last quarter of 2019 from the HBPLLF was prepared for genotyping-by-sequencing to supplement the sample collections analyzed by Mamoozadeh et al. (2020), which suggested the presence of a second putative stock (NPO2) in the North Pacific. In addition, DNA was re-isolated from the 12 Striped Marlin from Mamoozadeh et al. (2020) that comprised the putative NPO2 stock to investigate potential sample contamination given the high level of heterozygosity noted in those samples. Based on the DNA quantity and quality of the re-isolations, three of the 12 individuals from the NPO2 stock, all collected from Hawaii in 2015, were suitable for re-sequencing. These three individuals were included with the DNA isolated from 85 individuals collected from the HBPLLF in the fall of 2019, and the 88 Striped Marlin DNA isolations were loaded onto a 96-well plate at concentrations between 52.0 to 87.4 ng/μL and sent to DarT PL for DarTSeq™ 1.0 genotyping in September 2020. The resulting sequence data were received in December 2020.

The DarTseq™ genotyping method combines genomic complexity reduction and next-generation-sequencing methods to identify thousands of genome-wide SNPs (Sansaloni et al. 2011; Kilian et al. 2012). Briefly, genomic complexity reduction was achieved using a double restriction enzyme (RE) digestion with *PstI* and *SphI*, targeting low copy regions based on the representation size and genome fraction selected. Subsequent ligation reactions with custom RE-specific adapters were similar to those described in Elshire et al. (2011) and Kilian et al. (2012). The forward adapter was compatible with *PstI* and included an Illumina flowcell attachment sequence, a sequencing primer sequence, and a variable length barcode. The reverse adapter was compatible with *SphI* and included an Illumina flowcell attachment region. After RE

digestion and adapter ligation, fragments containing *PstI-SphI* overhangs were amplified by PCR, pooled at equimolar ratios into multiplex libraries, and sequenced in a single lane of an Illumina HiSeq 2500 platform (Illumina, Inc.).

Raw sequence data were processed using the proprietary DarTseq analytical pipeline DarTtoolbox, in which FASTQ files were analyzed for quality-based filtering, variant calling, and generation of final genotypes. First, raw sequence reads were filtered by average read quality score (Q score). Those sequences with Q scores < 25 for at least 50% of bases were removed as were those with Q scores < 30 in the barcode region. Based on the probability of incorrect base calls during sequencing, a Q score of 30 suggests the probability of an incorrect base call 1 in 1,000 times, or 99.9% sequencing accuracy. The increased selection criteria in the barcode region ensured reliable assignment of sequences to specific samples. Sequence reads were then de-multiplexed according to sample-specific barcodes and queried against NCBI GenBank and a proprietary DarT PL database for the identification and removal of reads associated with viral or bacterial contamination. Following raw sequence processing, co-analysis of the sequence data was performed by DarT PL on the 88 samples with those previously generated by Mamoozadeh et al. (2020), and all reads were aligned to the white marlin reference genome. Polymorphic positions were identified as SNP variants and major and minor alleles for each variant were identified. A matrix of SNP genotypes was generated based on the following DarT scores: “0” = major allele homozygote, “1” = alternate allele homozygote, “2” = heterozygote. SNP loci that met any of the following conditions were removed to achieve robust variant calling: monomorphic clusters (uninformative SNP loci that contain the same allelic state across all samples), clusters containing tri-allelic or

aberrant SNPs, clusters with overrepresented sequences, and/or loci lacking both allelic states (homozygote and heterozygote). To assess technical replication error and ensure accurate genotype calls, a proportion of loci were re-sequenced. Major and alternate allele frequencies, heterozygote and homozygote frequencies, polymorphism information content (PIC), call rate, and average reproducibility were calculated for the remaining SNP loci. The final genotype matrix supplied by DarT PL contained 68,224 SNP loci and associated metadata.

In-House Quality Filtering of SNP data

Once the co-analyzed dataset was received from DarT PL, additional quality filtering was conducted to ensure that only high-quality SNPs were retained using the *dartR* (Gruber et al. 2018) package in R version 4.0.4 (R Core Team 2021). Because several billfish species other than Striped Marlin were included in the original dataset, only Striped Marlin and their respective sequence data were retained, and uninformative loci that contained only one allele across all sample locations were removed by filtering out monomorphic loci. To minimize genotyping errors and missing data, quality control filters included removing loci based on read depth (coverage), the average count of sequence tags recovered for a particular locus, below 5x and above 75x. Loci with low coverage were removed to avoid retaining loci resulting from base pair miscalls, and those with high coverage were removed because they may represent a gene duplication event where the observed SNP resulted from multiple copies of the same sequence across the genome. Additionally, loci and individuals missing >10% of genotype calls were removed. Loci with less than 99% reproducibility were also removed, based on

comparisons of technical replicates for scoring consistency generated for one third of individual samples. If more than one SNP was identified on the same 69 bp sequence fragment (hereafter termed a secondary SNP), one SNP was retained at random to ensure independence of SNP loci. Loci resulting from genotyping error were removed by filtering for those loci with a minor allele frequency (MAF) <1%, the frequency of the second most common allele across all samples. The final filtering step included removing loci that did not conform to the expectations of Hardy-Weinberg Equilibrium (HWE) in more than one sample collection using an exact test (Wigginton et al. 2005). This was done by testing the statistical significance of HWE comparisons for each sample location using a critical value that was corrected by a modified false discovery rate (FDR; Benjamini and Yekutieli 2001; Narum 2006).

To screen for potential sample contamination, the R package *radiator* (Gosselin 2020) was used to assess levels of heterozygosity in individual samples and sample locations. If sample contamination was present, as evidenced by the presence of heterozygosity levels that were elevated compared to the rest of the sequenced individuals, the contaminated individuals were removed from the dataset.

Identification of Population Structure

Clustering methods were employed to determine genetic relationships among sample collections. These approaches were not constrained by the assumptions of Hardy-Weinberg equilibrium (HWE) and the full dataset was used for analysis (Jombart et al. 2009). A principal component analysis (PCA) was conducted in the R package *adegenet* (Jombart 2008; Jombart and Ahmed 2011) to identify genetically similar clusters of

individuals based on their sample locations by calculating Euclidean genetic distances between samples. Additionally, a discriminant analysis of principal components (DAPC; Jombart et al. 2010) was conducted in the R package *adegenet* to assess individual-based clustering. DAPC employed a PCA to maximize genetic variation between groups and minimize variation within groups to identify the most likely number of genetic clusters contained in the data (K), and individuals were then assigned to their most likely cluster. Successive K-means clusters were discovered using *find.clusters* and each K scenario was given a Bayesian information criterion (BIC) score. The K scenario with the lowest BIC score was selected as the most likely number of genetic clusters in the data. The number of retained principal components was determined using the function *xval*, which uses cross-validation procedures to optimize the number of principal components to be retained based on the group membership of 10% of individuals from the dataset (test set) predicted from the remaining 90% of individuals (training set). The optimal number of retained principal components was identified as that associated with the lowest mean squared error. Based on the results of the clustering analyses, individuals from each sample location were combined into genetically-distinct populations.

Following clustering analyses, the degree of genetic connectivity between populations was calculated using unbiased F-statistics (F_{ST}; Weir and Cockerham 1984). Because this approach is constrained by the assumptions of HWE, the full dataset with loci not conforming to the expectations of HWE removed was used to calculate F_{ST} in the R package *StAMPP* (Pembleton et al. 2013) and pairwise significance was assessed via 10,000 iterations of the data.

Identification of Genetic Diversity

Once the co-analyzed dataset was evaluated for the presence of population structure, levels of genetic diversity were determined for the populations. Genetic diversity statistics were calculated for each population using the full dataset with loci not conforming to the expectations of HWE removed. Observed (H_o) and expected (H_e) heterozygosities were calculated in the R packages *poppR* (Kamvar et al. 2014) and *dartR*, respectively. To assess potential inbreeding, an inbreeding coefficient (G_{IS}) was calculated using Genodive (Meirmans and Van Tiendren 2004).

Identification of Discriminatory SNPs

Due to the elevated costs associated with sequencing large numbers of samples using DarTSeq™, a cost-effective approach to investigate Striped Marlin stock composition within the central North Pacific was developed. To do this, a panel of discriminatory SNPs was created to allow rapid genotyping of the remaining HBPLLF samples. Because analyses of the DarTSeq™ dataset revealed the presence of two stocks within the HBPLLF, North Pacific and Oceania, a SNP panel consisting of those loci that best discriminated between the two stocks was assembled, and a genotyping assay was then developed for in-house genotyping.

To identify SNP loci that can best discriminate among the populations within the HBPLLF, SNPs were ranked based on their ability to separate both NPO and Oceania. The full SNP dataset with loci not conforming to the expectations of HWE removed was read into the Toolbox for the Evaluation and Ranking of SNPs (TRES) software (Kavakiotis et al. 2015). Prior to locus ranking, the dataset was divided into training

(80% individuals) and test (20% individuals) datasets, evenly separating the genetic clusters in TRES. The use of training and test datasets was implemented to prevent upwardly biasing the predicted assignment accuracy of the dataset (Anderson 2010). SNP loci with high discriminatory power were ranked based on three criteria: delta (Shriver et al. 1997), pairwise Wright's F_{ST} (Wright 1951), and informativeness for assignment (I_n; Rosenberg et al. 2003; Ding et al. 2011). Because the goal was to identify a final subset of 48 discriminatory SNPs, the training set was initially used to rank sets of 96, 192, and 384 SNPs using each of the three methods. Once the loci were ranked, the test datasets underwent PCA to visually assess the clustering and discriminatory accuracy of the ranked SNPs. The final list of loci was then submitted to Fluidigm's D3™ Assay Design Software (Fluidigm) for primer development.

SNP Panel Development and Genotyping

SNP panel primers were developed by Fluidigm with the following design restrictions: 1) sequences required a minimum of 60 base pairs in length, 2) a maximum of 250 base pairs were needed on either side of a SNP position, 3) SNP targets had to be bi-allelic (have only two alleles per locus), 4) there could not be another SNP within 20 base pairs on either side of the target SNP, and 5) sequences should not have a guanine-cytosine (GC) content greater than 65%. After submission of candidate SNP loci, Fluidigm returned custom primers for those loci that met the design criteria for primer design.

SNPType™ assays incorporate one of two alternate fluorescent molecules for discrimination of SNP alleles per locus. These assays are run on a Fluidigm system, a

high-throughput genotyping platform that conducts an allele-specific polymerase chain reaction (PCR) and adds fluorescent molecules (universal FAM and HEX probes) to the newly synthesized strands, imaging the resulting products. The genotyping results are processed using a native software to determine the fluorescence values for each sample and distinguish between two alleles at the targeted SNP location.

Once the primers were developed by Fluidigm and shipped to VIMS, they were tested for genotyping accuracy by comparing genotype calls from the Fluidigm with DarTSeq™ sequence genotypes for 47 Striped Marlin from the HBPLLF. After the genotyping accuracy of the SNP panel was confirmed, the remainder of the 2019-2020 sample collection was genotyped using the Fluidigm system. The resulting genotype data were used to assign individuals to their stock of origin. Using GENECLASS2 (Piry et al. 2004), assignment tests were conducted with a reference dataset consisting of the 83 individuals (both NPO and Oceania) that were initially DarT sequenced and assigned to stock of origin based on PCA and DAPC , using the Fluidigm-generated genotypes for the 48 loci in the SNP panel. Assignment tests were run using the Rannala and Mountain (1997) criterion (0.05 threshold). Individual assignment scores to either Oceania or NPO were produced and individuals with assignment scores below 90% were removed from the dataset. Assignment probabilities into either stock were calculated using the Monte Carlo resampling probability computation using the Peatkau et al. (2004) simulation algorithm, 10,000 simulated individuals, and an exclusion threshold of $p<0.05$. Following the assignment tests, the relationships between individual stock assignment and catch data were evaluated, including trends in stock composition by size, season, sex, and spawning condition.

Results

Sample Collection

NMFS fishery observers collected fin clips from and recorded associated catch data for 417 Striped Marlin caught in the HBPLLF between September 2019 and October 2020 (Appendix 1). No Striped Marlin were collected between March and May 2020 as observers were not allowed on fishing vessels due to the COVID-19 pandemic. The number of Striped Marlin sampled per month ranged from six in September 2019 to 95 in September 2020 with an average of 38 fish per month over the eleven months during which samples were collected (Figure 2). The monthly mean lengths of sampled Striped Marlin ranged from 131 cm EFL in February 2020 to 160 cm EFL in June 2020, with an overall mean length of 137 cm EFL (Figure 3). From the total sample collection, 203 (49%) were females, 175 (42%) were males, and 39 (9%) were unidentified. Females were the dominant sex of Striped Marlin sampled in most months, ranging from 56.2% in October 2019 to 83.3% in September 2019. Males exceeded females in November 2019, January, June, and July 2020, ranging from 54.0% in November 2019 to 66.7% in January and July 2020 (Figure 4). The greatest mean length for both sexes occurred in June 2020 (163.3 cm EFL, males; 162.1 cm EFL, females). The lowest mean length for females (131.1 cm EFL) occurred in February 2020, and the lowest mean length for males (125.0 cm EFL) occurred in September 2019 (Figure 5). Of the 417 Striped Marlin sampled from the HBPLLF, 13 (3.1%) were reported to be in an active spawning (ripe) condition. One ripe fish was sampled in September 2019 (16.7% of monthly samples, female), one in February 2020 (2.4%, male), five in June 2020 (13.9%, 2 females, 3

males), two in July 2020 (9.5%, 1 female, 1 male), three in September 2020 (3.5%, 3 females), and one in October 2020 (5.6%, male). Of these 13 individuals, four (30.8%) were reported to be at or greater than the reported length at 50% maturity for Striped Marlin in the central North Pacific (160 cm EFL; lengths = 160, female; 260, male; 165, female; 165, female). For the non-ripe Striped Marlin (96.9%), 37 fish (9.2%) were at or greater than the length at 50% maturity.

DarTSeq™ 1.0 Genotyping

The DarTSeq™ genotyping data for the 85 Striped Marlin sampled from the HBPLLF in 2019 (this study) and three re-sequenced NPO2 individuals initially analyzed by Mamoozadeh et al. (2020) were co-analyzed with the data for the 245 Striped Marlin analyzed in Mamoozadeh et al. (2020), as well as 468 samples of other billfish species. The dataset returned by DarT PL recovered 68,224 loci, along with associated metadata that included polymorphism information content (PIC) for each SNP locus (the diversity of alleles at a particular locus), trimmed sequence tags (read sequences containing SNP loci), and technical replicate scores (a measure of genotype scoring consistency used in the calculation of sequence reproducibility).

In-House Quality Filtering of SNP Data

Once the co-analyzed dataset was received from DarT PL, quality filtering steps were conducted to retain SNPs with high confidence and low genotyping errors. The dataset was first filtered to remove the 468 samples of various billfish species, resulting in the presence of 36,540 monomorphic SNPs (SNPs not found in Striped Marlin). These

monomorphic SNPs were removed from the dataset and subsequent filtering for read depth and call rate by locus (missing data per locus) removed 12,232 and 5,730 loci, respectively. Individual samples were then filtered for call rate (missing data per individual), resulting in the removal of 18 individuals (16 from Mamoozadeh et al. (2020) and 2 from the present study). Filtering for reproducibility based on technical replicates and the presence of secondary SNPs resulted in the removal of 2,303 and 1,755 SNPs, respectively. Filtering based on minor allele frequency (MAF; <1%) removed an additional 8,003 SNPs. Finally, filtering loci that did not conform to the expectations of Hardy-Weinberg Equilibrium (HWE) in more than one sample location (modified FDR = $p < 0.007$) resulted in the removal of 41 SNPs (Table 1).

To screen for possible contamination of samples submitted for DarT sequencing, the observed heterozygosities of Striped Marlin from each sample location, including those analyzed by Mamoozadeh et al. (2020), were calculated. For each of the three Striped Marlin from the putative second North Pacific stock (NPO2) that were re-sequenced in this study, heterozygosity levels dropped markedly (0.352 to 0.147, 0.374 to 0.156, and 0.387 to 0.163), and the resequenced values were more in line with the range of the observed individual heterozygosities in the other sample collections (0.117-0.257) (Figure 6). Differences in mean observed heterozygosity levels among sample locations were assessed using a 1-way ANOVA, which produced a p-value ≤ 0.001, indicating the presence of a significant difference among sample locations. After employing a Tukey HSD (honestly significant difference) test, the observed heterozygosity level of the putative NPO2 stock (samples from HAW2 and JAP2 in Figure 6) was found to be significantly higher than the rest of the sample collections ($p \leq 0.001$). Although only

three of the 12 Striped Marlin that comprised the putative NPO2 stock could be re-sequenced, the resulting heterozygosity levels for all three individuals were considerably lower compared to those of the first sequencing effort, suggesting that sample contamination during the initial sequencing effort may have occurred. Therefore, the 12 individuals identified as belonging to the putative NPO2 stock, all of which had high observed heterozygosities, were removed from the dataset prior to subsequent analyses.

Due to re-analysis of the data between Mamoozadeh (2018) and Mamoozadeh et al. (2020), the sample size for JAP2 (included in NPO2) changed from n=5 to n=6. The sixth Striped Marlin in Mamoozadeh et al. (2020) did not have the elevated heterozygosity levels reported for the other five individuals in the JAP2 sample collection, however, it clustered into the putative NPO2 stock. In the original analysis Mamoozadeh (2018), this individual was included in the JAP sample collection and clustered into the NPO stock. Due to uncertainties regarding the placement of this individual, it was removed from the dataset prior to assessing individual heterozygosities.

For the remaining samples, any individual with an observed heterozygosity of 0.225 or higher was removed from the dataset to avoid including potentially cross-contaminated individuals in the analysis. In addition to the 12 Striped Marlin that comprised the putative NPO2 stock, three from HAW19, one from HAW, one from EAUS, and one from ECU were removed due to individual heterozygosity levels greater than 0.225 (Figure 6).

Identification of Population Structure

A PCA was used to visually explore the population structure and magnitude of genetic differentiation among Striped Marlin from different sampling locations. The PCA of the full dataset resulted in 4.37% of the variance explained by principal component 1 and 1.82% of the variance explained by principal component 2 (Figure 7). The clustering pattern revealed distinct groupings consisting of individuals from the western Indian Ocean (WIO = South Africa, Kenya), Oceania (Oceania = western Australia, eastern Australia, New Zealand, Hawaii), North Pacific Ocean (NPO = Japan, Taiwan, Hawaii, California), and the eastern central Pacific Ocean (ECPO = Baja California, Ecuador, Peru). Of the 80 Striped Marlin collected from the HBPLLF in 2019 (HAW19), 54 fish clustered with the Oceania stock and 26 clustered with the North Pacific stock, suggesting a mixed-stock fishery in this region. Two of the re-sequenced Striped Marlin from the putative NPO2 stock clustered with the North Pacific stock and the third clustered with Oceania.

Individual-based ancestry assessed using DAPC returned results similar to those of the PCA. Using the full dataset, K=4 was determined to be the optimal number of clusters, indicated by the lowest BIC value (1163.820). The BIC values for K=3 and K=5 were 1166.722 and 1166.810, respectively, and increased as K increased. Using *xval*, the optimal number of principal components to retain was 80, based on the lowest mean square error (0.00419). Striped Marlin individuals sampled from the HBPLLF in 2019 were present in the North Pacific and Oceania clusters and the clustering pattern for the three re-sequenced fish from the putative NPO2 stock was identical to that of the PCA, with two fish clustering with the North Pacific stock and one with Oceania (Figure 8).

Based on the results of the clustering analyses, Striped Marlin that were sampled in a location that did not correspond to their genetic population (putative migrants) were placed into the population that corresponded with their genetic cluster. To characterize the degree of genetic connectivity among populations, unbiased F-statistics (F_{ST}; Weir and Cockerham 1984) were calculated. All pairwise comparisons were statistically significant, with p-values ≤ 0.001 (Table 2). Pairwise F_{ST} values between populations ranged from 0.0267 (NPO vs. ECPO) to 0.0886 (ECPO vs. WIO). For the two populations occurring in the HBPLLF, the level of differentiation between Oceania and the North Pacific stock was $F_{ST} = 0.0394$.

Identification of Genetic Diversity

Levels of genetic diversity within the four populations of Striped Marlin resolved in this study were similar, and the observed heterozygosity was slightly less than the expected heterozygosity in all populations ($H_O = 0.139$-0.156 and $H_E = 0.153$-0.166) (Table 3). The highest mean observed heterozygosity occurred in ECPO (0.156) and Oceania (0.156) and the lowest occurred in WIO (0.139). The highest mean expected heterozygosity, or genetic diversity, occurred in ECPO (0.166) and the lowest in WIO (0.153). Low levels of inbreeding were indicated for each population (0.053 in Oceania-0.088 in WIO; Table 3).

