Description of a new deep-water dogfish shark from Hawaii, with comments on the *Squalus mitsukurii* species complex in the West Pacific

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Abstract

Dogfish sharks of the genus *Squalus* are small, deep-water sharks with a slow rate of molecular evolution that has led to their designation as a series of species complexes, with low between-species diversity relative to other taxa. The largest of these complexes is named for the Shortspine spurdog (*Squalus mitsukurii* Jordan & Snyder), a medium-sized dogfish shark common to warm upper slope and seamount habitats, with a putative circumglobal distribution that has come under investigation recently due to geographic variation in morphology and genetic diversity. The Hawaiian population of *Squalus mitsukurii* was examined using both morphological and molecular analyses, putting this group in an evolutionary context with animals from the type population in Japan and closely-related congeners. External morphology differs significantly between the Hawaiian and Japanese *S. mitsukurii*, especially in dorsal fin size and relative interdorsal length, and molecular analysis of 1,311 base pairs of the mitochondrial genes ND2 and COI show significant, species-level divergence on par with other taxonomic studies of this genus. The dogfish shark in Hawaii represents a new species in the genus, and the name *Squalus hawaiiensis*, the Hawaiian spurdog, is designated after the type location.

Keywords

Chondrichthyes, DNA barcoding, Elasmobranchii, morphology, *Squalus hawaiiensis*, taxonomy
Introduction

Deep-water sharks like the dogfish sharks (Squaliformes, Squalidae) and the gulper sharks (Squaliformes, Centrophoridae) have proven confounding groups for systematists to resolve due to their highly conserved morphology, wide ranges, and patchy, infrequently-sampled distributions (Veríssimo et al. 2014; Cotton and Grubbs 2015; Veríssimo et al. 2017; Daly-Engel et al. submitted). Recent years have shown that DNA sequencing in conjunction with morphological analyses is an effective approach for elucidating the alpha taxonomy of deep-water sharks (Avise 2004; Ward et al. 2005; Last et al. 2007c; Ebert et al. 2010; Veríssimo et al. 2014; Pfleger et al. 2018). Findings from several studies have shown a mix of low genetic distances between well-established morphological species, and deep genetic splits between animals identified as conspecifics (Daly-Engel et al. 2010; Veríssimo et al. 2017; Daly-Engel et al. 2018; Pfleger et al. 2018; Daly-Engel et al. submitted).

Taxonomic delineation that incorporates DNA analysis has often relied upon consistencies among within- and between-species divergences in the barcoding gene (COI), as measured by percent nucleotide sequence variation (Avise 2004; Ward et al. 2005; Naylor et al. 2012). DNA barcoding is an effective, widely-used molecular method among taxonomists because the cytochrome oxidase I gene (COI) records a low rate of mutation compared with other loci (Avise 2004; Ward et al. 2005). While a reliable metric among distantly-related groups in which mutations accumulate consistently, COI may fail to elucidate shallow divergences among taxa with low genetic diversity. Complicating identification issues is the fact that deep-water sharks, whose cold environment results in low metabolic rates relative to other elasmobranchs, may undergo an overall slower rate of molecular evolution compared with shallow coastal species (Martin et al. 1992; Martin and Palumbi 1993). As a result, a number of investigators have found the more-rapidly evolving ND2 gene to be an effective genetic marker for estimating both inter- and intraspecific variation in dogfish sharks (Veríssimo et al. 2010; Naylor et al. 2012; Veríssimo et al. 2017; Pfleger et al. 2018).

Much work among shark systematists has focused on clarifying species delineations in dogfishes of the genus *Squalus*, an abundant, speciose, globally-distributed group of morphologically-similar, small-bodied demersal sharks that primarily inhabit circum-global shelf and slope habitats from 100 - 1000 m depth (Compagno et al. 2005; Last et al. 2007c). Within this genus, genetic and morphological examinations have revealed a series of species complexes characterized by relatively shallow evolutionary divergences among putative species (Last et al. 2007c; Gaither et al. 2016; Veríssimo et al. 2017). Such complexes are not unusual in nature, having been observed across a variety of phyla from insects (Perring 2001) and nematodes (Chilton et al. 1995) to bony fishes (Barluenga and Meyer 2004), and have been shown to harbor “cryptic” diversity not always apparent from morphology alone (Daly-Engel et al. Submitted). Taxonomic reevaluation of *Squalus* in the Indo-Pacific and elsewhere has revealed many undescribed species that were historically lumped together under a single name (Ward et al. 2007; Naylor et al. 2012; Viana et al. 2016; Pfleger et al. 2018): although the relatively shallow spiny dogfish *Squalus acanthias* Linnaeus comprises just one wide-ranging species apart from the North
Pacific (Ebert et al. 2010; Veríssimo et al. 2010), we now know that both the Shortspine dogfish shark *Squalus mitsukurii* Jordan & Snyder and the shortnose dogfish shark *Squalus megalops* Macleay comprise global species complexes (Veríssimo et al. 2010; Naylor et al. 2012; Veríssimo et al. 2017; Pfleger et al. 2018; Daly-Engel et al. Submitted).