Identification of Discriminatory SNPs

Upon the identification of a mixed-stock fishery for Striped Marlin in the HBPLLF, a panel of SNPs that could discriminate between all four Striped Marlin stocks

or just the North Pacific Ocean and Oceania stocks was developed and used to assign the additional 332 Striped Marlin collected from the HBPLLF during 2019 and 2020 to their stock of origin in a rapid and cost-effective manner. More SNPs than the goal of 48 were identified because it was expected that it would not be possible to develop assays for many loci due to design constraints. Based on I_n criteria, 384 SNPs were identified to be the most discriminatory among the four Striped Marlin stocks. Stock discrimination was visually determined using PCA and by comparing the amount of variation each locus explained (principal components 1 and 2). SNPs that best discriminated among all four populations were assessed first to allow for migrant detection if Striped Marlin sampled from the HBPLLF did not belong to either Oceania or the NPO. From this ranking of 384 SNPs, 78 were suitable for Fluidigm assay design. To best discriminate between Oceania and NPO, a ranking of 200 SNPs with the most discriminatory power was identified based on F_{ST}. From this ranking, there were only 20 SNPs that were not present in the rankings based on I_n for the four stocks and appropriate for Fluidigm assay design. In order to increase the number of discriminatory SNP loci for primer design, a final ranking was performed to discriminate between Oceania and NPO based on I_n. Unlike the first ranking, this one was done after putative migrants were moved from their capture location (stock) and into their genetic stock. This ranking identified 300 SNPs, but only 12 of these were not previously identified and appropriate for Fluidigm assay design. In all, a total of 110 SNPs were submitted to Fluidigm's D3™ Assay Design Software for conversion into SNPType assays in early April 2021.

SNP Genotyping

The Fluidigm primers were received in late April 2021 and tested in groups of 48 loci against 47 Striped Marlin samples with corresponding DarT genotype data and a no-template control on a 48.48 Dynamic Array™ IFC (integrated fluidic circuit; Fluidigm). The 47 individuals with corresponding DarT sequence data were used to identify any source of user error, and to ensure accurate genotype calls and genotype reproducibility by the Fluidigm Biomark™ HD. A final panel of 48 loci was selected based on accuracy of genotype calls and the ability to separate allele categories on Fluidigm's SNP Genotyping Analysis Software. For each of the 47 genotyped fish, the fluorescence reported for each allele of the target SNP was used to separate data into three clusters of alleles consisting of homozygous reference alleles (XX), homozygous alternate alleles (YY), or heterozygotes (XY).

During early testing of the SNP primers, when all 110 SNPs were run in order and not selected out of sequence for inclusion in a panel, the resulting Fluidigm genotypes matched those of the DarT data. However, when individual genotype calls from the final 48 locus panel were compared to the DarT data, there were several inconsistencies. Of the 48 loci genotyped across all 83 samples, 15 loci accounted for 15-77 mismatches each in comparison with the 'known' DarT genotypes. The majority of allele miscalls involved reference allele homozygotes (XX/YY) that were called heterozygotes (XY) based on their fluorescence, suggesting contamination of loci during the preparation of primers and IFC plate loading. Another assay failed, returning zero genotype calls across all individuals tested. These 16 loci were removed from the dataset. Of the 83 Striped Marlin with corresponding DarT data, ten individuals were removed due to missing data (n=4) or mismatches (≥ 25%). Between DarT and Fluidigm genotype calls (n=6)

Application of SNP Panel

The final panel of 32 SNP loci was used to genotype the 332 Striped Marlin of unknown stock origin. Seven individuals were removed based on missing data (samples missing more than 40% of genotype calls were removed). After comparing the clustering accuracy of the final 32 loci genotyped by DarT and the 32 loci used on the Fluidigm, the variance explained by principal components 1 and 2 was similar between both methods (17.2 and 6.0% for DarT PL and 19.6 and 7.9% for Fluidigm (Figures 9, 10, 11 and 12).

Assignment Testing

A total of 73 Striped Marlin (25 NPO; 48 Oceania) of the 83 fish with corresponding DarT data were genotyped at 32 SNP loci on the Fluidigm. These 73 individuals were used as a reference dataset for GENECLASS2 (Piry et al. 2004) and the 325 Striped Marlin of unknown origin comprised the test dataset and were assigned into either NPO or Oceania. It was observed that one 'known' individual that was assigned to Oceania based on PCA clustering analyses of DarT data consistently clustered with the NPO stock based on DAPC and assignment tests using the Fluidigm data. It was suspected that this individual may have been incorrectly assigned during the clustering analyses of the 83 individuals that were sent to DarT PL, and after consistently clustering with NPO, it was reassigned into its most likely stock of origin. The 325 Striped Marlin of unknown origin were assigned to one of the two stocks with an average assignment score of 98.04% (range: 51.87-100%). Of these, 20 individuals (6%) had assignment scores below 90% (ranging from 51.87 to 89.80%) and were subsequently removed from

the dataset. The remaining 305 individuals had an average assignment score of 99.54%. Striped Marlin assigning into Oceania had an average exclusion probability of 67.8% (ranging from 6.22-100.0%) for not belonging to NPO, and NPO had an average of 57.26% (ranging from 5.07-100.0%) for not belonging to Oceania. Of the 305 Striped Marlin collected from the HBPLLF with assignment scores greater than 90%, 104 (34.1%) of Oceania-assigned Striped Marlin collected from the HBPLLF could be significantly excluded (alpha = 0.05) from the NPO, based on exclusion probabilities generated for each assignment.

Relationships between stocks and biological information

Once the assignment tests were completed, the relationships between stock assignment and the biological information associated with each Striped Marlin were explored. Over the 11 months during which samples were collected, 156 (41.3%) of Striped Marlin assigned into NPO and 222 (58.7%) assigned into Oceania (Figure 13). More Striped Marlin assigned into Oceania during the months of October 2019 (83%), November 2019 (58%), July 2020 (67%), September 2020 (89%), and October 2020 (89%), whereas the majority of Striped Marlin assigned into NPO during January 2020 (71%), February 2020 (83%), and June 2020 (83%). In December 2019, assignment rates into both stocks were comparable (Figure 14). The greatest mean length for fish assigned to NPO occurred in July 2020 (160.0 cm EFL) and the lowest occurred in September 2020 (105.0 cm EFL). For individuals assigned to Oceania, the greatest mean length occurred in June 2020 (152 cm EFL) and the lowest in July 2020 (131 cm EFL) (Figure 15).

Sex ratios differed slightly between the two stocks. For Oceania, 51% of the assigned Striped Marlin were females, 40% were males, and 9% were unknown (Figure 16). For NPO, 44% were females, 48% were males, and 8% were unknown (Figure 17). From the total sample collection, 13 Striped Marlin were reported to be in an active spawning condition. One of the 13 did not assign into either population with a high assignment score (at least 90%) and was removed from the dataset. Of the remaining 12 fish identified by fisheries observers as being in an active spawning condition at the time of capture, 10 assigned into NPO and two assigned into Oceania. The spawning condition NPO-assigned fish were sampled in February (n=1; 2.4% of the monthly sample), June (n=5; 13.8%), July (n=1; 4.7%), and September 2020 (n=2; 2.35%); they consisted of six females and four males. The two Striped Marlin identified by fisheries observers as being in an active spawning condition and assigned to the Oceania stock were both males, sampled in July and October 2020.

The proportion of the two stocks of Striped Marlin represented in the HBPLLF samples changed over time. In October 2019, NPO accounted for 16.6% of the assigned Striped Marlin, and this value increased each month, peaking at 83.3% of the assigned fish in June 2020. Oceania comprised 66.6% of assigned fish in July 2020 and increased to 100% in August 2020, 89.4% in September 2020, and 88.8% in October 2020 (Figure 18). Six of the 11 actively-spawning Striped Marlin were sampled in quadrant four (five NPO; one Oceania), four were sampled in quadrant two (two NPO; two Oceania), and one was sampled in quadrant one (one NPO).

Based on sampling location (quadrant of capture), Oceania comprised the majority of stock assignments in quadrants 1, 2, and 3 of the HBPLLF (Figure 19). By

month and sampling quadrant, Striped Marlin sampled in quadrants 2 and 4 from October 2019 to December 2019 assigned largely with Oceania. In contrast, the majority of Striped Marlin sampled in January 2020 (40-70%) were taken in quadrants 1 and 2 and assigned mostly to NPO (Figure 20). From January 2020 to June 2020, the majority of sampled Striped Marlin assigned with NPO and were sampled in quadrants 1, 2, and 4. Striped Marlin assigning to Oceania made up the majority of catches from July 2020 to October 2020, and were mostly sampled in quadrants 1, 2, and 4. Very few Striped Marlin were sampled from quadrants 3 or 4 from August to October 2020, however, the majority of samples from these quadrants assigned into Oceania. Analysis of the spatial distribution of sampling revealed that the observed temporal changes in relative stock abundance occurred throughout HBPLLF.

Discussion

The goals of this study were to clarify the number of Striped Marlin stocks in the North Pacific and utilize temporal sampling to better understand the stock dynamics of Striped Marlin exploited by the HBPLLF. To determine the number of Striped Marlin stocks in the North Pacific, an existing SNP dataset for 256 Striped Marlin collected throughout the Pacific and Indian oceans (Mamoozadeh et al. 2020) was supplemented with SNP data from an additional 85 samples from the HBPLLF collected from September to December 2019. Three of 12 Striped Marlin reported to comprise a putative second stock in the North Pacific by Mamoozadeh et al. (2020) were re-sequenced based on suspicions of sample contamination evidenced by elevated observed heterozygosity levels. After re-sequencing, the observed heterozygosity of each of the three individuals

was reduced by approximately 50%, suggesting that sample contamination occurred in the previous study and prompting the removal of all 12 individuals comprising the putative second stock from the dataset. Analysis of a quality filtered dataset of over 1,500 SNPs across 308 individuals, including the three re-sequenced samples from the putative second stock, resolved a single stock occurring in the North Pacific (Japan, Taiwan, Hawaii, and California sample collections), but also revealed that a subset of the Striped Marlin collected from the HBPLLF clustered with the Oceania stock (western Australia, eastern Australia, New Zealand sample collections) described by Mamoozadeh et al. (2020). To explore the temporal patterning of the two stocks in the HBPLLF, a panel of 48 SNPs was developed to discriminate the NPO and Oceania stocks. This SNP panel was used to genotype an additional 325 Striped Marlin samples collected from the HBPLLF during 2019-2020 and assign them to stock of origin.

Stock Structure in the Central North Pacific

The results of this study do not support the existence of two North Pacific stocks as suggested by both Purcell and Edmands (2011) and Mamoozadeh et al. (2020). Purcell and Edmands (2011) collected Striped Marlin from throughout their range in the Pacific and analyzed collections of mature and immature fish from each location separately. If significant differences were not identified between mature and immature samples, they were combined for subsequent analyses, but if significant differences were detected, the samples were analyzed separately. Purcell and Edmands (2011) reported that mature Striped Marlin collected from Hawaii were genetically distinct from the other North Pacific sample collections, as well as immature fish collected from Hawaii. However, the

second putative North Pacific stock (mature Hawaiian fish) was only statistically significantly different following a correction of the microsatellite data for the presence of null alleles. Null allele frequencies of up to 33% were estimated for at least one locus for each locus-location combination. The correction for the presence of null alleles applied by Purcell and Edmands (2011) randomly incorporated null allele frequencies into existing non-null allele homozygotes within each location. Applying this correction resulted in an increase in significant pairwise F_{ST} comparisons between sample collections, including between mature and immature Striped Marlin collected off Hawaii. In most cases, microsatellite loci found to have null alleles in multiple sample collections are removed prior to genetic data analyses, but Purcell and Edmands (2011) opted to include them in their analyses (with correction) to maintain a robust number of loci. According to Putman and Carbone (2014), frequencies of null alleles up to 8% may cause minimal bias in estimates of population differentiation, however, correcting for null allele frequencies may not adequately reduce this bias and may exacerbate this bias. Chapuis and Estoup (2006) noted that correcting for null allele frequencies can result in inflated estimates of genetic differentiation (F_{ST}) in situations of low gene flow. As such, it is quite possible that the correction for null allele frequencies up to 33% in Purcell and Edmands (2011) resulted in upwardly biased estimates of differentiation between mature and immature Striped Marlin.

Another concern with the Purcell and Edmands (2011) study is the criteria used to identify immature and mature Striped Marlin. Fish length or weight was used to assign maturity status using values of length and weight at first maturity for Striped Marlin from the Coral Sea (Hanamoto 1977). The use of length or weight at first maturity instead of

length or weight at 50% maturity will result in the misclassification of many more immature fish as mature. As such, it is likely that the sample of "mature" Hawaiian fish analyzed by Purcell and Edmands (2011) actually consisted of many juveniles, clouding the biological rationale for the two groups.

Mamoozadeh et al. (2020) also identified a second putative stock (NPO2) of Striped Marlin within the North Pacific, which comprised 12 of 39 (30.7%) individuals collected off Hawaii and Japan and was consistently resolved across individual-based clustering methods. However, the authors noted that the mean observed heterozygosity reported for this stock was elevated (0.293) relative to the mean observed heterozygosities of the other stocks resolved in the study (0.137-0.164), suggesting the possibility of contamination. Intraspecific contamination can result in elevated estimates of genetic differentiation (F_{ST}) relative to uncontaminated samples, making it crucial to identify and remove the affected samples to avoid inaccurate designation of stock structure (Petrou et al. 2018). To test for contamination, the current study re-isolated DNA from the tissue samples and re-sequenced three of the 12 individuals comprising the NPO2 stock (all 12 individuals would have been re-sequenced, but as previously noted, low DNA quality in the nine remaining individuals prevented re-sequencing). Following re-isolation and re-sequencing of the three Striped Marlin samples from the putative NPO2 stock, the observed heterozygosity levels for each individual dropped by approximately 50%, suggesting that those three samples had been cross-contaminated during sample processing, and that the anomalously high observed heterozygosities for the other nine individuals in the putative NPO2 stock were also likely the result of contamination. It is probable that the conclusions of Mamoozadeh et al. (2020) were

impacted by the inclusion of cross-contaminated samples, with the cross-contaminated individuals clustering together and leading to the recognition of a spurious stock.

SNP Panel Validation

The results of this study suggest the presence of two genetic stocks of Striped Marlin occurring within the area of the CNP exploited by the HBPLLF, one comprised of North Pacific sample collections (Japan, Taiwan, Hawaii, and California), and the other composed of migrants from Oceania (western Australia, eastern Australia, New Zealand sample collections). To better understand the dynamics of the mixed stock fishery in the HBPLLF, a set of 110 SNPs with the highest power to discriminate the NPO and Oceania stocks was identified. The 73 Striped Marlin collected from the HBPLLF and assigned to stock of origin based on the full DarT dataset were used to validate the SNP loci and choose a final panel of 48 SNPs using a two-step process. The selected SNP loci were first validated for inclusion in the final SNP panel by comparing the DarTSeq™ genotypes of the 73 individuals with their Fluidigm SNPType genotypes to ensure that genotypes were called consistently between the two methods. Next, validation of the ability of the Fluidigm 48 SNP panel to discriminate between NPO and Oceania samples was tested. All of the 73 Striped Marlin clustered into their respective stocks of origin using the Fluidigm-obtained genotypes (100% assignment success). Validation of the SNP panel was crucial to ensure genotyping accuracy for individuals of unknown origin and to confirm that the panel had sufficient power to confidently discriminate stocks. Other studies have used similar methods to quickly discriminate stocks of another highly migratory pelagic fish, the Atlantic Bluefin Tuna, *Thunnus thynnus*, with varying levels

of success. To characterize the stock dynamics of the western and eastern stocks of Atlantic Bluefin Tuna using samples collected from throughout the Atlantic Ocean and Mediterranean Sea, Puncher et al. (2018) developed a panel of 95 SNPs that was used to genotype and assign Bluefin Tuna to their stock of origin. During panel validation, 75% of larval and young-of-the-year Bluefin Tuna (assumed to be of known stock origin) collected from the western Atlantic and 77.2% of those collected from the Mediterranean Sea used for SNP selection were correctly assigned to their stock of origin using the Rannala and Mountain (1997) criterion. Individuals with assignment scores below 70% were considered poorly assigned. A similar study of Atlantic Bluefin Tuna by Rodriguez-Ezpeleta et al. (2018) developed a panel of 96 SNPs and reported greater validation success rates compared to those of Puncher et al. (2018). In that study, a reference set of larval and young-of-the-year Atlantic Bluefin Tuna excluded from SNP discovery or selection resulted in 81% of samples collected from the Gulf of Mexico and 83% of samples collected from the Mediterranean Sea correctly assigning to basin of origin. Using the Rannala and Mountain (1997) criterion, individuals with assignment scores below 90% were considered unassigned. In the present study, the DarT-validated genotypes and 100% consistency of individual-based clustering into NPO and Oceania using Fluidigm-obtained genotypes suggests high confidence in the ability of the SNP panel to discriminate between the two stocks.

Assignment Tests

Once the genotyping accuracy and power of the 48 SNP panel was verified, the panel was used to genotype 325 Striped Marlin of unknown stock of origin collected

from the HBPLLF between September 2019 and October 2020 and assignment tests were conducted to assign these individuals to the NPO or Oceania stocks. Of the 48 SNPs, only 32 were used due to issues with contamination of 16 primer sets. The mean assignment score for the 325 individuals based on 32 SNP loci was 98.04%, however, 20 Striped Marlin (6%) had assignment scores below 90% and were removed. Of the remaining 305 fish, the high assignment scores (mean = 99.54%) clearly demonstrate the efficacy of the SNP panel. The assignment success achieved in the present study was greater than that reported in similar studies of pelagic fishes. Puncher et al. (2018) used 95 SNP loci to assign larval, young-of-the-year, and adult Atlantic Bluefin Tuna to the Atlantic or Mediterranean stock. Using the Rannala and Mountain (1997) criterion (threshold of 0.05) and an assignment score threshold of 70%, 66.7% of larval and young-of-year Atlantic Bluefin Tuna were confidently assigned to the western Atlantic Ocean, and 71.7% were confidently assigned to the Mediterranean Sea with assignment scores of at least 70%. For adult Atlantic Bluefin Tuna, mean assignment scores for the western Atlantic and Mediterranean Sea were 75.2% and 86.6%, respectively. Rodriguez-Ezpeleta et al. (2018) reported increased success in the assignment of adult Atlantic Bluefin Tuna compared to Puncher et al. (2018). Using an assignment threshold of 80%, 89% of samples assigned to the Gulf of Mexico and 98% assigned to the Mediterranean Sea based on 96 SNP loci using the Rannala and Mountain (1997) method. In the two studies focusing on Atlantic Atlantic Bluefin Tuna, the genetic differentiation between eastern and western stocks was an order of magnitude lower (F_{ST} = 0.003-0.008) than the estimated F_{ST} between NPO and Oceania Striped Marlin stocks (F_{ST} = 0.039). The elevated level of genetic differentiation between the two stocks for Striped Marlin may be

a driver of the higher percentage of assignment success achieved in the present study (Wilkinson et al. 2011).

Stock Composition in the HBPLLF

To explore the stock composition of Striped Marlin in the HBPLLF, analyses were conducted using a combined dataset consisting of 378 fish for which genotypes and stock assignments were obtained using the panel of 32 SNPs. The final dataset of Striped Marlin collected from the HBPLLF and subsequently assigned to stocks included 73 Striped Marlin initially analyzed with DarTSeq™ and 305 individuals of unknown origin and not used for SNP selection or validation that were genotyped with the 32 SNP panel. Of the 378 Striped Marlin, 156 (41.3%) assigned into NPO and 222 (58.7%) assigned into Oceania over the 11 months sampled. It should be noted that these 378 individuals were not sampled at random from the fishery and do not necessarily reflect the effort of the fleet operating in the HBPLLF. Samples were collected opportunistically by fisheries observers and the researcher had no control over the area or time in which sampling was conducted. Yearly observer coverage on deep-set longline trips in the HBPLLF is around 20%, captains that take observers fish the areas of their choice, and sampling kits were haphazardly given to observers by their supervisor with the goal of obtaining 50 samples per month. Unfortunately, no sampling occurred from March to May 2020 due to the COVID-19 pandemic.

The finding of co-occurring stocks of Striped Marlin in the CNP is not unprecedented. Mamoozadeh et al. (2020) reported that four of the 21 (19%) Striped Marlin sampled from the HBPLLF clustered into a western South Pacific stock,

comprising individuals collected from eastern Australia and New Zealand. Although associated catch data were unavailable for many of the Striped Marlin analyzed in Mamoozadeh et al. (2020), one of the four migrants collected from the HBPLLF in their study was collected in November 2014, a month in which Oceania fish accounted for 60.47% of the assigned Striped Marlin in the present study. Similarly, Purcell and Edmands (2011) noted significant heterogeneity between juvenile and adult Hawaiian Striped Marlin, with adult Hawaiian fish found to be significantly different from juveniles and other North Pacific fish. While they attributed the difference to life stage, the possibility remains that the presence of migrants from Oceania in their samples may have contributed to the genetic heterogeneity they observed.

Changes in the proportion of the Oceania and NPO stocks within the HBPLLF were evident throughout the year, suggesting stock-specific ingress and/or egress within the fishery. The proportion of NPO Striped Marlin increased from the late fall to the early summer months (November-June), suggesting that NPO Striped Marlin are immigrating into the fishery and/or Oceania fish are leaving the fishery. Conversely, the proportion of Oceania Striped Marlin increased starting in the summer and peaked in the fall months (July-October). Samples were obtained from the HBPLLF during September and October of 2019 and 2020. The proportions of Oceania Striped Marlin sampled were similar for both months across years (September 2019, 83.33%; September 2020, 89.41%; October 2019, 85.29%; October 2020, 88.89%), supporting annual temporal stability of stock composition for at least two months across years.

Humphreys and Brodziak (2019) suggested that the CNP likely serves as a juvenile nursery and feeding ground for sub-adult Striped Marlin, characterized by

juvenile-sized fish and relatively limited spawning activity compared to other regions of the Pacific. Analysis of over two decades of longline catch data from the HBPLLF found that the majority of Striped Marlin caught in the fishery are small in size (mean length = 134 cm EFL) and reproductively immature (Sculley 2019). The results of the present study corroborate these findings. The 378 genotyped Striped Marlin from the HBPLLF had a mean EFL of 139 cm (range = 91-260 cm). Those assigned to the NPO had a mean EFL of 142 cm (range = 91-260 cm), slightly larger than those from Oceania (which have a mean EFL of 137 cm; range = 104-183 cm), but the mean size of those assigned to either stock was well below the length at 50% maturity (160 cm) reported for the CNP (Humphreys and Brodziak 2019). Only 30 Striped Marlin assigned to NPO (19.5% of all NPO) were at or greater than the length at 50% maturity for CNP Striped Marlin. For the fish that assigned to Oceania, only one (0.45% of all Oceania) was at or greater than the length at 50% maturity reported for western South Pacific Striped Marlin (181 cm EFL; Kopf et al. 2011).

Although the HBPLLF is largely catching sub-adult fish, 13 (3.1%) of the Striped Marlin analyzed in this study were reported by observers to be in an active spawning condition at the time of capture (mean length = 157.4 cm). Nine of these 13 Striped Marlin were found to be smaller than the reported length at 50% maturity for the CNP (160 cm; Humphreys and Brodziak 2019), indicating that the majority of these fish were young or possibly first-time spawners. The four individuals that were at or larger than 160 cm assigned to NPO. Of the 13 spawning-condition fish, 10 (76.9%; 4 males and 6 females) assigned to the NPO stock, and were collected across multiple months (September 2019, n=1; September 2020, n=2; February 2020, n=1; June 2020, n=5; and

July 2020, n=1). The June 2020 sample had the highest proportion of spawning-condition NPO fish (13.8%) as well as the highest proportion of Striped Marlin assigned to NPO (83.33%) across the 11-month sampling period. The 10 actively spawning Striped Marlin that assigned to NPO were collected in quadrants 1 (n=1), 2 (n=4), 4 (n=5) with the majority collected in quadrants 2 and 4, representing the eastern half of the HBPLLF range.

Striped Marlin spawning has been found to occur across a broad latitudinal band throughout their range (Kopf et al. 2012), however, the CNP is not recognized as a major spawning area for the North Pacific stock and low numbers of larvae have been collected from the region in the summer months (Hyde et al. 2006; Nishikawa et al. 1985). Humphreys and Brodziak (2019) noted that Striped Marlin spawning in the CNP is highly seasonal and short in duration, although active spawning Striped Marlin were identified across five non-consecutive months in the present study. Only 10 (2.3%) Striped Marlin assigned to NPO were found to be in an active spawning condition, and it is likely that major spawning activity for NPO Striped Marlin does not occur in the CNP. Spawning activity for the NPO stock is believed to occur in the western North Pacific, near Taiwan, during the late spring and summer months (Nakamura 1949; Chang et al. 2018).

Of the 13 Striped Marlin in spawning condition collected from the HBPLLF, only two were assigned to Oceania. These included two males, one collected during July 2020 in quadrant 4 (127 cm EFL) and one collected during October 2020 in quadrant 2 (139 cm EFL). The size of these individuals suggests that they were likely young spawners; both were well below the 181 cm size at 50% maturity for western South Pacific Striped

Marlin. According to the exclusion probabilities generated using the methods of Paetkau et al. (2004) (alpha = 0.05), one of these individuals was significantly excluded from assigning to NPO and the other, although not significantly excluded from either NPO or Oceania, had a 99.9% probability of assignment to the Oceania stock.

Spawning activity for Oceania Striped Marlin is reported to occur near the Coral Sea, Fiji, and south of French Polynesia (Kopf et al. 2012). Based on gonadosomatic indices, spawning in the western South Pacific reaches a peak during November and December and lasts from September to March for males and October to January for females. The length at 50% maturity for female Striped Marlin in this region is 181 cm EFL, similar to that of the western North Pacific, and about 20 cm greater than that reported for the CNP (Kopf et al. 2012; Chang et al. 2018).

Although Striped Marlin in spawning condition from both NPO and Oceania stocks occur in the HBPLLF, the very low frequency of occurrence of mature individuals in the area suggests that major spawning activity for the two stocks occurs elsewhere. It does not appear that gene flow is occurring between the two stocks. The estimated F_{ST} between Oceania and NPO is 0.039 (p-value $\leq$ 0.001), indicating a significant level of differentiation. These genetic differences may be maintained by differences in spawning time and area for the two stocks.

Differences in spawning movements could account for some of the changes in Striped Marlin stock composition in the HBPLLF. As discussed above, the majority of spawning activity for NPO occurs in the western North Pacific and peaks in the spring and early summer months, with some limited spawning occurring in the CNP. One might expect mature NPO Striped Marlin to leave the HBPLLF in the months before this time

to reach spawning grounds in the western North Pacific, increasing the relative proportion of Oceania fish in the HBPLLF. However, this study noted an increase in the proportion of NPO fish in the HBPLLF during the winter and spring, counter to expectations. Most of the spawning activity for Oceania occurs in the western South Pacific, peaking during November and December, and the results of this study show a decrease in the relative abundance of Oceania Striped Marlin in the HBPLLF during the fall which would coincide with the movements of Oceania adults from the HBPLLF to the spawning grounds. The situation is somewhat similar to the mixing of Atlantic Bluefin Tuna on feeding grounds and the subsequent separation of stocks to their respective spawning grounds (Carlsson et al. 2007).

Seasonal changes in the relative abundance of the NPO and Oceania stocks of Striped Marlin in the HBPLLF may also be influenced by differential recruitment of juveniles from major spawning grounds in the western North Pacific and western South Pacific to the HBPLLF. Striped Marlin juveniles exhibit very rapid growth, with growth rates of 3.1 mm d^{-1} reported for the first six months of life and 1.5 mm d^{-1} over the next six months, some of the fastest growth rates among bony fishes (Kopf et al. 2011). The proportion of NPO Striped Marlin in the HBPLLF peaked in February (82.93%) and June 2020 (83.33%) while Oceania Striped Marlin peaked in September (89.41%) and October 2020 (89.41%). These increases in the proportion of each stock may be explained by the recruitment of young Striped Marlin into the HBPLLF roughly six to nine months after spawning in their respective areas. Striped Marlin spawned during November or December in Oceania would reach approximately 140 cm EFL by the first year, and may migrate to and utilize the CNP as a juvenile feeding area around September and October.

Sculley (2019) reported an influx of age-0 Striped Marlin into the HBPLLF from September through March, which may represent recruiting Oceania age-0 juveniles. The growth of these individuals is consistent with the increase in mean size of Oceania Striped Marlin that occurred from September 2019 to June 2020 in this study.

For NPO Striped Marlin, spawning peaks from June to July in the western North Pacific (Chang et al. 2018), resulting in recruitment to the HBPLLF around March. Given the temporal gap in sampling of Striped Marlin in the current study due to the COVID-19 pandemic, no data are available to infer the stock dynamics of the HBPLLF from March-May 2020, but it is assumed that the proportion of NPO fish remains high during this time. The recruitment of age-0 NPO Striped Marlin spawned in June and July in the western North Pacific into the HBPLLF during March-May would result in a high proportion of NPO fish in the fishery over these months. According to Sculley (2019), the Striped Marlin that recruit into the HBPLLF become a larger component of the catch in March and they integrate into the catch at around 150 cm EFL. Taken together, the observation of differential seasonal recruitment of juvenile Striped Marlin from NPO or Oceania into the HBPLLF appears to be consistent with the observed seasonal changes in stock composition.

Due to the highly migratory nature of Striped Marlin, broad movements associated with feeding or changing environmental conditions likely occur throughout the year, and these could be stock-specific. The shifts in stock composition of Striped Marlin in the HBPLLF may be influenced by the movement of NPO fish out of the range of the HBPLLF eastward, towards California. The mean length of NPO Striped Marlin occurring in the HBPLLF decreased from September 2019 (mean length = 160 cm), to

February 2020 (mean length = 129 cm). It is possible that during this period larger individuals were leaving the fishery and moving to feeding grounds in upwelling areas of the eastern North Pacific associated with the California Current. According to previous genetic studies of Pacific Striped Marlin, fish from California consistently cluster with Hawaii and the rest of the North Pacific sample locations into a North Pacific-wide stock (NPO; McDowell and Graves 2008; Purcell and Edmands 2011; Mamoozadeh et al. 2020). Striped Marlin in the eastern North Pacific range from 100-170 cm EFL, similar to the lengths reported for the fish in the present study (Bromhead et al. 2004). Tag-recapture data indicate that 40-60 kg Striped Marlin (which equates to an EFL of 150-180 cm) tagged off California have been recaptured off Hawaii from late autumn to early winter (Hinton and Maunder 2011). However, there have been no recaptures of Striped Marlin tagged off Hawaii in the waters off California, although the total number of recaptures is low (Ortiz et al. 2003). After being spawned in the western North Pacific, some NPO Striped Marlin may utilize both the CNP and waters near California as juvenile feeding areas. Following the winter months, these growing fish may move west back to the CNP, accounting for the increase of NPO Striped Marlin in the spring months. Those early and first-time spawning Striped Marlin may then leave the CNP and move towards the western North Pacific for spawning from April to August.

Taken together, there are at least three hypotheses for the temporal changes in Striped Marlin stock composition that occur in the HBPLLF, including stock-specific differences in spawning, recruitment, and feeding movements. The latter two hypotheses appear to fit best with the observed seasonal shifts in stock composition. However, there

are likely many additional factors that could explain the changes in stock composition in the HBPLLF and additional research is needed to address these questions.

Implications for Fisheries Management

The results of this study strongly support the presence of a single stock of Striped Marlin in the North Pacific, and a total of three stocks in the Pacific Ocean. Striped Marlin collected from Japan, Taiwan, Hawaii, and California form a North Pacific stock (NPO), collections from Baja California, Ecuador, and Peru form an eastern central Pacific stock (ECPO), and collections from eastern Australia, western Australia, New Zealand, and Hawaii form an Oceania stock (OCEANIA). The presence of the two stocks co-occurring in the area of the CNP fished by the HBPLLF indicates that the fishery is exploiting a mixed-stock aggregation, a finding that is not currently accounted for in stock assessments or regional management plans.

The current stock delineations of Pacific Striped Marlin recognized by the relevant RFMOs are more aligned with RFMO jurisdictional boundaries and not necessarily consistent with biological data. The Western and Central Pacific Fisheries Commission (WCPFC) recognizes stocks of Striped Marlin in the western and central North Pacific and in the western South Pacific, and the Inter-American Tropical Tuna Commission (IATTC) recognizes a single stock in the eastern Pacific Ocean. These three management units do not correspond with the three genetically distinct Pacific stocks resolved in the present study. The stock mixing occurring in the CNP (presence of Striped Marlin from NPO and Oceania) adds further complexity to the development of effective management plans for Pacific Striped Marlin, and each of the three managed

stocks are in differing states of exploitation or over-exploitation. To better manage Striped Marlin stocks in the Pacific, joint management efforts between the WCPFC and IATTC will be required, especially for the stocks that are currently in an overfished state. The results of the present study are highly relevant not only because the western and central North Pacific stock is currently overfished and experiencing overfishing (WCPFC 2019), but because Striped Marlin managed in the western South Pacific stock are exploited by the HBPLLF. This suggests that there is fishing mortality not incorporated into the stock assessments for western South Pacific Striped Marlin.

The SNP panel developed in the present study allows for rapid genotyping and assignment of Striped Marlin to determine the stock of origin. In mixed-stock fisheries, genomic resources, including the SNP panel developed in this study, can provide estimates of stock-specific productivity, and potentially improve management and stock-rebuilding plans, especially for stocks that are overfished or experiencing overfishing.

Future Research

The results of this study indicate that multiple stocks of Striped Marlin utilize the area of the CNP exploited by the HBPLLF. Although Striped Marlin that assigned to both NPO and Oceania were present throughout the 14-month sample period (September 2019-October 2020), samples were not collected from March-May 2020 due to a lack of effort corresponding to the COVID-19 pandemic. To gain a more complete understanding of Striped Marlin stock dynamics in the HBPLLF throughout the year, sampling should be conducted in these months. Additionally, monthly sampling should be conducted over consecutive years to determine the temporal stability of the changes in stock composition

observed in the present study. Now that a SNP panel is available to discriminate between NPO and Oceania Striped Marlin, fin clips can be taken from fish that are to be tagged with conventional or satellite tags, and those individuals can be genotyped and assigned to their stock of origin. The ability to combine the known stock of origin with tagging information will lead to an improved understanding of stock-specific Striped Marlin movements.

Future efforts to understand the temporal patterning of Striped Marlin stock composition in the HBPLLF should employ preferential sampling of various size classes. To characterize temporal patterns of adult Striped Marlin leaving the HBPLLF to respective spawning grounds in the western North or western South Pacific, targeted sampling of adult fish >160 cm should occur in the months prior to their peak spawning periods. For NPO Striped Marlin, sampling should occur in the winter and spring months during which time they may move to the western North Pacific for spawning, which peaks during the spring and summer. For Oceania Striped Marlin, sampling should occur in the summer and fall months, prior to spawning, which peaks in November and December in the western South Pacific. Similarly, targeted sampling of young (<160 cm) Striped Marlin that may move out of the range of the HBPLLF to feeding grounds prior to spawning may characterize stock-specific movements of juveniles within the CNP.

To better understand the differential recruitment dynamics of Striped Marlin in the HBPLLF, preferential sampling of age 0-1 fish should occur throughout the year. Small Striped Marlin around 140 cm are likely age 0-1 fish that recently recruited from spawning grounds in the western North or western South Pacific. Sampling these fish for genotyping and stock assignment throughout the year may characterize any temporal and

stock-specific patterns of recruitment of Striped Marlin from NPO or Oceania into the HBPLLF. Sampling effort concentrated in the fall and spring months may identify recent recruits from Oceania and NPO, respectively.

The SNP panel developed in the present study could be applied to Striped Marlin caught in other regions of the Pacific, including the western South Pacific. The possibility remains that fisheries operating in Oceania may exploit migrant Striped Marlin from the NPO stock, given the potential life-stage dependent movements of Striped Marlin suggested in the present study. Similarly, SNP panels can be developed to genotype and assign Striped Marlin from other areas of potential mixing, including between NPO and eastern central Pacific (ECPO) or between Oceania and western Indian Ocean (WIO) stocks.

In addition to movements associated with spawning, recruitment, or feeding, there are several environmental variables that may drive the movements of Striped Marlin in the CNP, including sea surface temperature, salinity, dissolved oxygen, and chlorophyll concentration. These variables could be compared to changes in the stock composition of Striped Marlin over time to characterize stock-specific responses to environmental changes. Additionally, further investigation into SNP loci under selection may be warranted to identify any stock-specific adaptations to environmental variables.

Conclusions

This study utilized NGS and SNP genotyping to resolve the stock structure of Striped Marlin in the CNP. A single central North Pacifc Stock (NPO) was resolved but mixing of the NPO and western South Pacific (Oceania) stock was noted in the CNP.

Genetic analyses of Striped Marlin collected from the HBPLLF over a 14 month period indicated that the relative proportions of NPO and Oceania Striped Marlin changed seasonally in the fishery, suggesting that Striped Marlin from NPO and Oceania undergo differential movement into and out of the HBPLLF throughout the year. Factors that may drive the observed temporal changes in the stock composition of Striped Marlin include stock-specific movements to different spawning grounds in the western North and western South Pacific, stock-specific movements to feeding grounds out of the range of the HBPLLF, and seasonally displaced recruitment into the HBPLLF for Striped Marlin spawned in the western North or western South Pacific.

Additional research is required to determine the biological and ecological drivers of this dynamic mixed-stock fishery. The results of this study may lead to improved management measures for Striped Marlin in the CNP and suggest joint management efforts by the WCPFC and IATTC to better manage this trans-boundary species.

Table 1. Quality filtering steps for the SNP dataset received from Diversity Arrays Technology (DarT PL, Canberra, Australia) containing 344 Striped Marlin and 68,224 SNPs.

Filter	Removal Threshold	Number of SNPs post-filter
Monomorphic SNPs		31,684
Read Depth	<5x and >75x	19,452
Call Rate (Loci)	<90%	13,722
Call Rate (Individual)	<90%	326 individuals removed
Reproducibility	<99%	11,419
Secondary SNPs	At random	9,664
Minor Allele Frequency	<1%	1,611
Hardy-Weinberg Equilibrium	P < 0.007 in >1 sample location	1,570
Individual Heterozygosity	>0.225	18 individuals removed
FINAL		1,570 SNPs; 308 individuals

Table 2. Pairwise F_{ST} values (below diagonal) calculated between Striped Marlin populations analyzed in this study, based on DarT sequence data. Fish sampled in an area that did not correspond to their genetic stock (putative migrants) were placed into their respective genetic stock. P-values associated with each pairwise comparison are shown in the above diagonal. NPO = North Pacific Ocean, ECPO = eastern central Pacific Ocean, WIO = Western Indian Ocean.

	Oceania	NPO	ECPO	WIO
Oceania	-	0	0	0
NPO	0.0394	-	0	0
ECPO	0.0522	0.0267	-	0
WIO	0.0402	0.0856	0.0886	-

Table 3. Genetic diversity metrics calculated for each Striped Marlin population resolved via clustering analyses of the DarT data: number of individuals (N) that comprised each population, observed heterozygosity (H_O), expected heterozygosity (H_E), and inbreeding coefficient (G_{IS}). Fish sampled in an area that did not correspond to their genetic stock (putative migrants) were placed into their respective genetic stock. NPO = North Pacific Ocean, ECPO = eastern central Pacific Ocean, WIO = Western Indian Ocean.

	N	H_O	H_E	G_{IS}
Oceania	129	0.156	0.165	0.053
NPO	76	0.153	0.164	0.069
ECPO	75	0.156	0.166	0.058
WIO	34	0.139	0.153	0.088

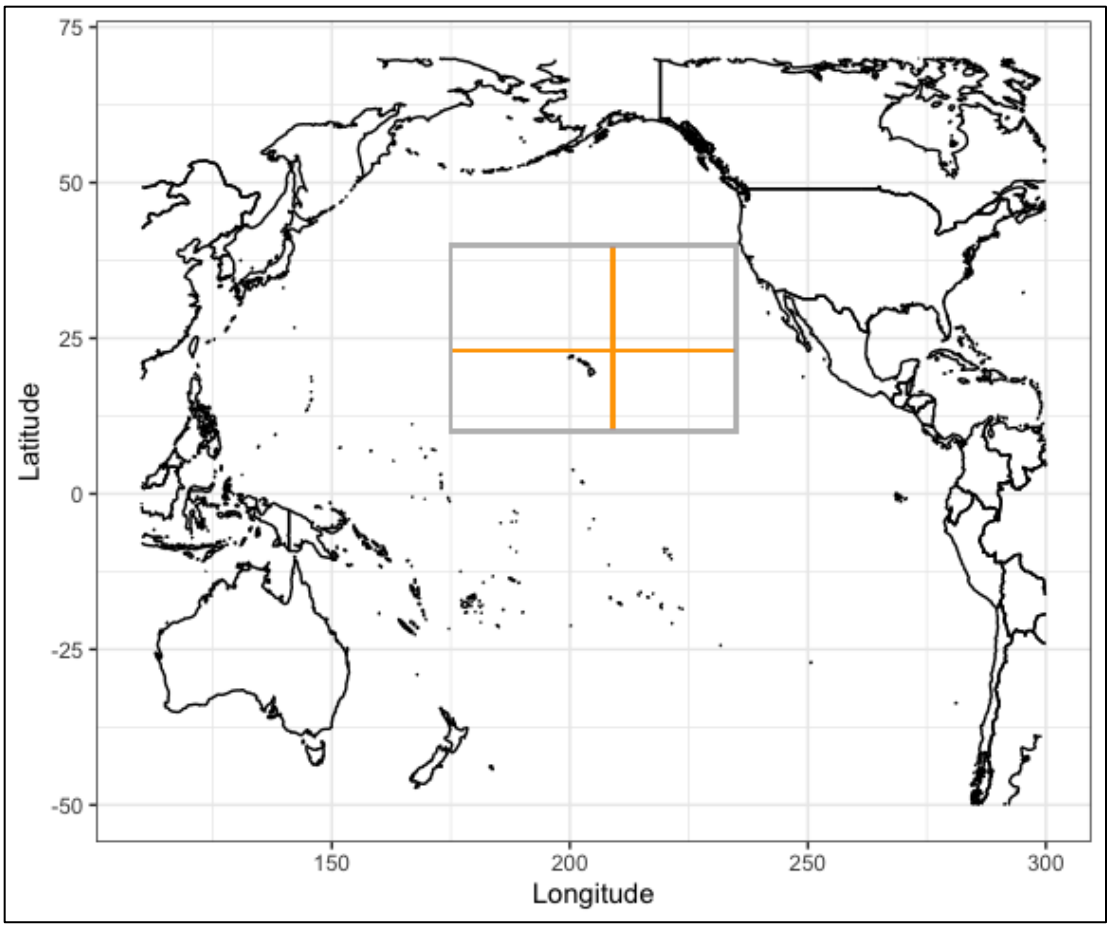

Figure 1. Range of the Hawaii-based pelagic longline fishery (gray box) where Striped Marlin were sampled from September 2019 to October 2020. The orange lines delineate the four quadrants (quadrant 1 = upper left, quadrant 2 = upper right, quadrant 3, lower left, quadrant 4, lower right).