Recent taxonomic studies on *Squalus* have focused on *Squalus mitsukurii*, a putative circumglobal species found on continental and insular shelves and upper slopes and on seamounts between 100 and 950 m depth (Compagno et al. 2005). Re-examination of local *S. mitsukurii* stocks has revealed many new species, including four from the West Pacific alone: *S. formosus* White & Iglesias (2011), *S. chloroculus* Last, White, & Motomura (Last et al. 2007b), *S. montalbani* Whitley (Last et al. 2007b), and *S. griffini* Phillips (Duffy and Last 2007). Other revisions of *S. mitsukurii* have been done in the Atlantic using either genetic tools or morphological characters (Viana et al. 2016; Veríssimo et al. 2017), though not both (but see Pfleger et al. 2018).

Along the Hawaiian Archipelago in the Central Pacific, the Shortspine spurdog (*Squalus cf. mitsukurii*) is the only *Squalus* species known, aggregating in large numbers on or near the bottom at a depth of 100–950 m (Wilson and Seki 1994). Observable differences between specimens of *S. mitsukurii* in Hawaii and its conspecifics from the West Pacific first came to light during a genetic study (Daly-Engel et al. 2010), and subsequent research showed that growth (L∞, k) and reproductive parameters (size-at-maturity) for *Squalus cf. mitsukurii* in Hawaii differed from published data (putatively as *S. mitsukurii*) from other regions (Cotton et al. 2011). Together with the relative geographic isolation of the Hawaiian Islands and the high levels of endemism observed there [25% of fish species in Hawaii are endemic, the most in the Indo-Pacific region (Roberts et al. 2002; Randall 2007; Briggs and Bowen 2011)] make this population a likely candidate for redescription.

We undertook a taxonomic evaluation of *Squalus mitsukurii* from the Hawaiian Islands using molecular and morphological data, couching these in the evolutionary context of closely-related, previously-recognized congeners from the West Pacific. DNA barcoding with COI can discriminate among species in the genus *Squalus* (Ward et al. 2007), but low resolution in this marker may fail to identify cryptic diversity. We therefore supplemented DNA sequences derived from the COI barcoding gene with data from ND2, a faster-evolving mitochondrial gene with the potential to distinguish evolutionary relationships with a high degree of resolution (Avise 2004; Naylor et al. 2012). In addition, morphological and meristic comparisons were made comparing *S. cf. mitsukurii* from Hawaii with measurements taken from the Japanese holotype, and reported by Last et al. (2007c) and in Viana et al. (2016).

**Materials and methods**

**Tissue collections**

Whole specimens and genetic samples of *Squalus cf. mitsukurii* were collected primarily during longline surveys conducted on the insular slope around the Hawaiian Island of Oahu. Survey methods are described in Daly-Engel et al. (2010) and Cotton et al.
(2011). Additional specimens and samples were collected from bottom fish surveys from Maui to Lisianski Atoll, spanning nearly 2,000 km of the Hawaiian Archipelago. Because the 2010 genetic study showed extremely low diversity, we deemed 5–10 specimens adequate for taxonomic evaluation, a number on par with other revisions in this genus (Ward et al. 2007; Pfleger et al. 2018). To that end, five whole mature females and three whole mature male _S. cf. mitsukurii_ from Oahu were retained as voucher specimens for morphometric and genetic analyses. Small (< 1 cm³) samples of fin or muscle tissue were taken using scissors and stored in 2 mL vials containing 1.5 mL 20% dimethylsulfoxide (DMSO) saturated salt (NaCl) buffer (Seutin et al. 1991) or >70% ethanol (EtOH).

Genetic examination of 130 tissue samples from 25–30 _Squalus_ dogfish species has shown that _S. cf. mitsukurii_ from Hawaii clustered closely with _S. nasutus_ Last, Marshall, & White from Australia, _S. japonicus_ Ishikawa from Japan and elsewhere, and _S. mitsukurii_ from Japan (Daly-Engel et al. Submitted), and well apart from other congeners in the region; hence the current analysis focuses on these species. Because it is impossible to extract undamaged DNA from the formalin-fixed _S. mitsukurii_ holotype, we referenced DNA extracted from two specimens identified as _S. mitsukurii_ by expert Japanese systematist Dr. Sho Tanaka (Tanaka et al. 1975; Yano and Tanaka 1984; Yano et al. 2017) collected from Suruga Bay in mainland Japan, which is approximately 100 kilometers from the type locality of Misaki. Tissue samples of _S. nasutus_ (N = 2) and _S. japonicus_ (N = 8) were obtained from Australia and Japan (Appendix 1).