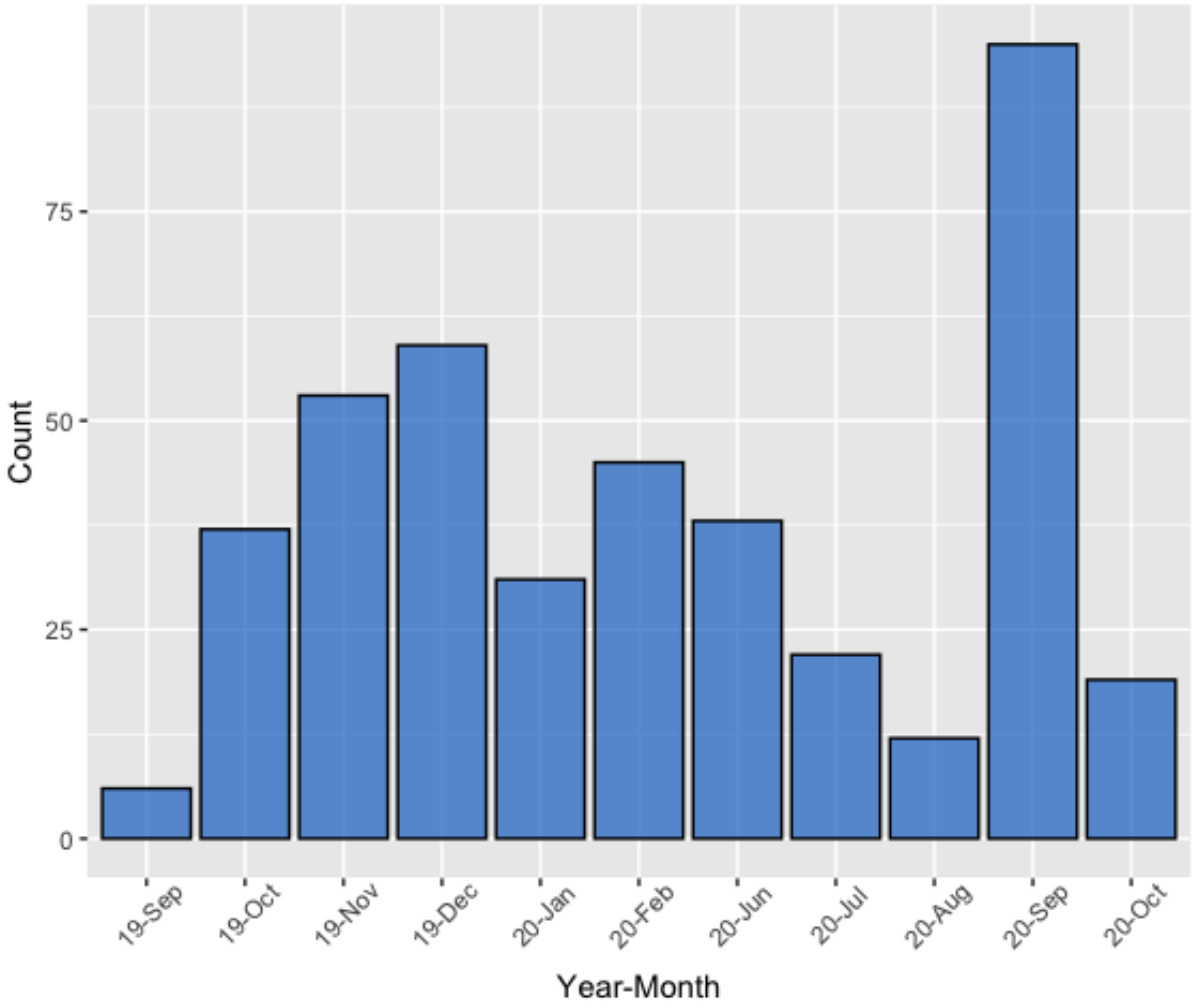

Figure 2. Numbers of Striped Marlin sampled from the Hawaii-based pelagic longline fishery by NMFS observers from September 2019 to October 2020. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic.

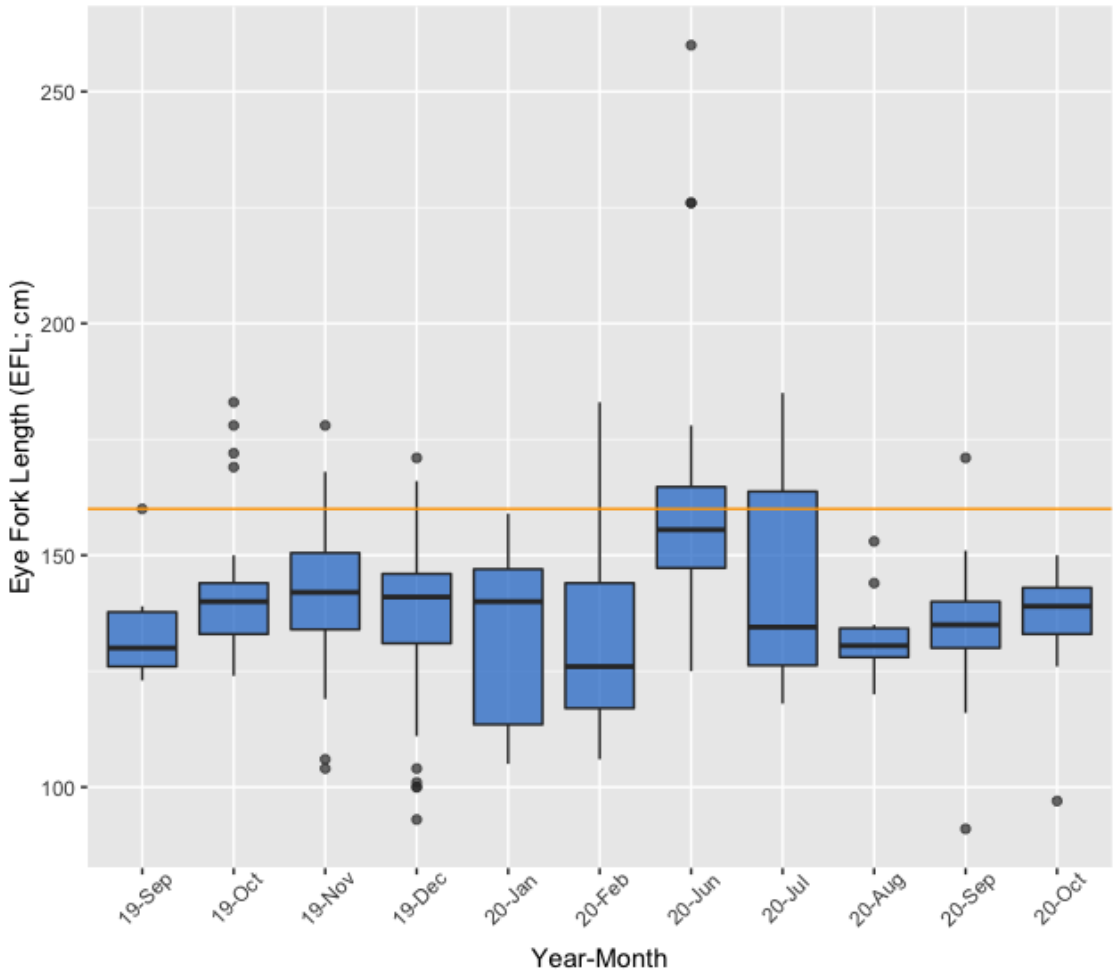

Figure 3. Length distribution of 417 Striped Marlin sampled from September 2019 to October 2020 from the Hawaii-based pelagic longline fishery. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic. For each month, the minimum, median, and maximum lengths within the interquartile range (IQR) are represented by the minimum lines, boxes, and maximum lines, respectively. Outliers from each IQR are represented by filled circles. The orange line at 160 cm EFL represents the length at 50% maturity for Striped Marlin in the central North Pacific (Humphreys and Brodziak 2019).

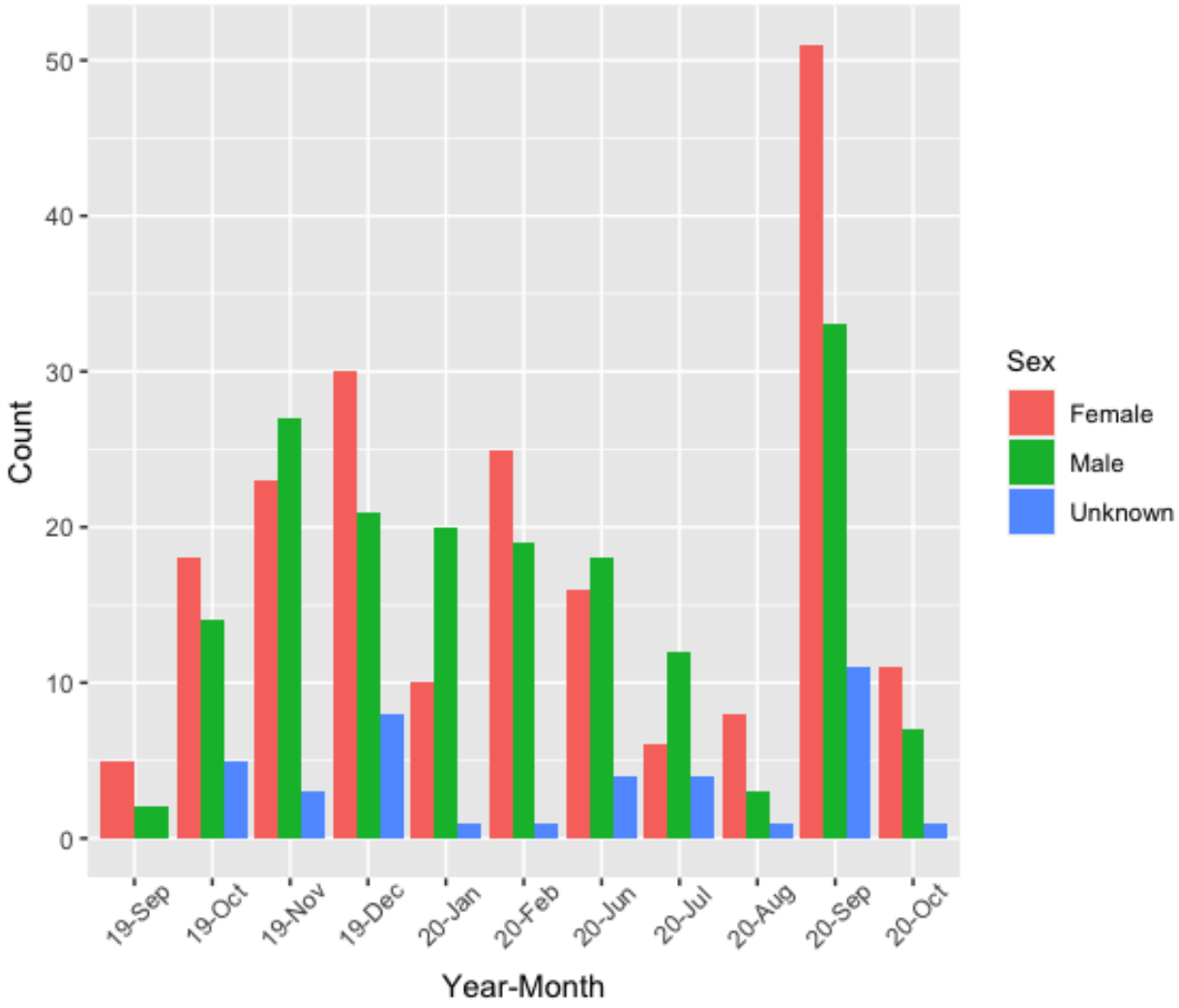

Figure 4. Sex distribution for the 417 Striped Marlin sampled from September 2019 to October 2020 from the Hawaii-based pelagic longline fishery. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic. Fish sex is coded as red = females, green = males, and blue = unknown.

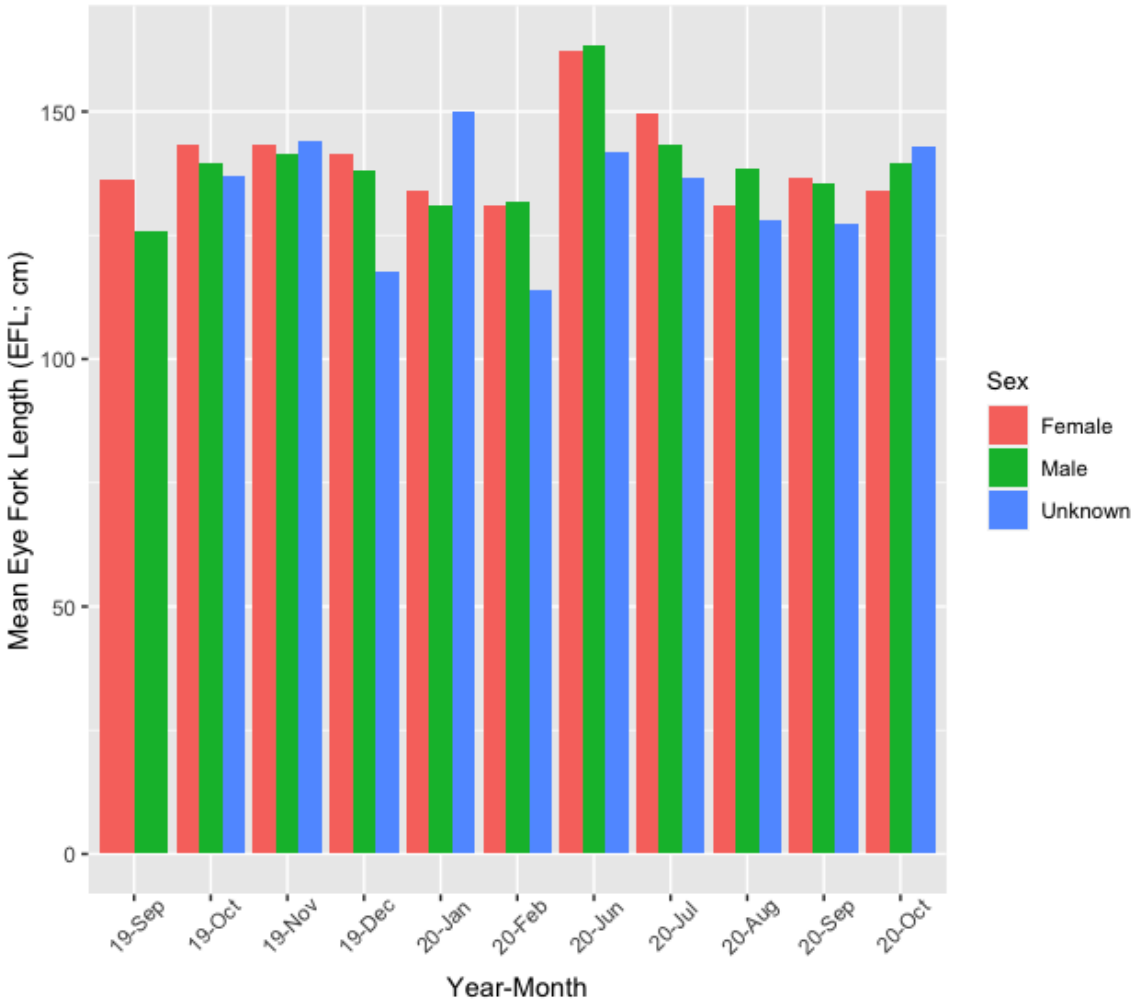

Figure 5. Mean length by sex for the 417 Striped Marlin sampled from September 2019 to October 2020 from the Hawaii-based pelagic longline fishery. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic. Fish sex is coded as red = females, green = males, and blue = unknown.

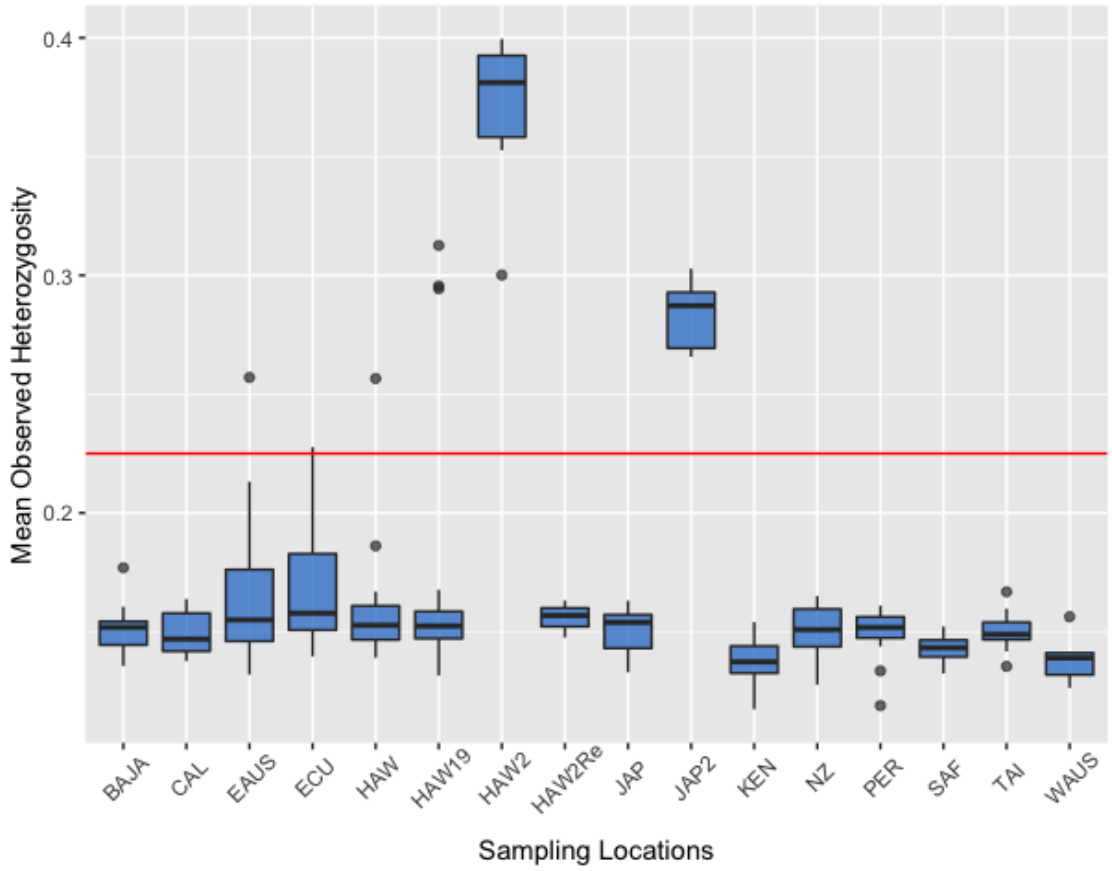

Figure 6. Observed heterozygosity levels for individual Striped Marlin from each sample collection including those from Mamoozadeh et al (2020). For each sample location, the minimum, median, and maximum heterozygosity levels of individual Striped Marlin within the interquartile range (IQR) are represented by the minimum lines, boxes, and maximum lines, respectively. Outliers from each IQR are represented by filled circles. The red line at 0.225 represents the heterozygosity threshold over which individuals were removed from the dataset due to concerns of contamination. HAW2 and JAP2 represent the 12 individuals that comprised the NPO2 stock in Mamoozadeh et al. (2020). HAW2Re represents the three individuals from HAW2 that were re-sequenced in the present study.

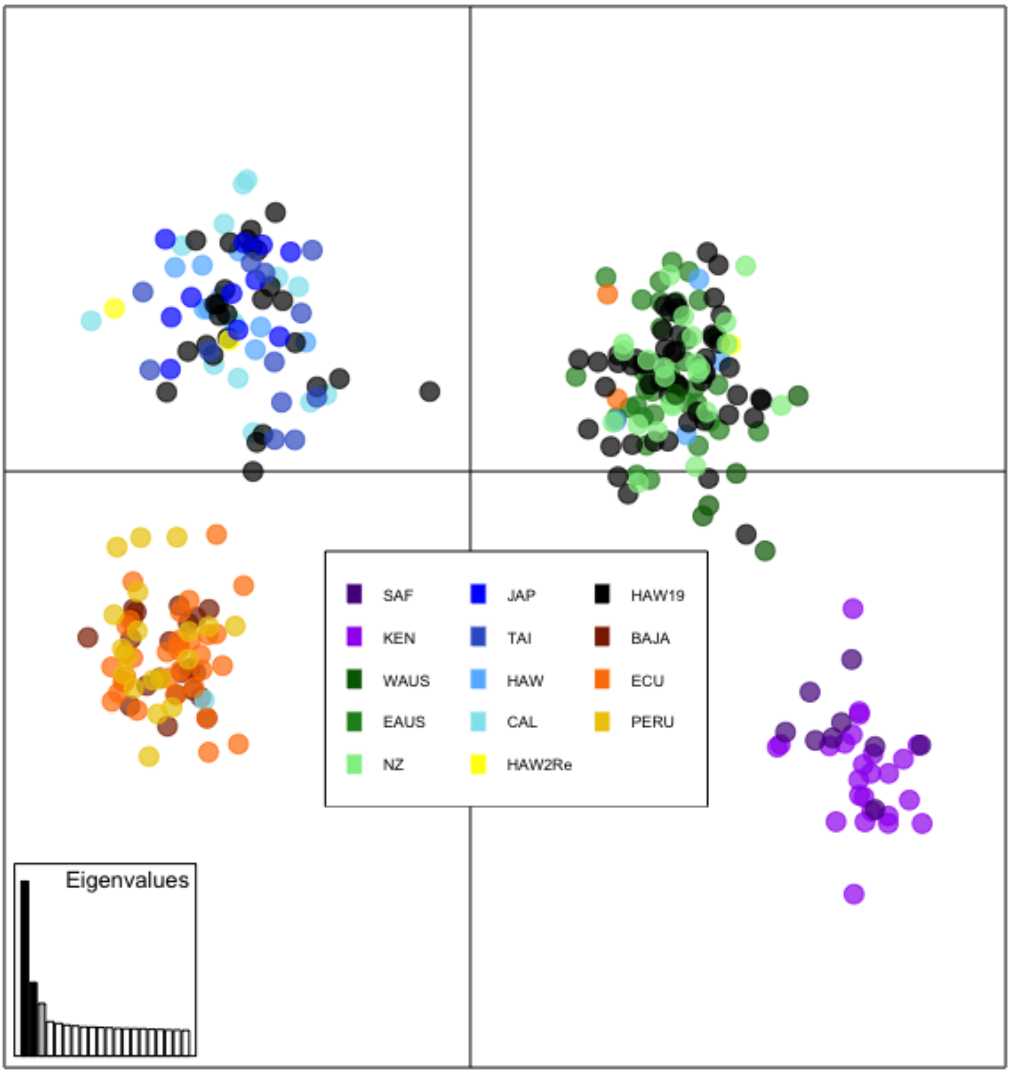

Figure 7. Principal component analysis (PCA) of co-analyzed dataset consisting of 308 Striped Marlin (80 present study, 228 Mamoozadeh et al. (2020)) and 1,611 SNPs. Principal components 1 (x-axis) and 2 (y-axis) are displayed, accounting for 4.38% and 1.84% of the variance in the dataset, respectively.

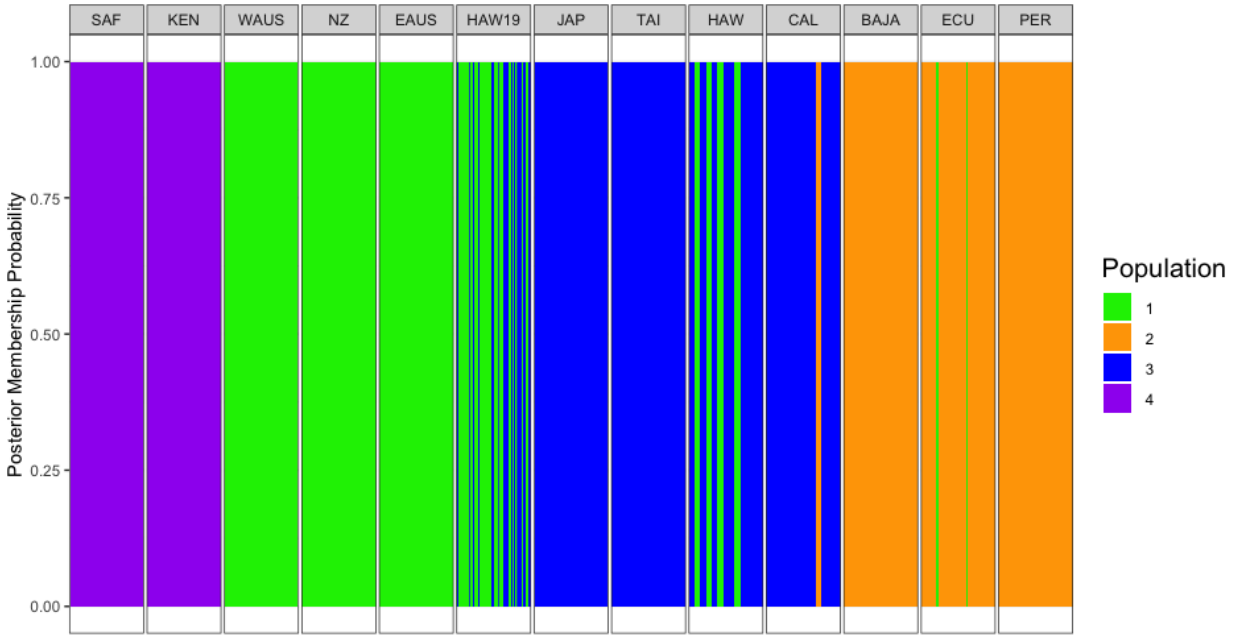

Figure 8. Discriminant analysis of principal components (DAPC) of the co-analyzed dataset consisting of 305 Striped Marlin and 1,611 SNPs. Sample locations are given at the top of the figure and individual Striped Marlin are represented by colored lines, corresponding to their assigned cluster. Population codes represent ECPO (1), WIO (2), Oceania (3), and NPO (4).

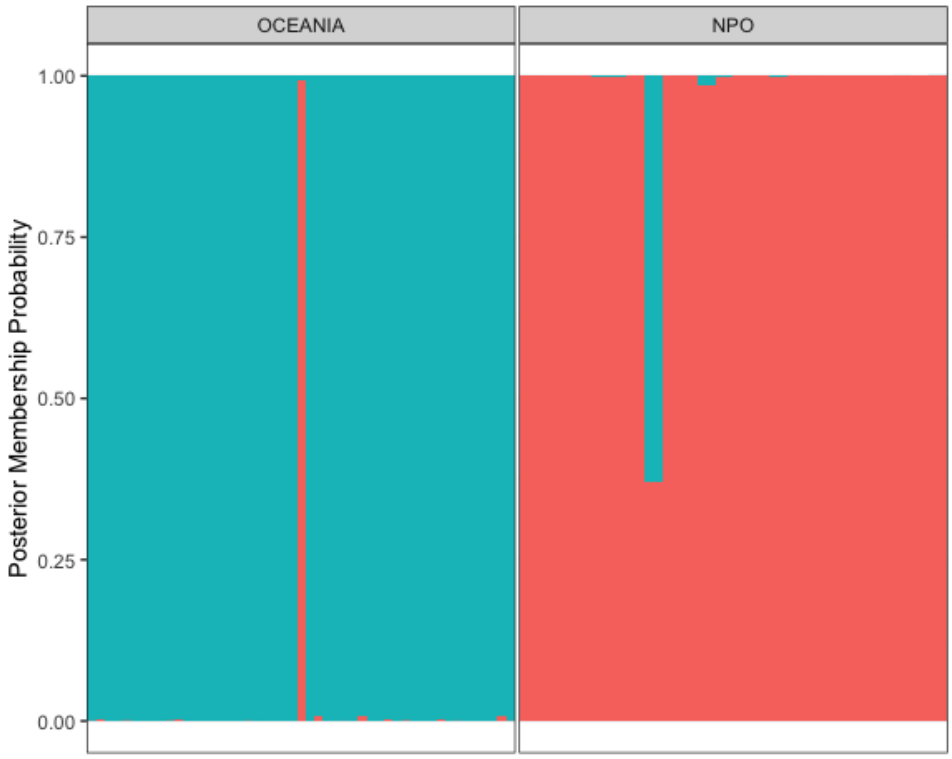

Figure 9. Discriminant analysis of principal components (DAPC) based on the available DarT data for 73 sequenced Striped Marlin at the final 32 loci used for the Fluidigm panels. 24 Striped Marlin clustered with NPO and 49 clustered with Oceania. It was discovered that one individual (HAW_191027) was incorrectly assigned with Oceania when it should have been assigned with NPO, as is shown in the DAPC

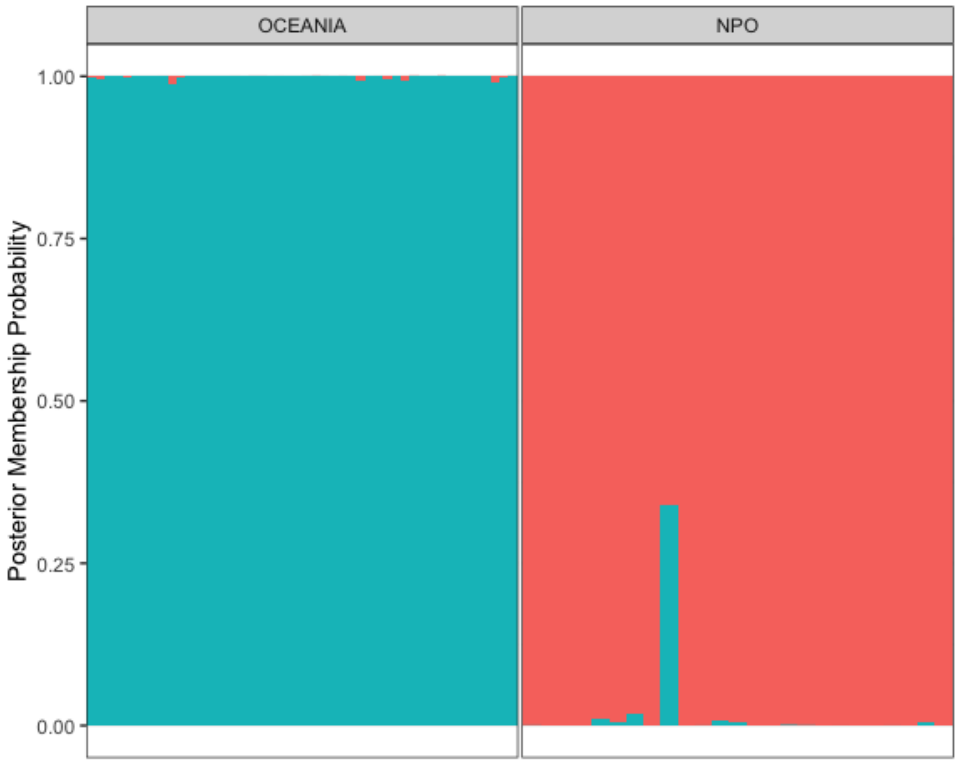

Figure 10. DAPC of 73 of the 83 Striped Marlin that have accompanying DarT data, based on their Fluidigm-obtained genotypes with 48 loci. 48 Striped Marlin clustered with Oceania and 25 clustered with NPO.

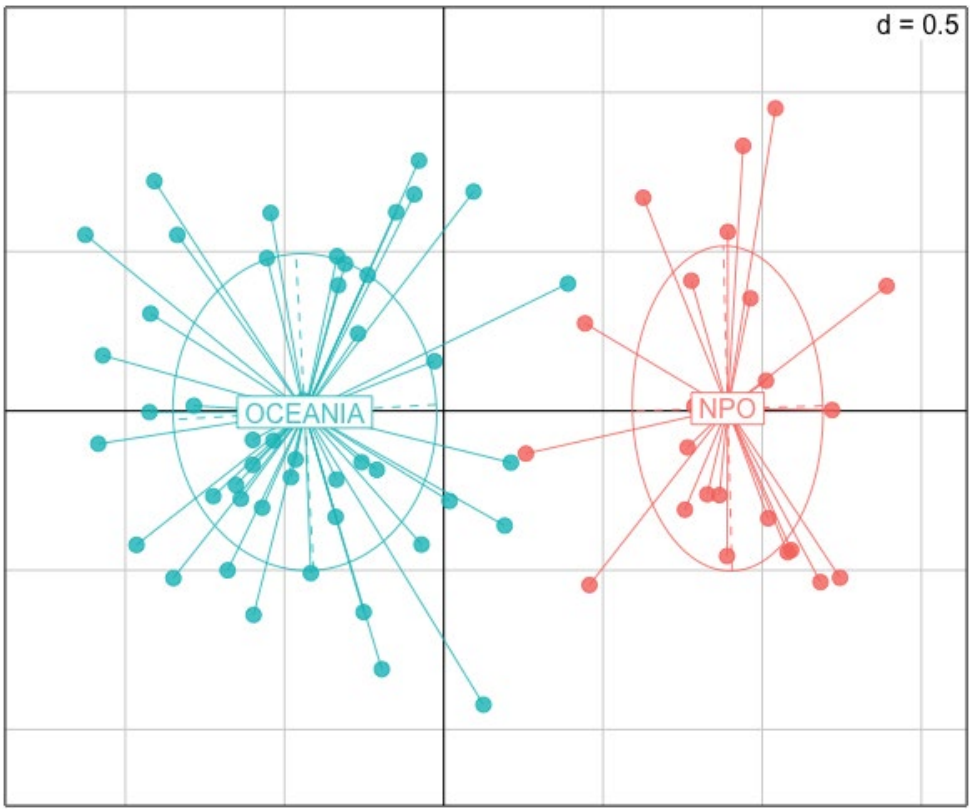

Figure 11. Principal component analysis (PCA) of 73 Striped Marlin based on the DarT data for the 32 loci selected for the Fluidigm panel. Ten individuals were removed from the dataset due to elevated levels of missing data or heterozygosities. Of the 73 individuals, 49 clustered into Oceania and 24 clustered into NPO. Principal components 1 (x-axis) and 2 (y-axis) accounted for 20.26 and 7.73 % of the variance, respectively.

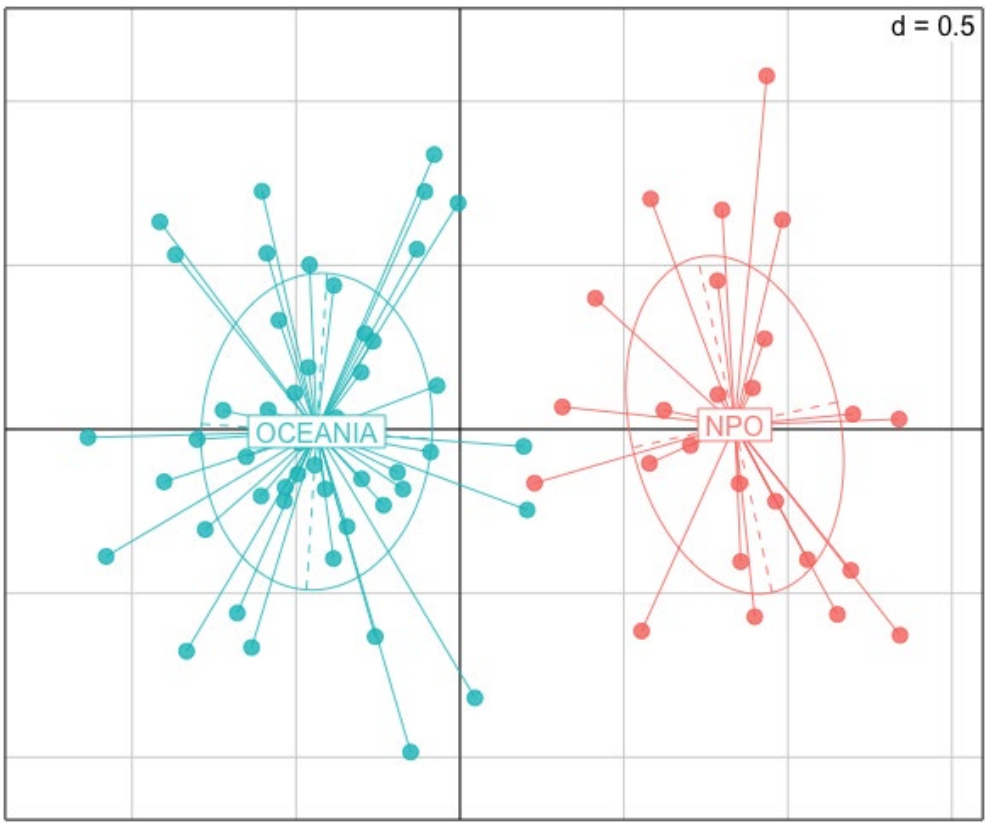

Figure 12. Principal component analysis (PCA) of 73 Striped Marlin with corresponding DarT data using the 32 loci genotyped on the Fluidigm. Of the 73 individuals, 48 clustered into Oceania and 25 clustered into NPO. Principal components 1 (x-axis) and 2 (y-axis) accounted for 19.6 and 7.9 % of the variance, respectively.

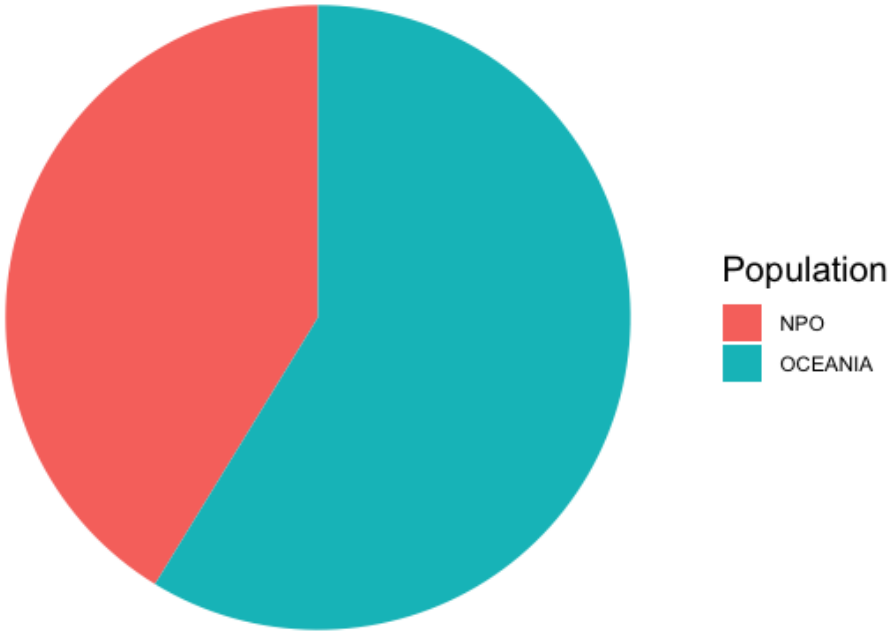

Figure 13. Proportion of Striped Marlin sampled between September 2019 and October 2020 from the Hawaii-based pelagic longline fishery that assigned into either NPO and Oceania (n = 378). NPO accounted for (156) 41.3% of assigned samples and Oceania accounted for (222) 58.7%

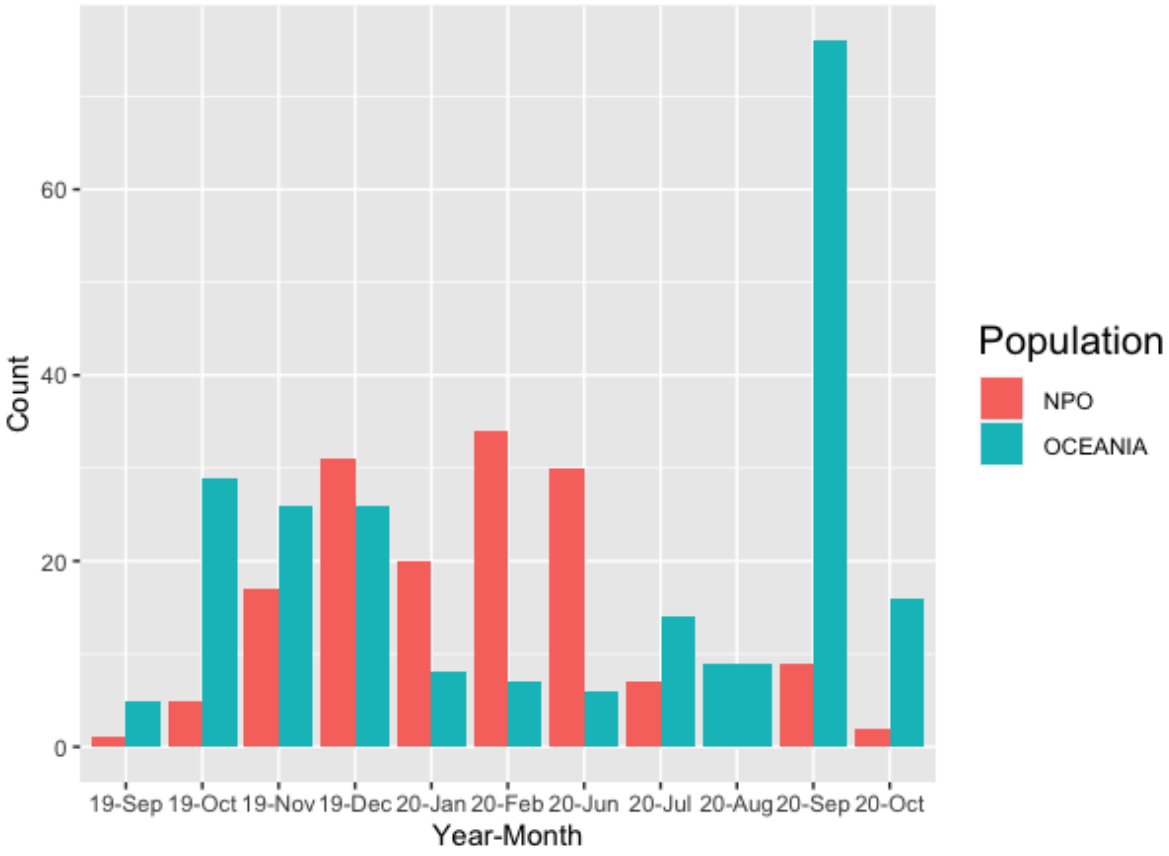

Figure 14. Number of Striped Marlin sampled between September 2019 and October 2020 from the Hawaii-based pelagic longline fishery that were assigned to the NPO or Oceania stocks by month. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic.