**Genetic analysis**

DNA was extracted from fin clips using a DNeasy Blood & Tissue Kit from Qiagen (Germantown, MD). Primers were obtained from Integrated DNA Technologies, Inc. (Coralville, Iowa). PCR reactions consisting of 7 μL BioMix Red from Bioline (London, UK) at the recommended concentration, 1 μL (3 μg) template DNA, and 1 μL (1.0 μM) each primer (10 μL total PCR volume). PCR amplification on a C1000 Touch Thermal Cycler (Bio-Rad; Hercules, California) consisted of an initial denaturation at 95 °C for 4 minutes followed by 36 cycles of 1 min at 95 °C, followed by 30s at 58 °C, and 30s at 72 °C with a final extension at 72 °C for 20 minutes. DNA from two mitochondrial genes were sequenced for a total of 1,131 base pairs (bp; Table 1): Cytochrome Oxidase I (COI; 602 bp), and NADH dehydrogenase 2 (ND2; 529 bp). COI primers were standard barcoding primers by Folmer et al. (1994), and NADH 2 primers that were utilized were designed by Veríssimo et al. (2010; Table 1). PCR products were cleaned with ExoFAP (Thermo Fisher Scientific, Waltham, Massachusetts) and sequenced on an Applied Biosystems 3730XL DNA Analyzer at the University of Arizona Genetics Core.

DNA sequences were trimmed in Geneious v9.1.4 (Kearse et al. 2012) and aligned using Mafft (Katoh et al. 2002) implemented in Geneious. MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) was used to construct Bayesian inference phylogenetic trees: first, analyses of Markov Chain Monte Carlo (MCMC) chains were run for 10,000,000 generations while sampling one tree per 100
Figure 1. Phylogenetic tree of concatenated ND2 and COI sequences. Bayesian phylogenetic tree of concatenated mitochondrial ND2 and COI sequences for *Squalus* species used in this study, which was concordant with maximum likelihood methods. Numbers at nodes represent maximum likelihood bootstrap support/Bayesian posterior probability.

Morphometrics and meristics

Morphological measurements were used to discriminate between Japanese *S. mitsukurii*, including the holotype as measured by Last et al. (2007c) and Viana et al. (2016), and *S. cf. mitsukurii* collected from Hawaii. Measurements were performed on fresh
specimens in accordance with conventional techniques used for sharks (Compagno 1984), including taxon-specific adaptations (e.g. fin spine measurements) used in recent publications (Last et al. 2007c; Veríssimo et al. 2014). A suite of 82 morphological and meristic measurements were recorded for eight specimens. Measurements were taken by two readers for each individual, and the average measurement between the two readers is reported for three specimens to be designated as a holotype and two paratypes, along with the minimum and maximum values measured across the five remaining specimens. Vertebral meristic data were obtained for six specimens, including the three type specimens, using X-radiographs conducted at the Shepherd Spring Animal Hospital in Crawfordville, Florida. Dermal denticles from a male specimen (72.5 cm TL) were imaged by the Florida State University’s Biological Science Imaging Resource (BSIR) using a scanning electron microscope with Everhart-Thornley Detector (SEM ETD; FEI Nova 400 NanoSEM; BAL-TEC CPD030 Critical Point Dryer) at 15 kV, with a spot size of 3 at magnifications of 195–800×.

**Results**

**Genetic analyses**

Mitochondrial DNA sampled from four conspecific shark taxa in the genus *Squalus* from the Central and West Pacific (*S. mitsukurii, S. nasutus, S. japonicus,* and *S. hawaiiensis* sp. n.)

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**Table 1.** Details and diversities of genetic loci amplified in *Squalus hawaiiensis* sp. n. Abbreviations: COI = Cytochrome oxidase I; ND2 = ND2 dehydrogenase 2; N = number of individual specimens included in the analysis; T_a = annealing temperature; π = nucleotide diversity; S = segregating sites; I = informative sites; H = number of haplotypes; h = haplotype diversity.

| Gene | F primer | R primer | # bp | N  | π    | S  | I  | H  | model | Citation       |
|------|----------|----------|------|----|------|----|----|----|-------|----------------|
| COI  | LCO      | HCO      | 602  | 20 | 0.0038 | 8  | 8  | 6  | HKY   | (Folmer et al. 1994) |
| ND2  | ND2F     | ND2R     | 529  | 20 | 0.0069 | 15 | 10 | 9  | TRN   | (Veríssimo et al. 2010) |

**Table 2.** Genetic distances expressed as a percent divergence between *Squalus* species. Lower wedge is average between-species divergence in concatenated ND2 and COI genes; upper wedge is between-species divergence in each gene expressed as ND2/COI. Shaded boxes show within-species variation in concatenated sequences (top) and ND2/COI (bottom).

| S. mitsukurii (N = 2) | S. japonicus | S. hawaiiensis sp nov | S. nasutus |
|-----------------------|--------------|-----------------------|-----------|
| 0.09                  | 1.07/0.30    | 1.01/0.50             | 1.70/0.70 |
| 0.20/0.00             |              |                       |           |
| S. japonicus (N = 8)  |              |                       |           |
| 0.71                  | 0.12         | 0.84/0.50             | 1.07/0.70 |
| 0.13/0.18             |              |                       |           |
| S. hawaiiensis sp nov (N = 8) | 0.73 | 1.90 | 0.00 | 1.01/0.80 |
| 0.00/0.00             |              |                       |           |
| S. nasutus (N = 2)    |              |                       |           |
| 1.15                  | 0.87         | 0.91                  | 0.09      |
| 0.20/0.00             |              |                       |           |
S. cf. *mitsukurii* clustered into four genetically distinct genetic groups with a high degree of confidence using both Maximum Likelihood (89–98% bootstrap support) and Bayesian methodology (1.00 posterior probability), except for *S. japonicus* (80% bootstrap support, 0.80 posterior probability). COI and ND2 trees were concordant, though jModeltest showed slightly different best-fit models of molecular evolution for each (Table 1), and the concatenated tree is shown (Figure 1). As expected, ND2 showed roughly twofold-higher diversity (? = 0.0069) than COI (? = 0.0038), though the evolutionary patterns they describe are similar (Table 1). TCS networks illustrate distinct genetic separation between the four taxa, with some haplotypes being closely related, but none shared (Figure 2).

Among the four species examined here, interspecific divergence across 1,131 bp of concatenated mtDNA ranged from 0.71% between *S. mitsukurii* and *S. japonicus* to 1.90% between *S. japonicus* and *S. cf. mitsukurii* (average = 1.05±0.18%). Average pairwise genetic distance between *S. cf. mitsukurii* and the three named species was 1.18%, greater than the average distance linking named pairs (0.91%). Intraspecific divergence ranged from 0.00% among eight *S. cf. mitsukurii* to 1.12% in the same number of *S. japonicus*. Such lack of diversity is consistent with a 2010 population genetic study of *Squalus* from Hawaii that recovered only eight CO1 haplotypes in 112 individuals, and only five haplotypes in the 91 sharks sampled from Oahu (Daly-Engel et al. 2010).
Haplotype diversity was also low in *S. nasutus* and *S. mitsukurii*, likely because these were represented by just two samples each. Novel DNA sequences have been made publicly available via GenBank (Appendix 1).

*Squalus hawaiiensis* sp. n.
http://zoobank.org/105A6FF0-9FFD-4425-BE9C-85019A911B25

**Diagnosis.** A large species of *Squalus* of the ‘mitsukurii group’ with the following combination of characters: body relatively slender, trunk height 8.7–12.4% TL (mean 10.1% TL, n=8; Figure 3); snout is angular and short to moderate in length, mouth width 1.35–1.60 (1.48) times horizontal prenarial length and pre-oral length is 1.92–2.06 (1.97) times the prenarial length (Figure 4); pre-first dorsal length 30.3–31.5 (30.2)% TL; pre-second dorsal length 63.6–67.0 (65.5)% TL; interdorsal space 26.7–30.0 (28.6)% TL; pelvic-caudal space 25.2–29.3 (27.1)% TL; relatively small, upright dorsal fins; first dorsal fin length 11.4–12.8 (12.2)% TL, height 6.5–7.8 (7.3)% TL, inner margin length 4.9–5.7 (5.4)% TL; second dorsal fin length 10.6–11.7 (11.1)% TL, height 4.0–4.6 (4.4)% TL, inner margin length 4.3–4.9 (4.6)% TL; first dorsal fin spine length 46.6–114.5 (55.6)% of first dorsal fin height; second dorsal spine length 104.5–114.5 (109.0)% of second dorsal fin height; caudal bar triangular, extending from the caudal fork nearly to the anterior edge of the lower caudal, distinct upper caudal blotch and fringe in juveniles, upper caudal blotch diffuse in adults but extending to the posterior margin of the upper caudal fin, upper and lower caudal fins white tipped; flank denticles tricuspid (Figure 5A–C); teeth are similar in appearance in the upper and lower jaw, with numbers ranging from 26–28 in the upper jaw and 23 in the lower jaw; 41–45 monospondylous centra, 85–89 precaudal centra, 112–116 total centra; adult maximum size at least 101 cm TL.

**Description.** Morphometric data are provided in Table 3. *Squalus hawaiiensis* sp. n. is a relatively large dogfish shark with a fusiform body, a relatively short snout, and small dorsal fins. The nape is modestly humped over the pectoral fins, particularly in large females. Head length is 21.4–23.9% TL. The snout is relatively short but angular and relatively pointed in dorsal view, with a pre-narial length that is 49–52% of the pre-oral length and 1.06–1.31 times eye length. Pre-oral length is 2.04–2.42 times the internarial space. Pre-vent length is 50.4–53.6% of the TL. Mouth width is 0.69–0.83 times the pre-oral length. Eye is large (3.9–4.9% of TL) and strongly notched posteriorly. Upper and lower labial furrows pronounced. Upper labial furrow length 1.9–2.5% TL, 24.9–33.0% of mouth width, and 19.3–24.7% of pre-oral length. Inner nostril labial furrow space is 1.89–2.27 times labial furrow length. Pre-first dorsal fin length is 30.3–31.5% of TL, pre-second dorsal space is 63.6–67.0% of TL and the interdorsal space ranges from 26.7% to 30.0% of TL. The first dorsal fin is rounded at the apex. First dorsal fin length measures 1.62–1.81 times first dorsal fin height. First dorsal fin length is 1.02–1.16 times second dorsal fin length and the height of the first dorsal fin is 1.57–1.80 times the height of the second dorsal fin. Second dorsal fin length 2.36–2.79 times the second dorsal fin height. Dorsal fin spines are stout, with the spine on
the second dorsal fin typically longer (4.1–5.0%TL) than the spine on the first dorsal fin (3.6–4.6%TL). First dorsal spine length is 0.39–0.65 (mean: 0.53%) times the first dorsal fin height. Second dorsal spine length is 0.84–1.15 (mean: 1.04%) times the second dorsal fin height. The pectoral fins are well developed with an anterior margin that is 12.8–16.0% of the TL. The pectoral inner margin is 6.4–7.4% of total length and free rear tip is rounded (Figure 6A–C).