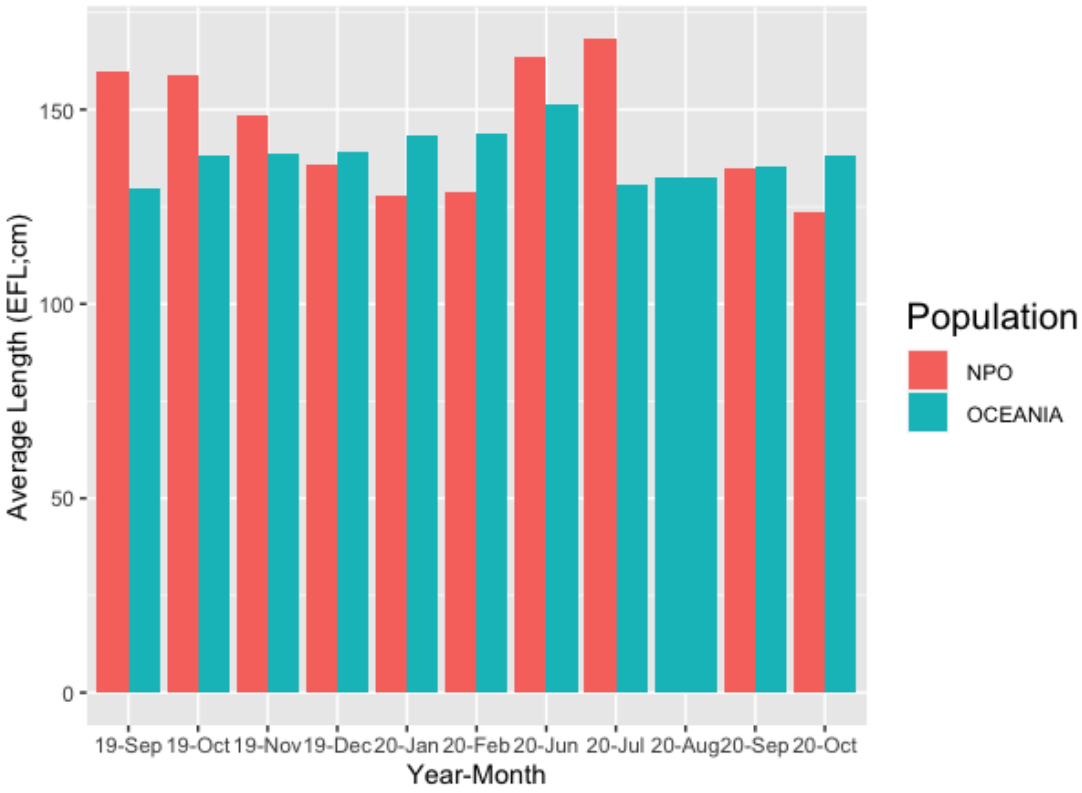

Figure 15. Monthly mean length (cm; EFL) of Striped Marlin assigned to the NPO or Oceania stocks sampled from the Hawaii-based pelagic longline fishery between September 2019 and October 2020. No samples were collected from March 2020 to May 2020 due to the COVID-19 pandemic. There were no individuals assigned to NPO in August 2020.

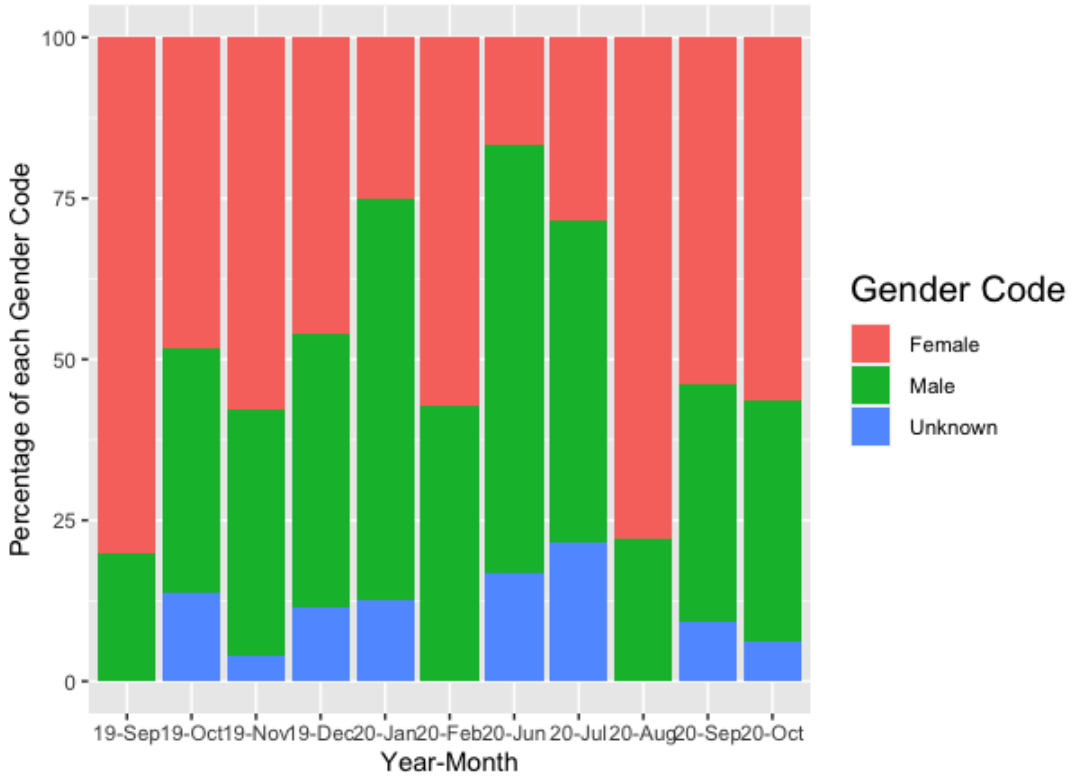

Figure 16. Monthly sex composition of Striped Marlin sampled from the Hawaii-based pelagic longline fishery from September 2019 to October 2020 and assigned to the Oceania stock.
Fish sex is coded as red = Female, green = Male, and blue = Unknown.

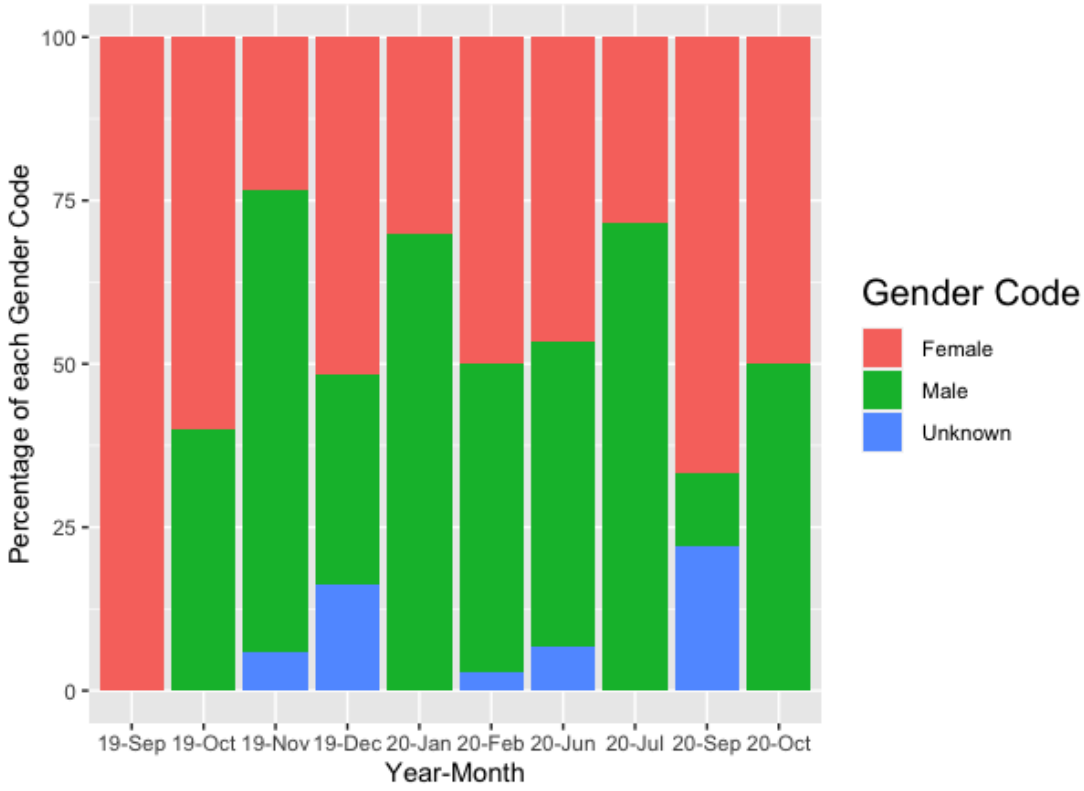

Figure 17. Monthly sex composition of Striped Marlin sampled from the Hawaii-based pelagic longline fishery from September 2019 to October 2020 and assigned to the NPO stock.
Fish sex is coded as red = Female, green = Male, and blue = Unknown.

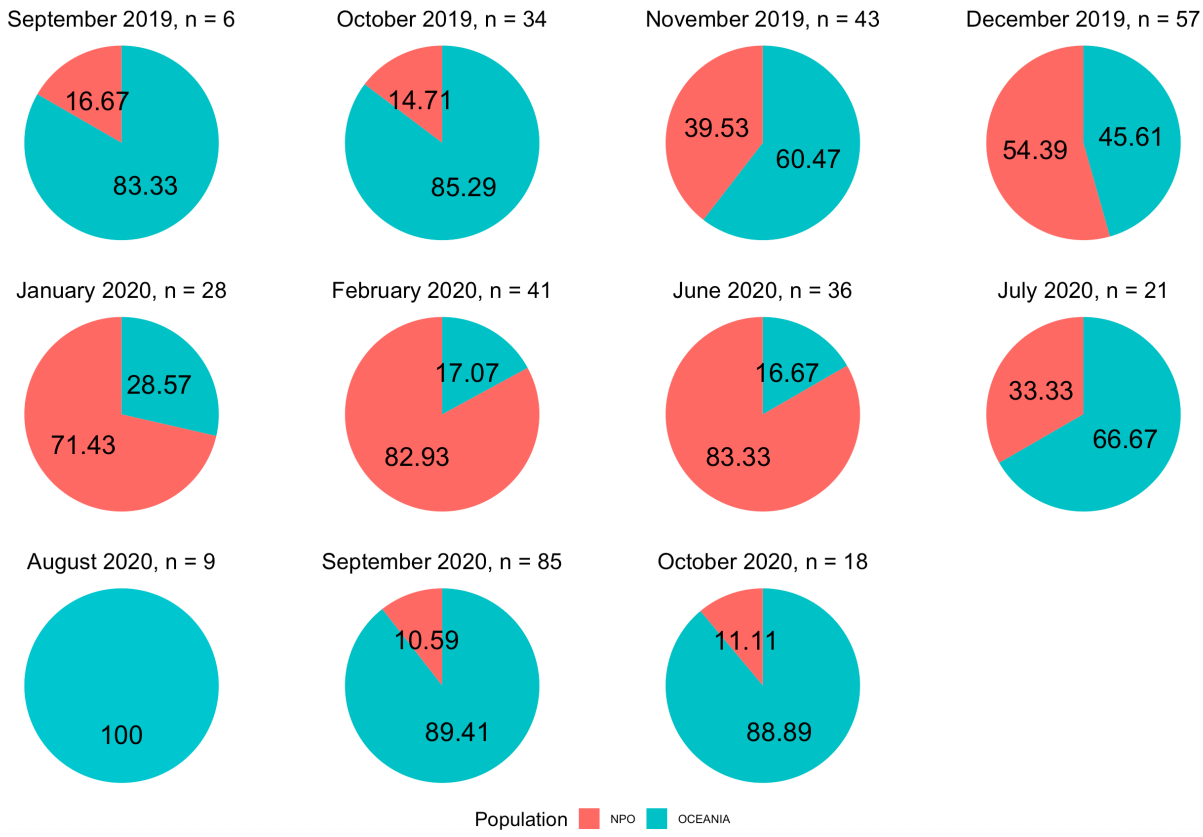

Figure 18. Proportion of Striped Marlin assigned to NPO or Oceania from October 2019 to October 2020. Labels above each pie chart denote the month, year, and number of samples for each month. Numbers on each pie chart represent the percentage of Striped Marlin that make up each monthly collection by stock.

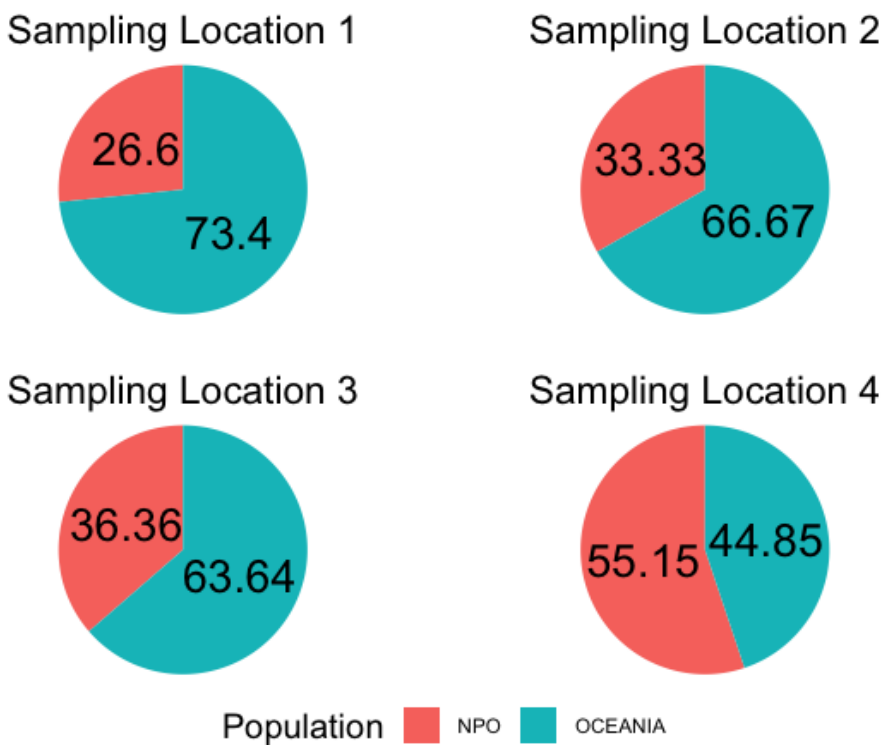

Figure 19. Proportion of Striped Marlin sampled between September 2019 and October 2020 from the Hawaii-based pelagic longline fishery that were assigned to the NPO or Oceania stocks by quadrant (Figure 1). Quadrant 1 (n=94), 2 (n=108), 3 (n=11), 4 (n=165).

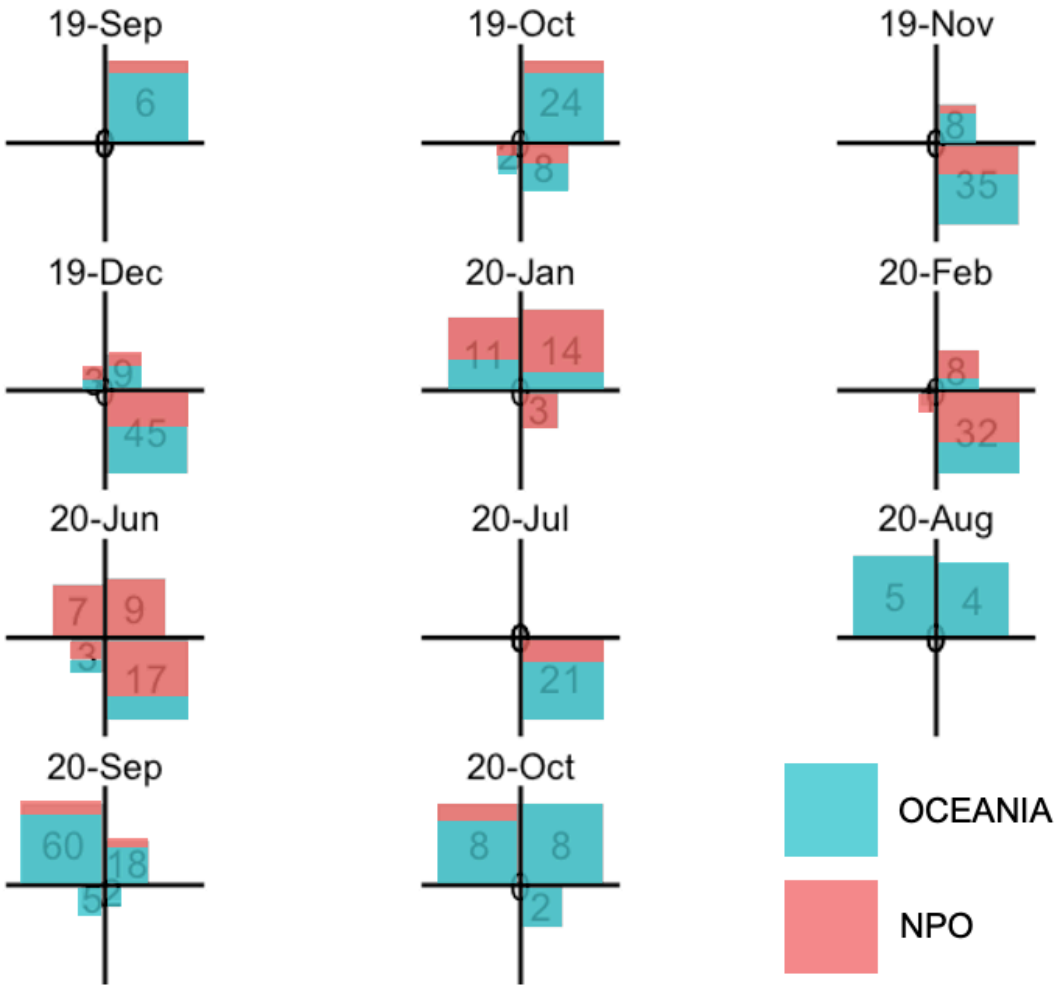

Figure 20. Numbers, catch location (quadrant), and stock composition of Striped Marlin sampled between September 2019 and October 2020 from the Hawaii-based pelagic longline. Quadrant 1 (Figure 1) = upper left, quadrant 2 = upper right, quadrant 3 = lower left, quadrant 4 = lower right. NPO = red, Oceania = blue.

Appendix 1: Sample names and associated catch data for 417 striped marlin collected by NMFS fisheries observers operating in the Hawaii-based Pelagic longline fishery from September 2019 to October 2020. The 'Assignment' column gives the stock assignment for striped marlin into NPO or Oceania based on genotypes derived from the DarTSeq™ (D) or Fluidigm (F) platforms. Individuals that were removed during DarT data filtering are represented by '-' and those that were unassigned due to assignment scores <90% are represented by '%.'