*Squalus hawaiiensis* is morphologically similar to other species in the “*mitsukurii*” group. It is distinguished morphologically by a very long inter-dorsal space which ranges from 26.7% to 30.0% of TL compared to 18.7–25.5% in *Squalus mitsukurii* (Last et al. 2007a) and 23.5–24.6% in *Squalus formosus* (White and Igléias 2011), both from Taiwan and southern Japan, and to 23.5–25.6 in *S. edmundsi*, 20.6–23.8%
Table 3. Morphological data from *Squalus hawaiiensis* sp. n. and *S. mitsukurii* from Japan. Morphological data from type specimens of two *Squalus* species expressed as a percentage of total length (TL) in cm following the methods of Last et al. (2007b). Morphometrics from the holotype, two paratypes a and b, and the range of values from five additional specimens of *Squalus hawaiiensis* sp. n. are shown; type specimens are listed with FLMNH catalog number and genetic ID from Figure 1. Morphometrics for *S. mitsukurii* were taken directly from published studies, including two independent sets for the *S. mitsukurii* holotype: 1Last et al. (2007b) and 2Viana et al. (2016). Also shown are the minimum and maximum values from Last et al. (2007b) for four *S. mitsukurii* paratypes from Japan; “Min” and “Max” represent a range of values for these paratypes, not including holotype values. Abbreviations: ♀ = male, ♂ = female, bolded numbers indicate non-overlapping size ranges between *S. mitsukurii* and *S. hawaiiensis*.

|                  | *S. hawaiiensis* sp. n. | *S. mitsukurii* (Japan) |
|------------------|-------------------------|-------------------------|
|                  | Holotype (♀ UF241161, Sha116) | Paratype♂ (♂, UF241162, Sha114) | Paratype♂ (♂, UF241163, Sha117) | Min | Max | Holotype1 | Holotype1 | Min | Max |
| STL | Stretched total length | 774.5 | 628 | 502.5 | – | – | – | – |
| TL | Total length | 750.5 | 608 | 487.5 | 353 | 836 | 719 | 710 | 266 | 855 |
| PCL | Precaudal length | 81.3 | 82.6 | 80.3 | 80.3 | 83.1 | 76.6 | 77.5 | 78.2 | 79.0 |
| FL | Fork Length | 90.2 | 91.3 | 89.8 | 88.4 | 92.5 | – | – | – | – |
| PD2 | Pre-second dorsal length | 65.8 | 65.6 | 64.6 | 63.6 | 67.0 | 59.8 | 61.0 | 58.6 | 61.2 |
| PD1 | Pre-first dorsal length | 31.5 | 30.4 | 30.9 | 30.3 | 31.3 | 30.9 | 32.4 | 28.5 | 32.3 |
| SVL | Pre-vent length | 53.1 | 52.4 | 51.1 | 50.4 | 53.6 | 51.5 | 50.0 | 48.9 | 52.2 |
| PP2 | Prepelvic length | 52.2 | 50.1 | 48.6 | 48.9 | 52.4 | 48.5 | 47.9 | 47.4 | 50.1 |
| PP1 | Prepectoral length | 22.5 | 24.3 | 23.1 | 22.0 | 23.3 | 23.3 | 24.6 | 19.9 | 23.9 |
| HDL | Head Length | 21.8 | 23.9 | 22.9 | 21.4 | 22.4 | 23.4 | 24.2 | 20.9 | 23.5 |
| PG1 | Prebranchial length | 18.3 | 19.2 | 19.1 | 17.9 | 20.7 | 19.5 | 20.4 | 18.0 | 20.1 |
| PSP | Prespiracular length | 12.2 | 12.9 | 13.2 | 12.0 | 12.9 | 12.8 | 12.8 | 12.1 | 13.3 |
| POB | Preorbital length | 7.6 | 7.8 | 7.8 | 7.4 | 7.8 | 7.5 | 7.3 | 7.3 | 7.9 |
| PRN | Prenarial length | 4.9 | 5.2 | 5.4 | 4.8 | 5.1 | 5.5 | 5.6 | 5.0 | 5.4 |
| PINL | Pre-inner nostril | 5.0 | 5.2 | 5.3 | 4.9 | 5.1 | – | – | – | – |
| POR | Preoral length | 9.9 | 10.1 | 10.4 | 9.6 | 10.2 | 10.8 | 10.3 | 9.4 | 10.6 |
| INLF | Inner nostril- labial furrow space | 4.3 | 4.7 | 4.8 | 4.3 | 4.7 | 4.4 | 4.3 | 4.2 | 4.7 |
| MOW | Mouth width | 7.7 | 7.6 | 7.2 | 7.0 | 8.1 | 6.2 | 8.6 | 6.3 | 7.5 |
| ULA | Labial furrow length | 1.9 | 2.5 | 2.1 | 1.9 | 2.3 | 2.4 | 2.5 | 2.1 | 2.5 |
| INW | Internarial space | 4.4 | 4.9 | 4.4 | 4.0 | 4.8 | 4.7 | 4.0 | 4.9 |
| INO | Interorbital space | 8.0 | 7.8 | 8.0 | 6.7 | 7.8 | 8.1 | 9.3 | 7.9 | 8.4 |
| EYL | Eye length | 4.3 | 4.9 | 4.5 | 3.9 | 4.7 | 3.4 | 3.6 | 3.8 | 4.7 |
| EYH | Eye height | 3.0 | 3.1 | 2.9 | 1.7 | 3.5 | 1.3 | 0.9 | 1.8 | 2.5 |
| SPL | Spiracle length | 1.2 | 1.4 | 1.7 | 1.2 | 1.6 | 1.2 | 1.3 | 1.2 | 1.5 |
Description of a new deep-water dogfish shark from Hawaii...

|                     | S. hawaiiensis sp. n. | S. mitsukurii (Japan) |
|---------------------|-----------------------|-----------------------|
|                     | Holotype\(^{a}\) (♀ UF241161, Sha116) | Paratype\(^{a}\) (♂ UF241162, Sha114) | Holotype\(^{b}\) (♀ UF241163, Sha117) | Min | Max |
| GS1 First gill-slit height | 1.7 | 1.6 | 1.4 | 1.5 | 1.9 | 1.9 | 1.7 | 1.6 | 1.7 |
| GS5 Fifth gill-slit height | 2.2 | 1.9 | 2.2 | 2.0 | 2.4 | 2.1 | 2.3 | 1.8 | 2.0 |
| IDS Interdorsal space | **27.8** | **28.9** | **26.7** | **28.1** | **30.0** | **21.3** | **21.1** | **18.7** | **25.5** |
| DCS Dorsal-caudal space | 10.2 | 12.1 | 11.4 | 10.9 | 11.6 | 9.8 | 10.6 | 9.9 | 11.2 |
| PPS Pectoral-pelvic space | 26.2 | 22.9 | 22.8 | 23.6 | 27.7 | 22.5 | 21.8 | 21.3 | 24.5 |
| PCA Pelvic-caudal space | 25.4 | 29.0 | 27.4 | 25.2 | 29.3 | 22.7 | 23.7 | 22.3 | 27.4 |
| D1L First dorsal length | 12.5 | 11.4 | 11.9 | 11.6 | 12.8 | 14.5 | 13.6 | 12.5 | 15.7 |
| D1A First dorsal anterior margin | 11.0 | 9.1 | 10.6 | 10.0 | 11.1 | 12.0 | 12.0 | 10.5 | 11.1 |
| D1B First dorsal base length | **7.2** | **6.2** | **6.9** | **6.4** | **7.4** | 8.3 | 8.2 | 7.8 | 7.8 |
| D1H First dorsal height | 7.7 | 6.5 | 7.8 | 6.9 | 7.7 | 8.5 | 9.8 | 4.5 | 8.3 |
| D1I First dorsal inner margin | 5.5 | 5.2 | 5.4 | 4.9 | 5.7 | 6.3 | 6.2 | 4.9 | 6.4 |
| D1P First dorsal posterior margin | 8.1 | 7.7 | 8.0 | 7.6 | 9.0 | 9.7 | 9.3 | 4.6 | 7.9 |
| D1ES First dorsal spine length | 4.6 | 4.2 | 3.8 | 3.6 | 4.4 | 3.3 | 3.9 | 3.5 | 4.8 |
| D1BS First dorsal spine base width | 0.9 | 0.8 | 0.9 | 0.7 | 1.0 | 0.8 | 1.0 | 0.6 | 0.8 |
| D2L Second dorsal length | 9.4 | 9.7 | 9.7 | 9.2 | 9.9 | – | – | – | – |
| D2L* Second dorsal length (incl. cartilage) | **11.5** | **11.1** | **10.8** | **10.6** | **11.7** | 12.7 | 12.3 | 12.0 | 13.9 |
| D2A Second dorsal anterior margin | 6.9 | 6.5 | 7.3 | 6.7 | 7.4 | – | – | – | – |
| D2A* Second dorsal anterior margin (incl. cartilage) | **9.5** | **8.1** | **8.6** | **8.3** | **9.2** | 10.2 | 10.2 | 10.4 | 10.7 |
| D2B Second dorsal base length | 5.0 | 4.9 | 4.9 | 5.2 | 5.5 | – | – | – | – |
| D2B* Second dorsal base length (incl. cartilage) | **6.8** | **6.4** | **6.3** | **5.9** | **6.9** | 7.2 | 7.2 | 8.0 | 9.2 |
| D2H Second dorsal height | 4.3 | 4.1 | 4.6 | 4.0 | 4.6 | 4.5 | 6.8 | 3.0 | 4.6 |
| D2I Second dorsal inner margin | 4.6 | 4.7 | 4.6 | 4.3 | 4.9 | 5.1 | 5.3 | 4.2 | 5.4 |
| D2P Second dorsal posterior margin | 5.4 | 5.7 | 5.5 | 4.8 | 6.3 | 5.2 | 6.3 | 4.1 | 4.4 |
| D2ES Second dorsal spine length | 4.1 | 4.7 | 5.0 | 4.1 | 4.6 | 3.8 | 4.2 | 3.8 | 5.0 |
|                | S. hawaiiensis sp. n. | S. mitsukurii (Japan) |
|----------------|-----------------------|-----------------------|