Original Specimen ID	New Specimen ID	Year-Month	Area	Sex	Length (cm; EFL)	Spawning Condition	Assignment	Platform
LL6849 5 4 7	STM_HAW190901	19-Sep	2	F	139	N	OCEANIA	D
LL6849 3 5 5	STM_HAW190902	19-Sep	2	F	160	Y	NPO	D
LL6849 3 2 2	STM_HAW190903	19-Sep	2	F	126	N	OCEANIA	D
LL6849 1 2 3	STM_HAW190904	19-Sep	2	F	123	N	OCEANIA	D
LL6849 8 4 13	STM_HAW190905	19-Sep	2	F	134	N	OCEANIA	D
LL6849 11 3 5	STM_HAW190906	19-Sep	2	M	126	N	OCEANIA	D
LL6885 5 2 9	STM_HAW191001	19-Oct	2	M	144	N	-	D
LL6885 8 3 10	STM_HAW191002	19-Oct	2	F	169	N	OCEANIA	D
LL6886 14 3 10	STM_HAW191003	19-Oct	4	F	146	N	OCEANIA	D
LL6885 4 2 4	STM_HAW191004	19-Oct	2	M	135	N	OCEANIA	D
LL6885 11 2 4	STM_HAW191005	19-Oct	2	F	140	N	OCEANIA	D
LL6885 2 9 2	STM_HAW191006	19-Oct	2	U	140	U	OCEANIA	F
LL6885 8 1 4	STM_HAW191007	19-Oct	2	F	124	N	OCEANIA	D
LL6885 5 1 15	STM_HAW191008	19-Oct	2	U	145	U	OCEANIA	D
LL6886 11 5 8	STM_HAW191009	19-Oct	4	F	183	N	NPO	D
LL6885 4 3 8	STM_HAW191010	19-Oct	2	F	134	N	-	D
LL6885 3 1 11	STM_HAW191011	19-Oct	2	F	127	U	OCEANIA	D
LL6885 4 4 11	STM_HAW191012	19-Oct	2	U	130	U	OCEANIA	D
LL6885 12 4 12	STM_HAW191013	19-Oct	2	U	140	U	-	D
LL6886 11 1 3	STM_HAW191014	19-Oct	4	F	141	N	NPO	D
LL6886 15 4 4	STM_HAW191015	19-Oct	4	M	135	N	OCEANIA	D

LL6885 1 3 8	STM_HAW191016	19-Oct	2	F	134	N	OCEANIA	D
LL6885 8 1 5	STM_HAW191017	19-Oct	2	F	125	N	OCEANIA	D
LL6885 4 3 10	STM_HAW191018	19-Oct	2	F	146	N	OCEANIA	D
LL6885 7 3 11	STM_HAW191019	19-Oct	2	M	142	N	OCEANIA	D
LL6882 12 2 8	STM_HAW191020	19-Oct	2	M	143	U	NPO	D
LL6882 1 2 10	STM_HAW191021	19-Oct	2	M	137	U	OCEANIA	D
LL6882 9 2 12	STM_HAW191022	19-Oct	2	M	142	U	OCEANIA	D
LL6882 1 2 11	STM_HAW191023	19-Oct	2	U	129	U	OCEANIA	D
LL6885 11 2 13	STM_HAW191024	19-Oct	2	M	133	N	OCEANIA	D
LL6885 8 1 15	STM_HAW191025	19-Oct	2	M	142	N	OCEANIA	D
LL6882 1 1 9	STM_HAW191026	19-Oct	2	F	128	U	OCEANIA	D
LL6896 1 5 8	STM_HAW191027	19-Oct	3	F	178	N	NPO	D
LL6896 1 4 14	STM_HAW191028	19-Oct	3	M	130	N	OCEANIA	D
LL6882 9 1 13	STM_HAW191029	19-Oct	2	M	133	U	OCEANIA	D
LL6882 9 1 12	STM_HAW191030	19-Oct	2	M	148	U	OCEANIA	D
LL6885 5 4 8	STM_HAW191031	19-Oct	2	F	130	N	OCEANIA	D
LL6885 4 3 7	STM_HAW191032	19-Oct	2	F	134	N	OCEANIA	D
LL6885 8 3 8	STM_HAW191033	19-Oct	2	F	135	N	OCEANIA	F
LL6886 11 4 2	STM_HAW191034	19-Oct	4	M	150	N	NPO	F
LL6886 11 6 13	STM_HAW191035	19-Oct	4	M	142	N	OCEANIA	F
LL6886 12 3 6	STM_HAW191036	19-Oct	4	F	134	N	OCEANIA	F
LL6886 13 2 9	STM_HAW191037	19-Oct	4	F	172	N	OCEANIA	F
LL6911 4 2 5	STM_HAW191101	19-Nov	4	F	150	N	-	D
LL6911 3 4 10	STM_HAW191102	19-Nov	4	F	147	N	-	D
LL6911 2 4 7	STM_HAW191103	19-Nov	4	M	166	N	-	D
LL6911 3 1 3	STM_HAW191104	19-Nov	4	F	138	N	-	D
LL6911 7 2 2	STM_HAW191105	19-Nov	4	F	134	N	-	D
LL6911 5 2 8	STM_HAW191106	19-Nov	4	M	0	N	-	D

LL6911 5 4 15	STM_HAW191107	19-Nov	4	F	144	N	NPO	F
LL6911 8 2 1	STM_HAW191108	19-Nov	4	M	161	N	NPO	D
LL6912 8 2 14	STM_HAW191109	19-Nov	4	M	135	N	NPO	D
LL6912 8 1 3	STM_HAW191110	19-Nov	4	F	136	N	OCEANIA	D
LL6912 8 1 12	STM_HAW191111	19-Nov	4	M	134	N	OCEANIA	D
LL6917 4 1 6	STM_HAW191112	19-Nov	4	F	133	N	OCEANIA	D
LL6917 7 1 8	STM_HAW191113	19-Nov	4	M	146	N	OCEANIA	D
LL6917 8 5 4	STM_HAW191114	19-Nov	4	M	159	N	NPO	D
LL6924 2 4 2	STM_HAW191115	19-Nov	4	M	133	N	OCEANIA	D
LL6924 7 5 3	STM_HAW191116	19-Nov	4	M	159	N	NPO	F
LL6920 2 3 1	STM_HAW191117	19-Nov	4	F	178	N	OCEANIA	D
LL6920 7 2 4	STM_HAW191118	19-Nov	4	M	146	N	-	D
LL6920 9 3 1	STM_HAW191119	19-Nov	4	F	141	N	OCEANIA	F
LL6920 9 3 2	STM_HAW191120	19-Nov	4	M	130	N	OCEANIA	D
LL6926 3 1 13	STM_HAW191121	19-Nov	4	F	104	N	OCEANIA	D
LL6926 6 1 12	STM_HAW191122	19-Nov	4	U	156	N	NPO	D
LL6920 4 1 12	STM_HAW191123	19-Nov	4	F	161	N	OCEANIA	F
LL6911 5 3 1	STM_HAW191124	19-Nov	4	M	136	N	NPO	F
LL6911 5 3 9	STM_HAW191125	19-Nov	4	M	142	N	OCEANIA	F
LL6911 5 5 10	STM_HAW191126	19-Nov	4	M	147	N	NPO	F
LL6911 7 8 3	STM_HAW191127	19-Nov	4	U	0	U	-	F
LL6912 3 2 13	STM_HAW191128	19-Nov	4	U	132	U	OCEANIA	F
LL6912 4 1 4	STM_HAW191129	19-Nov	4	F	160	N	NPO	F
LL6912 4 2 11	STM_HAW191130	19-Nov	4	M	148	N	NPO	F
LL6912 5 3 15	STM_HAW191131	19-Nov	4	F	152	N	OCEANIA	F
LL6914 2 2 4	STM_HAW191132	19-Nov	2	M	119	N	OCEANIA	F
LL6914 2 3 10	STM_HAW191133	19-Nov	2	M	137	N	OCEANIA	F
LL6914 7 2 4	STM_HAW191134	19-Nov	2	M	142	N	OCEANIA	F

LL6914 7 2 9	STM_HAW191135	19-Nov	2	M	106	N	%	F
LL6914 8 1 1	STM_HAW191136	19-Nov	2	F	132	N	OCEANIA	F
LL6914 8 2 8	STM_HAW191137	19-Nov	2	M	140	N	OCEANIA	F
LL6914 8 2 9	STM_HAW191138	19-Nov	2	F	139	N	OCEANIA	F
LL6914 9 1 3	STM_HAW191139	19-Nov	2	F	168	N	NPO	F
LL6914 9 2 1	STM_HAW191140	19-Nov	2	F	140	N	OCEANIA	F
LL6917 12 1 2	STM_HAW191141	19-Nov	4	M	143	N	%	F
LL6917 13 1 14	STM_HAW191142	19-Nov	4	F	136	N	OCEANIA	F
LL6917 14 1 12	STM_HAW191143	19-Nov	4	M	132	N	NPO	F
LL6920 1 1 7	STM_HAW191144	19-Nov	4	F	130	N	OCEANIA	F
LL6920 1 1 12	STM_HAW191145	19-Nov	4	F	150	N	OCEANIA	F
LL6920 4 1 11	STM_HAW191146	19-Nov	4	M	131	N	NPO	F
LL6920 9 1 1	STM_HAW191147	19-Nov	4	M	147	N	NPO	F
LL6924 3 2 14	STM_HAW191148	19-Nov	4	F	128	N	OCEANIA	F
LL6924 4 4 6	STM_HAW191149	19-Nov	4	M	151	N	NPO	F
LL6924 6 2 13	STM_HAW191150	19-Nov	4	F	151	N	OCEANIA	F
LL6924 6 2 14	STM_HAW191151	19-Nov	4	M	136	N	OCEANIA	F
LL6924 7 5 2	STM_HAW191152	19-Nov	4	M	151	N	NPO	F
LL6926 1 1 2	STM_HAW191153	19-Nov	4	F	143	N	NPO	F
LL6926 7 2 9	STM_HAW191201	19-Dec	4	U	100	U	NPO	D
LL6926 7 7 3	STM_HAW191202	19-Dec	4	F	155	N	NPO	D
LL6920 16 4 2	STM_HAW191203	19-Dec	4	M	146	N	NPO	D
LL6926 13 2 4	STM_HAW191204	19-Dec	4	U	138	U	OCEANIA	D
LL6926 9 1 4	STM_HAW191205	19-Dec	4	F	166	N	NPO	D
LL6920 18 3 9	STM_HAW191206	19-Dec	4	M	138	N	OCEANIA	D
LL6920 18 1 14	STM_HAW191207	19-Dec	4	M	133	N	OCEANIA	D
LL6920 18 1 11	STM_HAW191208	19-Dec	4	M	142	N	NPO	D
LL6920 17 4 2	STM_HAW191209	19-Dec	4	F	164	N	NPO	D

LL6920 17 2 4	STM_HAW191210	19-Dec	4	F	142	N	OCEANIA	D
LL6920 15 2 9	STM_HAW191211	19-Dec	4	F	146	N	OCEANIA	D
LL6920 14 2 10	STM_HAW191212	19-Dec	4	M	130	N	NPO	D
LL6920 13 5 11	STM_HAW191213	19-Dec	4	M	142	N	OCEANIA	D
LL6938 7 2 1	STM_HAW191214	19-Dec	4	M	158	N	NPO	D
LL6938 9 3 7	STM_HAW191215	19-Dec	4	M	140	N	OCEANIA	D
LL6938 11 1 2	STM_HAW191216	19-Dec	2	F	155	N	NPO	D
LL6938 4 6 12	STM_HAW191217	19-Dec	2	M	131	N	NPO	D
LL6938 5 1 15	STM_HAW191218	19-Dec	4	F	118	N	NPO	D
LL6938 4 1 9	STM_HAW191219	19-Dec	2	M	139	N	NPO	D
LL6938 4 2 13	STM_HAW191220	19-Dec	2	F	135	N	OCEANIA	D
LL6938 4 6 11	STM_HAW191221	19-Dec	2	F	148	N	NPO	D
LL6938 2 4 5	STM_HAW191222	19-Dec	4	F	153	N	-	D
LL6938 3 1 9	STM_HAW191223	19-Dec	2	M	114	N	NPO	D
LL6938 3 4 7	STM_HAW191224	19-Dec	2	F	143	N	OCEANIA	D
LL6938 1 1 14	STM_HAW191225	19-Dec	4	F	145	U	OCEANIA	D
LL6938 2 3 8	STM_HAW191226	19-Dec	4	F	141	N	OCEANIA	D
LL6949 2 2 1	STM_HAW191227	19-Dec	1	F	171	N	NPO	D
LL6949 4 1 6	STM_HAW191228	19-Dec	1	F	111	N	-	D
LL6949 6 2 8	STM_HAW191229	19-Dec	1	F	146	N	NPO	D
LL6920 12 1 10	STM_HAW191230	19-Dec	4	U	158	N	NPO	F
LL6920 12 4 3	STM_HAW191231	19-Dec	4	U	147	N	OCEANIA	F
LL6920 13 3 4	STM_HAW191232	19-Dec	4	M	146	N	OCEANIA	F
LL6920 14 1 10	STM_HAW191233	19-Dec	4	F	115	N	NPO	F
LL6920 18 1 5	STM_HAW191234	19-Dec	4	F	126	N	NPO	F
LL6920 18 1 13	STM_HAW191235	19-Dec	4	M	146	N	OCEANIA	F
LL6920 18 1 15	STM_HAW191236	19-Dec	4	F	145	N	NPO	F
LL6924 11 2 15	STM_HAW191237	19-Dec	4	M	127	N	OCEANIA	F

LL6926 7 5 15	STM_HAW191238	19-Dec	4	F	139	N	NPO	F
LL6926 8 1 12	STM_HAW191239	19-Dec	4	U	93	U	NPO	F
LL6926 9 3 10	STM_HAW191240	19-Dec	4	U	101	U	NPO	F
LL6926 9 5 2	STM_HAW191241	19-Dec	4	M	131	U	NPO	F
LL6926 12 3 14	STM_HAW191242	19-Dec	4	U	100	U	NPO	F
LL6926 12 5 1	STM_HAW191243	19-Dec	4	F	143	N	NPO	F
LL6926 12 7 13	STM_HAW191244	19-Dec	4	U	104	U	OCEANIA	F
LL6926 13 1 4	STM_HAW191245	19-Dec	4	F	154	N	NPO	F
LL6926 13 1 5	STM_HAW191246	19-Dec	4	F	116	N	NPO	F
LL6938 1 1 15	STM_HAW191247	19-Dec	4	F	140	N	OCEANIA	F
LL6938 1 4 6	STM_HAW191248	19-Dec	4	M	140	U	NPO	F
LL6938 2 4 1	STM_HAW191249	19-Dec	4	M	147	N	NPO	F
LL6938 2 5 8	STM_HAW191250	19-Dec	4	M	134	N	OCEANIA	F
LL6938 2 5 9	STM_HAW191251	19-Dec	4	F	134	N	OCEANIA	F
LL6938 3 6 6	STM_HAW191252	19-Dec	2	M	138	N	OCEANIA	F
LL6938 4 1 10	STM_HAW191253	19-Dec	2	F	141	N	OCEANIA	F
LL6938 5 1 12	STM_HAW191254	19-Dec	4	M	138	N	OCEANIA	F
LL6938 5 1 14	STM_HAW191255	19-Dec	4	F	113	N	NPO	F
LL6938 5 4 8	STM_HAW191256	19-Dec	4	M	142	N	OCEANIA	F
LL6938 7 1 14	STM_HAW191257	19-Dec	4	F	144	N	OCEANIA	F
LL6938 8 3 13	STM_HAW191258	19-Dec	4	F	155	N	OCEANIA	F
LL6949 4 3 4	STM_HAW191259	19-Dec	1	F	143	N	OCEANIA	F
LL6949 8 1 8	STM_HAW200101	20-Jan	1	M	149	N	NPO	F
LL6949 8 2 15	STM_HAW200102	20-Jan	1	F	145	N	OCEANIA	F
LL6949 9 1 4	STM_HAW200103	20-Jan	1	M	145	N	OCEANIA	F
LL6949 9 2 1	STM_HAW200104	20-Jan	1	M	152	N	OCEANIA	F
LL6949 9 2 2	STM_HAW200105	20-Jan	1	M	119	N	OCEANIA	F
LL6949 9 2 3	STM_HAW200106	20-Jan	1	F	136	N	NPO	F

LL6949 10 1 3	STM_HAW200107	20-Jan	1	F	107	N	NPO	F
LL6949 10 3 2	STM_HAW200108	20-Jan	1	M	157	N	NPO	F
LL6949 12 3 15	STM_HAW200109	20-Jan	1	M	148	N	NPO	F
LL6949 13 2 2	STM_HAW200110	20-Jan	1	M	147	N	OCEANIA	F
LL6975 1 0 53	STM_HAW200111	20-Jan	2	F	105	N	%	F
LL6975 1 0 57	STM_HAW200112	20-Jan	2	M	110	N	NPO	F
LL6975 1 0 61	STM_HAW200113	20-Jan	2	F	148	N	NPO	F
LL6975 2 0 1	STM_HAW200114	20-Jan	2	F	144	N	NPO	F
LL6975 2 0 63	STM_HAW200115	20-Jan	2	M	145	N	NPO	F
LL6975 3 0 2	STM_HAW200116	20-Jan	2	F	115	N	NPO	F
LL6975 3 0 10	STM_HAW200117	20-Jan	2	M	140	N	OCEANIA	F
LL6975 3 0 39	STM_HAW200118	20-Jan	2	F	147	N	OCEANIA	F
LL6975 4 0 4	STM_HAW200119	20-Jan	2	M	106	N	NPO	F
LL6975 4 0 20	STM_HAW200120	20-Jan	2	M	116	N	NPO	F
LL6975 4 0 22	STM_HAW200121	20-Jan	2	M	109	N	NPO	F
LL6975 4 0 37	STM_HAW200122	20-Jan	2	U	150	U	OCEANIA	F
LL6975 4 0 59	STM_HAW200123	20-Jan	2	M	120	N	NPO	F
LL6975 5 0 5	STM_HAW200124	20-Jan	2	M	159	U	-	F
LL6975 5 0 19	STM_HAW200125	20-Jan	2	M	110	N	NPO	F
LL6975 5 0 20	STM_HAW200126	20-Jan	2	M	135	N	NPO	F
LL6975 5 0 42	STM_HAW200127	20-Jan	2	F	145	N	%	F
LL6975 5 0 45	STM_HAW200128	20-Jan	1	M	131	N	NPO	F
LL6988 3 0 6	STM_HAW200129	20-Jan	4	M	112	N	NPO	F
LL6988 3 0 7	STM_HAW200130	20-Jan	4	M	111	N	NPO	F
LL6988 3 0 14	STM_HAW200131	20-Jan	4	F	147	N	NPO	F
LL6988 6 0 4	STM_HAW200201	20-Feb	4	F	144	N	NPO	F
LL6988 11 0 63	STM_HAW200202	20-Feb	3	F	115	N	NPO	F
LL6988 12 0 41	STM_HAW200203	20-Feb	4	M	125	N	NPO	F

LL6988 12 0 46	STM_HAW200204	20-Feb	4	F	110	N	%	F
LL6988 13 0 82	STM_HAW200205	20-Feb	4	F	144	N	%	F
LL6993 2 0 24	STM_HAW200206	20-Feb	4	F	157	N	OCEANIA	F
LL6993 4 0 17	STM_HAW200207	20-Feb	4	F	140	N	%	F
LL6993 9 0 1	STM_HAW200208	20-Feb	4	F	132	N	NPO	F
LL6993 13 0 11	STM_HAW200209	20-Feb	4	F	151	N	OCEANIA	F
LL6996 2 0 12	STM_HAW200210	20-Feb	2	M	111	N	NPO	F
LL6996 3 0 35	STM_HAW200211	20-Feb	2	F	146	N	NPO	F
LL6996 3 0 46	STM_HAW200212	20-Feb	2	F	118	N	NPO	F
LL6996 3 0 64	STM_HAW200213	20-Feb	2	M	136	N	OCEANIA	F
LL6996 6 0 28	STM_HAW200214	20-Feb	2	F	157	N	NPO	F
LL6996 8 0 5	STM_HAW200215	20-Feb	2	M	151	N	NPO	F
LL6996 8 0 25	STM_HAW200216	20-Feb	2	M	109	N	NPO	F
LL6996 8 0 53	STM_HAW200217	20-Feb	2	F	106	N	NPO	F
LL7010 3 0 26	STM_HAW200218	20-Feb	4	M	149	N	NPO	F
LL7010 3 0 41	STM_HAW200219	20-Feb	4	M	126	N	NPO	F
LL7010 4 0 17	STM_HAW200220	20-Feb	4	M	133	N	OCEANIA	F
LL7010 5 0 25	STM_HAW200221	20-Feb	4	M	152	N	NPO	F
LL7010 5 0 33	STM_HAW200222	20-Feb	4	M	138	Y	NPO	F
LL7010 5 0 36	STM_HAW200223	20-Feb	4	M	132	N	OCEANIA	F
LL7010 5 0 40	STM_HAW200224	20-Feb	4	F	142	N	NPO	F
LL7010 5 0 45	STM_HAW200225	20-Feb	4	F	143	N	NPO	F
LL7010 6 0 31	STM_HAW200226	20-Feb	4	M	119	N	NPO	F
LL7010 6 0 44	STM_HAW200227	20-Feb	4	M	152	N	NPO	F
LL7010 6 0 55	STM_HAW200228	20-Feb	4	F	114	N	OCEANIA	F
LL7010 6 0 61	STM_HAW200229	20-Feb	4	U	114	U	NPO	F
LL7010 7 0 2	STM_HAW200230	20-Feb	4	M	152	N	NPO	F
LL7010 7 0 29	STM_HAW200231	20-Feb	4	F	114	N	%	F