|                | Holotype (♀ UF241161, Sha116) | Paratype (♂ UF241162, Sha114) | Paratype (♂ UF241163, Sha117) | Min | Max | Holotype (♀) | Holotype (♂) | Min | Max |
| D2BS | Second dorsal spine base width | 0.8 | 0.8 | 0.9 | 0.7 | 0.9 | 0.7 | 0.9 | 0.7 | 0.9 |
| P1A | Pectoral anterior margin | 16.0 | 12.8 | 13.6 | 12.9 | 15.6 | 15.0 | 15.2 | 11.7 | 16.1 |
| P1I | Pectoral inner margin | 6.6 | 6.8 | 7.1 | 6.4 | 7.4 | 8.2 | 9.5 | 7.0 | 7.5 |
| P1B | Pectoral base length | 5.6 | 5.4 | 5.3 | 5.0 | 5.8 | 6.8 | 5.3 | 5.0 | 6.1 |
| P1P | Pectoral posterior margin | 12.2 | 9.9 | 9.9 | 10.1 | 12.3 | 11.0 | 11.7 | 7.6 | 11.4 |
| P2L | Pelvic length | 9.9 | 11.4 | 10.9 | 9.3 | 10.7 | 10.8 | 11.5 | 9.6 | 10.3 |
| P2H | Pelvic height | 3.9 | 3.4 | 3.1 | 3.0 | 5.2 | 5.6 | – | 4.0 | 4.9 |
| P2I | Pelvic inner margin | 4.6 | 5.7 | 5.9 | 3.9 | 6.0 | 5.8 | 6.3 | 2.0 | 3.1 |
| CDM | Dorsal caudal margin | 20.7 | 20.1 | 21.1 | 19.4 | 21.4 | 22.6 | 24.4 | 21.2 | 21.3 |
| CPV | Preventral caudal margin | 11.2 | 9.9 | 10.3 | 10.2 | 12.0 | 12.3 | 12.1 | 10.2 | 12.2 |
| CPU | Upper postventral caudal margin | 16.6 | 15.0 | 15.4 | 14.3 | 16.6 | 16.4 | – | 13.2 | 16.2 |
| CPL | Lower postventral caudal margin | 5.2 | 4.0 | 3.2 | 3.7 | 5.4 | 4.8 | – | 3.4 | 5.6 |
| CFW | Caudal fork width | 6.7 | 6.7 | 6.6 | 6.5 | 7.2 | 6.7 | 7.0 | 5.9 | 6.7 |
| CEL | Caudal fork length | 8.5 | 8.1 | 8.5 | 8.2 | 9.3 | 9.2 | – | 9.3 | 10.3 |
| HANW | Head width at nostrils | 7.2 | 7.7 | 7.6 | 6.5 | 7.3 | 7.7 | 7.3 | 7.6 | 7.7 |
| HAMW | Head width at mouth | 10.8 | 11.1 | 10.5 | 9.9 | 10.6 | 11.5 | 12.2 | 10.1 | 10.8 |
| HDW | Head width | 13.6 | 11.7 | 10.8 | 11.7 | 15.8 | 14.8 | 22.5 | 11.5 | 13.8 |
| TRW | Trunk width | 15.0 | 10.6 | 10.7 | 11.7 | 14.2 | – | 18.3 | 8.2 | 10.7 |
| ABW | Abdomen width | 15.1 | 10.9 | 9.6 | 10.0 | 14.4 | – | 15.5 | 6.4 | 9.6 |
| TAW | Tail width | 7.1 | 7.1 | 5.9 | 5.9 | 7.9 | 6.3 | – | 4.7 | 6.7 |
| CPW | Caudal peduncle width | 3.0 | 3.0 | 2.7 | 2.4 | 3.4 | 2.5 | – | 2.4 | 3.1 |
| HDH | Head height | 8.2 | 8.3 | 8.2 | 8.1 | 10.7 | 8.5 | 12.7 | 7.5 | 11.7 |
| TRH | Trunk height | 9.2 | 8.7 | 8.8 | 8.8 | 12.4 | – | 10.3 | 7.9 | 9.1 |
| ABH | Abdomen height | 11.1 | 9.3 | 9.2 | 8.6 | 14.2 | – | 15.5 | 6.4 | 9.6 |
| TAH | Tail height | 6.3 | 5.9 | 5.3 | 5.7 | 8.8 | 7.2 | – | 5.3 | 6.2 |
| CPH | Caudal peduncle height | 2.3 | 2.2 | 2.2 | 2.3 | 2.5 | 2.6 | – | 2.3 | 2.5 |
| CLO | Clasper outer length | 4.5 | 3.8 | 5.1 | 5.1 | – | – | 1.7 | 2.6 |
| CLI | Clasper inner length | 7.7 | 6.3 | 8.4 | 8.4 | – | – | 5.2 | 6.0 |
| CLB | Clasper base width | 1.7 | 1.2 | 1.6 | 1.6 | – | – | 0.9 | 1.1 |
Figure 5. SEM images of dermal denticles. Three views of dermal denticles from adult male (TL = 72.5 cm) *Squalus hawaiiensis*.