LL7010 7 0 30	STM_HAW200232	20-Feb	4	F	120	N	NPO	F
LL7010 8 0 14	STM_HAW200233	20-Feb	4	M	116	N	NPO	F
LL7010 8 0 36	STM_HAW200234	20-Feb	4	F	122	N	NPO	F
LL7010 8 0 44	STM_HAW200235	20-Feb	4	F	122	N	NPO	F
LL7010 8 0 56	STM_HAW200236	20-Feb	4	M	107	N	NPO	F
LL7010 8 0 58	STM_HAW200237	20-Feb	4	M	132	N	NPO	F
LL7010 8 0 64	STM_HAW200238	20-Feb	4	F	119	N	NPO	F
LL7010 8 0 72	STM_HAW200239	20-Feb	4	F	126	N	NPO	F
LL7010 9 0 45	STM_HAW200240	20-Feb	4	F	123	U	NPO	F
LL7010 9 0 67	STM_HAW200241	20-Feb	4	F	117	N	NPO	F
LL7010 10 0 2	STM_HAW200242	20-Feb	4	M	147	N	NPO	F
LL7010 11 0 6	STM_HAW200243	20-Feb	4	F	113	N	NPO	F
LL7010 12 0 9	STM_HAW200244	20-Feb	4	M	117	N	NPO	F
LL7010 12 0 23	STM_HAW200245	20-Feb	4	F	183	N	OCEANIA	F
LL7063 3 0 27	STM_HAW200601	20-Jun	2	F	151	N	NPO	F
LL7063 5 0 9	STM_HAW200602	20-Jun	2	F	175	N	NPO	F
LL7063 5 0 17	STM_HAW200603	20-Jun	2	F	143	N	%	F
LL7063 5 0 24	STM_HAW200604	20-Jun	2	M	147	N	NPO	F
LL7063 5 0 48	STM_HAW200605	20-Jun	2	F	151	Y	NPO	F
LL7063 6 0 13	STM_HAW200606	20-Jun	2	F	163	N	NPO	F
LL7063 8 0 13	STM_HAW200607	20-Jun	1	F	145	N	NPO	F
LL7063 11 0 35	STM_HAW200608	20-Jun	1	F	154	N	NPO	F
LL7063 11 0 46	STM_HAW200609	20-Jun	1	M	151	N	NPO	F
LL7063 14 0 25	STM_HAW200610	20-Jun	1	F	169	N	NPO	F
LL7063 15 0 4	STM_HAW200611	20-Jun	1	F	141	N	NPO	F
LL7067 3 0 2	STM_HAW200612	20-Jun	4	M	164	N	NPO	F
LL7067 3 0 7	STM_HAW200613	20-Jun	4	M	164	N	NPO	F
LL7067 8 0 5	STM_HAW200614	20-Jun	4	M	171	N	NPO	F

LL7067 8 0 13	STM_HAW200615	20-Jun	4	U	125	U	OCEANIA	F
LL7067 9 0 8	STM_HAW200616	20-Jun	4	M	161	N	NPO	F
LL7067 10 0 12	STM_HAW200617	20-Jun	4	U	155	Y	NPO	F
LL7067 11 0 8	STM_HAW200618	20-Jun	4	M	148	N	NPO	F
LL7067 11 0 10	STM_HAW200619	20-Jun	4	M	130	N	OCEANIA	F
LL7067 11 0 21	STM_HAW200620	20-Jun	4	F	178	N	NPO	F
LL7068 1 0 7	STM_HAW200621	20-Jun	2	M	140	N	%	F
LL7068 1 0 18	STM_HAW200622	20-Jun	2	M	164	N	NPO	F
LL7068 4 0 18	STM_HAW200623	20-Jun	2	M	144	Y	NPO	F
LL7074 4 0 47	STM_HAW200624	20-Jun	2	F	148	N	NPO	F
LL7074 8 0 20	STM_HAW200625	20-Jun	2	F	156	N	NPO	F
LL7076 1 0 5	STM_HAW200626	20-Jun	3	U	138	U	NPO	F
LL7076 1 0 26	STM_HAW200627	20-Jun	3	U	150	U	NPO	F
LL7077 1 0 11	STM_HAW200628	20-Jun	4	M	159	N	OCEANIA	F
LL7077 2 0 13	STM_HAW200629	20-Jun	4	F	162	N	NPO	F
LL7077 7 0 6	STM_HAW200630	20-Jun	1	M	133	N	NPO	F
LL7077 8 0 20	STM_HAW200631	20-Jun	1	M	149	N	NPO	F
LL7079 10 0 44	STM_HAW200632	20-Jun	4	M	163	N	OCEANIA	F
LL7079 10 0 49	STM_HAW200633	20-Jun	4	F	226	N	NPO	F
LL7079 11 0 23	STM_HAW200634	20-Jun	4	M	226	N	NPO	F
LL7079 11 0 24	STM_HAW200635	20-Jun	4	M	260	Y	NPO	F
LL7079 11 0 35	STM_HAW200636	20-Jun	4	M	165	N	OCEANIA	F
LL7079 11 0 70	STM_HAW200637	20-Jun	4	F	165	Y	NPO	F
LL7081 4 0 14	STM_HAW200638	20-Jun	3	F	167	N	OCEANIA	F
LL7067 14 0 4	STM_HAW200701	20-Jul	4	M	160	N	NPO	F
LL7067 14 0 11	STM_HAW200702	20-Jul	4	U	158	N	%	F
LL7067 14 0 15	STM_HAW200703	20-Jul	4	M	185	N	NPO	F
LL7067 14 0 25	STM_HAW200704	20-Jul	4	F	118	N	OCEANIA	F

LL7067 17 0 3	STM_HAW200705	20-Jul	4	M	160	N	NPO	F
LL7067 17 0 13	STM_HAW200706	20-Jul	4	M	168	N	NPO	F
LL7067 17 0 34	STM_HAW200707	20-Jul	4	M	166	N	NPO	F
LL7081 7 0 16	STM_HAW200708	20-Jul	4	F	169	N	OCEANIA	F
LL7081 15 0 17	STM_HAW200709	20-Jul	4	F	165	Y	NPO	F
LL7094 3 0 17	STM_HAW200710	20-Jul	4	U	119	U	OCEANIA	F
LL7094 4 0 6	STM_HAW200711	20-Jul	4	M	126	N	OCEANIA	F
LL7094 4 0 7	STM_HAW200712	20-Jul	4	M	126	N	OCEANIA	F
LL7094 5 0 31	STM_HAW200713	20-Jul	4	F	128	N	OCEANIA	F
LL7094 5 0 32	STM_HAW200714	20-Jul	4	M	127	Y	OCEANIA	F
LL7094 8 0 20	STM_HAW200715	20-Jul	4	M	131	N	OCEANIA	F
LL7094 9 0 16	STM_HAW200716	20-Jul	4	F	145	N	OCEANIA	F
LL7094 9 0 34	STM_HAW200717	20-Jul	4	M	121	N	OCEANIA	F
LL7094 9 0 35	STM_HAW200718	20-Jul	4	M	128	N	OCEANIA	F
LL7094 13 0 27	STM_HAW200719	20-Jul	4	M	121	N	OCEANIA	F
LL7094 14 0 8	STM_HAW200720	20-Jul	4	F	173	N	NPO	F
LL7099 9 0 48	STM_HAW200721	20-Jul	4	U	135	U	OCEANIA	F
LL7099 9 0 50	STM_HAW200722	20-Jul	4	U	134	U	OCEANIA	F
LL7108 15 3 34	STM_HAW200801	20-Aug	2	F	135	U	OCEANIA	F
LL7108 15 3 35	STM_HAW200802	20-Aug	2	F	134	U	OCEANIA	F
LL7108 16 0 7	STM_HAW200803	20-Aug	1	F	144	N	OCEANIA	F
LL7108 16 0 8	STM_HAW200804	20-Aug	1	M	134	N	OCEANIA	F
LL7108 16 0 28	STM_HAW200805	20-Aug	1	F	130	U	OCEANIA	F
LL7108 16 0 29	STM_HAW200806	20-Aug	1	F	130	U	OCEANIA	F
LL7108 16 0 33	STM_HAW200807	20-Aug	1	M	128	N	OCEANIA	F
LL7108 16 0 57	STM_HAW200808	20-Aug	1	M	153	N	-	F
LL7134 1 0 78	STM_HAW200809	20-Aug	2	U	128	N	-	F
LL7134 2 0 16	STM_HAW200810	20-Aug	2	F	120	N	%	F

LL7134 2 0 25	STM_HAW200811	20-Aug	2	F	131	N	OCEANIA	F
LL7134 2 0 26	STM_HAW200812	20-Aug	2	F	125	N	OCEANIA	F
LL7130 2 0 6	STM_HAW200901	20-Sep	1	M	151	N	NPO	F
LL7130 5 0 27	STM_HAW200902	20-Sep	1	U	0	Y	NPO	F
LL7130 7 0 7	STM_HAW200903	20-Sep	1	F	144	N	OCEANIA	F
LL7130 7 0 8	STM_HAW200904	20-Sep	1	F	146	N	OCEANIA	F
LL7130 7 0 81	STM_HAW200905	20-Sep	1	U	0	N	NPO	F
LL7130 8 0 2	STM_HAW200906	20-Sep	1	F	138	N	OCEANIA	F
LL7130 9 0 95	STM_HAW200907	20-Sep	1	F	136	N	NPO	F
LL7130 10 0 38	STM_HAW200908	20-Sep	1	F	131	N	NPO	F
LL7130 10 0 39	STM_HAW200909	20-Sep	1	F	132	N	OCEANIA	F
LL7130 10 0 74	STM_HAW200910	20-Sep	1	F	171	N	OCEANIA	F
LL7130 11 0 34	STM_HAW200911	20-Sep	1	F	139	N	OCEANIA	F
LL7130 11 0 71	STM_HAW200912	20-Sep	1	U	140	U	OCEANIA	F
LL7130 12 0 24	STM_HAW200913	20-Sep	1	F	135	N	%	F
LL7130 12 0 28	STM_HAW200914	20-Sep	1	F	143	N	-	F
LL7130 12 0 85	STM_HAW200915	20-Sep	1	M	133	N	%	F
LL7130 13 0 35	STM_HAW200916	20-Sep	1	M	133	N	OCEANIA	F
LL7130 13 0 36	STM_HAW200917	20-Sep	1	F	143	N	OCEANIA	F
LL7130 13 0 37	STM_HAW200918	20-Sep	1	M	136	N	OCEANIA	F
LL7130 13 0 90	STM_HAW200919	20-Sep	1	M	141	N	OCEANIA	F
LL7130 14 0 61	STM_HAW200920	20-Sep	1	F	136	N	OCEANIA	F
LL7130 14 0 66	STM_HAW200921	20-Sep	1	F	147	N	OCEANIA	F
LL7130 15 0 7	STM_HAW200922	20-Sep	1	M	140	N	-	F
LL7130 15 0 11	STM_HAW200923	20-Sep	1	F	151	N	NPO	F
LL7130 15 0 29	STM_HAW200924	20-Sep	1	F	144	N	NPO	F
LL7130 15 0 42	STM_HAW200925	20-Sep	1	F	129	N	OCEANIA	F
LL7130 16 0 65	STM_HAW200926	20-Sep	1	F	132	N	OCEANIA	F

LL7130 16 0 72	STM_HAW200927	20-Sep	1	F	137	N	OCEANIA	F
LL7130 16 0 73	STM_HAW200928	20-Sep	1	U	138	N	OCEANIA	F
LL7134 3 0 6	STM_HAW200929	20-Sep	2	F	136	N	OCEANIA	F
LL7134 4 0 26	STM_HAW200930	20-Sep	1	U	127	U	OCEANIA	F
LL7134 4 0 55	STM_HAW200931	20-Sep	1	F	131	N	OCEANIA	F
LL7134 5 0 10	STM_HAW200932	20-Sep	1	U	134	U	OCEANIA	F
LL7134 6 0 29	STM_HAW200933	20-Sep	1	F	130	N	OCEANIA	F
LL7134 7 0 88	STM_HAW200934	20-Sep	1	U	130	N	OCEANIA	F
LL7134 8 0 16	STM_HAW200935	20-Sep	2	F	125	N	OCEANIA	F
LL7134 9 0 28	STM_HAW200936	20-Sep	2	F	140	Y	NPO	F
LL7140 3 1 1	STM_HAW200937	20-Sep	1	M	127	N	OCEANIA	F
LL7140 3 1 2	STM_HAW200938	20-Sep	1	F	130	N	OCEANIA	F
LL7140 5 4 53	STM_HAW200939	20-Sep	1	U	91	N	NPO	F
LL7140 6 1 2	STM_HAW200940	20-Sep	1	M	145	N	OCEANIA	F
LL7140 7 1 14	STM_HAW200941	20-Sep	1	F	140	N	OCEANIA	F
LL7140 7 2 23	STM_HAW200942	20-Sep	1	M	126	N	OCEANIA	F
LL7140 7 2 24	STM_HAW200943	20-Sep	1	M	132	N	OCEANIA	F
LL7140 8 2 24	STM_HAW200944	20-Sep	2	F	128	N	OCEANIA	F
LL7140 10 8 117	STM_HAW200945	20-Sep	2	F	132	N	OCEANIA	F
LL7141 12 0 2	STM_HAW200946	20-Sep	3	M	136	U	OCEANIA	F
LL7141 14 0 28	STM_HAW200947	20-Sep	3	M	141	U	OCEANIA	F
LL7141 15 0 20	STM_HAW200948	20-Sep	3	F	130	N	OCEANIA	F
LL7144 1 0 16	STM_HAW200949	20-Sep	2	F	139	N	OCEANIA	F
LL7144 1 0 46	STM_HAW200950	20-Sep	2	M	132	N	%	F
LL7144 1 0 54	STM_HAW200951	20-Sep	2	F	132	N	OCEANIA	F
LL7144 2 0 19	STM_HAW200952	20-Sep	2	F	143	N	%	F
LL7144 2 0 22	STM_HAW200953	20-Sep	2	F	139	N	OCEANIA	F
LL7144 4 0 49	STM_HAW200954	20-Sep	2	U	129	N	OCEANIA	F

LL7144 4 0 61	STM_HAW200955	20-Sep	2	F	139	N	OCEANIA	F
LL7144 4 0 62	STM_HAW200956	20-Sep	2	U	0	N	-	F
LL7144 5 0 55	STM_HAW200957	20-Sep	2	M	132	N	OCEANIA	F
LL7144 5 0 81	STM_HAW200958	20-Sep	2	M	135	N	OCEANIA	F
LL7144 6 0 18	STM_HAW200959	20-Sep	2	M	127	N	OCEANIA	F
LL7144 6 0 26	STM_HAW200960	20-Sep	2	M	133	N	OCEANIA	F
LL7144 7 0 4	STM_HAW200961	20-Sep	1	F	140	N	OCEANIA	F
LL7144 7 0 5	STM_HAW200962	20-Sep	1	F	129	N	OCEANIA	F
LL7144 7 0 19	STM_HAW200963	20-Sep	1	F	129	N	OCEANIA	F
LL7144 7 0 20	STM_HAW200964	20-Sep	1	F	128	N	OCEANIA	F
LL7144 7 0 24	STM_HAW200965	20-Sep	1	M	135	N	OCEANIA	F
LL7144 7 0 29	STM_HAW200966	20-Sep	1	F	116	N	%	F
LL7144 7 0 49	STM_HAW200967	20-Sep	1	M	139	N	%	F
LL7144 7 0 60	STM_HAW200968	20-Sep	1	M	130	N	OCEANIA	F
LL7144 7 0 61	STM_HAW200969	20-Sep	1	F	143	N	OCEANIA	F
LL7144 7 0 66	STM_HAW200970	20-Sep	1	F	125	N	OCEANIA	F
LL7144 7 0 70	STM_HAW200971	20-Sep	1	F	128	N	OCEANIA	F
LL7144 7 0 72	STM_HAW200972	20-Sep	1	M	133	U	OCEANIA	F
LL7144 7 0 73	STM_HAW200973	20-Sep	1	M	136	U	OCEANIA	F
LL7146 2 0 44	STM_HAW200974	20-Sep	4	M	141	N	OCEANIA	F
LL7146 4 0 59	STM_HAW200975	20-Sep	4	U	130	N	OCEANIA	F
LL7146 11 0 20	STM_HAW200976	20-Sep	2	M	145	N	OCEANIA	F
LL7146 11 0 34	STM_HAW200977	20-Sep	2	F	128	N	OCEANIA	F
LL7146 12 0 4	STM_HAW200978	20-Sep	2	M	128	N	OCEANIA	F
LL7146 13 0 17	STM_HAW200979	20-Sep	2	F	135	N	OCEANIA	F
LL7148 9 0 49	STM_HAW200980	20-Sep	1	M	147	U	OCEANIA	F
LL7153 1 0 52	STM_HAW200981	20-Sep	3	M	140	N	OCEANIA	F
LL7153 3 0 19	STM_HAW200982	20-Sep	3	F	149	N	OCEANIA	F

LL7153 4 0 6	STM_HAW200983	20-Sep	1	M	137	N	OCEANIA	F
LL7153 4 0 12	STM_HAW200984	20-Sep	1	F	141	N	OCEANIA	F
LL7153 4 0 30	STM_HAW200985	20-Sep	1	M	138	N	OCEANIA	F
LL7153 4 0 42	STM_HAW200986	20-Sep	1	M	129	N	OCEANIA	F
LL7153 4 0 49	STM_HAW200987	20-Sep	1	F	144	N	OCEANIA	F
LL7153 4 0 51	STM_HAW200988	20-Sep	1	M	127	N	OCEANIA	F
LL7153 4 0 79	STM_HAW200989	20-Sep	1	F	130	N	OCEANIA	F
LL7153 5 0 14	STM_HAW200990	20-Sep	1	F	133	U	OCEANIA	F
LL7153 5 0 31	STM_HAW200991	20-Sep	1	F	136	N	OCEANIA	F
LL7153 7 0 94	STM_HAW200992	20-Sep	1	M	131	N	OCEANIA	F
LL7155 2 0 40	STM_HAW200993	20-Sep	1	M	131	N	OCEANIA	F
LL7155 5 0 11	STM_HAW200994	20-Sep	1	F	140	N	OCEANIA	F
LL7155 6 0 23	STM_HAW200995	20-Sep	1	F	145	Y	%	F
LL7148 12 0 42	STM_HAW201001	20-Oct	1	M	138	U	OCEANIA	F
LL7148 14 0 55	STM_HAW201002	20-Oct	1	M	138	U	OCEANIA	F
LL7148 15 0 13	STM_HAW201003	20-Oct	1	F	97	U	NPO	F
LL7155 7 0 10	STM_HAW201004	20-Oct	1	F	142	N	OCEANIA	F
LL7155 7 0 12	STM_HAW201005	20-Oct	1	M	150	N	NPO	F
LL7155 13 0 8	STM_HAW201006	20-Oct	1	M	129	N	OCEANIA	F
LL7155 14 0 36	STM_HAW201007	20-Oct	1	F	126	N	OCEANIA	F
LL7155 17 0 17	STM_HAW201008	20-Oct	1	F	146	N	OCEANIA	F
LL7155 17 0 22	STM_HAW201009	20-Oct	1	F	139	N	%	F
LL7156 3 0 7	STM_HAW201010	20-Oct	4	F	145	N	OCEANIA	F
LL7156 5 0 37	STM_HAW201011	20-Oct	4	F	146	N	OCEANIA	F
LL7156 13 0 37	STM_HAW201012	20-Oct	2	F	132	N	OCEANIA	F
LL7156 13 0 44	STM_HAW201013	20-Oct	2	F	137	N	OCEANIA	F
LL7156 14 0 27	STM_HAW201014	20-Oct	2	F	132	N	OCEANIA	F
LL7156 14 0 28	STM_HAW201015	20-Oct	2	M	143	N	OCEANIA	F

LL7156 14 0 40	STM_HAW201016	20-Oct	2	M	140	N	OCEANIA	F
LL7156 15 0 32	STM_HAW201017	20-Oct	2	M	139	Y	OCEANIA	F
LL7168 7 0 17	STM_HAW201018	20-Oct	2	U	143	U	OCEANIA	F
LL7168 8 0 20	STM_HAW201019	20-Oct	2	F	134	U	OCEANIA	F

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