in *S. grahami* (White et al. 2007), 21.7–25.9% in *S. montalbani* (Last et al. 2007b), all from Australia and 22.6–26.0% in *S. griffini* (Duffy and Last 2007) from New Zealand, but overlaps with *S. chloroculus* (23.7–27.5%) from Australia (Last et al. 2007b), *S. nasutus* (24.4–28.0%) from Australia, Indonesia, and the Philippines (Last et al. 2007a) and *S. japonicus* from Japan (28.0–29.5%TL) (Chen et al. 1979). *Squalus hawaiiensis* is further distinguished from *S. mitsukurii* by having smaller first and second dorsal fin lengths and anterior margins and a longer body or torso (longer pre-caudal and pre-second dorsal lengths but shorter dorsal caudal margin; Table 3). The longer torso is reflected in differences in the ranges of the following ratios between *S. mitsukurii* type specimens (reported in Last et al. 2007) and all *S. mitsukurii* measured here (N=8): pre-first dorsal length 1.45–1.73 vs. 1.01–1.16 times interdorsal space; prepectoral length 1.09–1.28 vs. 0.74–0.86 times interdorsal space; prepectoral length 1.02–1.07 vs. 0.78–0.89 times pelvic-caudal space. Based on data from Chen et al. (1979), *S. mitsukurii* has higher vertebral meristic counts (45–51 monospondylyous centra, 87–93 precaudal centra, 118–127 total centra) than *S. hawaiiensis* (41–45
monospondylous centra, 85–89 precaudal centra, 112–116 total centra). *Squalus chloroculus* has a caudal bar that extends much higher on the upper caudal fin and lacks the upper caudal blotch characteristic of *S. hawaiiensis* (Figure 7A–C). *Squalus chloroculus* also has much shorter first dorsal fin spines (2.3–3.3%TL) and second dorsal fin spines (2.5–3.9%TL) than *S. hawaiiensis*. *Squalus nasutus* has a much longer snout with pre-narial lengths of 5.9–7.5%TL and pre-oral lengths of 11.1–12.7%TL compared to 4.8–5.4%TL and 9.6–10.4%TL respectively for *S. hawaiiensis*. Based on the morphometrics from Chen et al. (1979), the closely related *S. japonicus* differs from *S. hawaiiensis* in having a smaller mouth (6.4–6.9%TL compared to 7.0–8.1%TL) and shorter first and second dorsal fin lengths. First dorsal fin length in *S. japonicus* is 10.1–11.0%TL compared to 11.4–12.8%TL in *S. hawaiiensis*. Second dorsal fin length is 7.9–8.4%TL *S. japonicus* compared to 10.6–11.7%TL in *S. hawaiiensis*.

**Color.** In life (based on many captured specimens): dorsal surface uniformly dark gray to brown, light gray to white ventrally. Dorsal fins uniformly gray to brown with think black tips that narrow with age, free rear tips slightly paler. Caudal fin mostly

![Figure 6. Holotype. A First dorsal fin B second dorsal fin C pectoral fin of Squalus hawaiiensis holotype (UF241161, female 750.5 mm TL).](image)
Description of a new deep-water dogfish shark from Hawaii...

Figure 7. Caudal fin of Squalus hawaiiensis sp. n. A Holotype (UF241161, female 750.5 mm TL) B fresh adult male C fresh adult female.

dusky with a broken white trailing edge, dark caudal bar triangular, extending from the caudal fork nearly to the anterior edge of the lower caudal (Figure 8A–B). Upper caudal blotch diffuse in adults, extending to a short length of the posterior margin of the upper caudal fin, upper and lower caudal fins white tipped; pectoral and pelvic fins greyish dorsally, darker in the middle and with well-defined white posterior margin; Juveniles with much more pronounced fin markings; dorsal fins with black fringes, dark blotch in pectoral fins, caudal bar distinct on lower caudal from the fork to the anterior edge, well-defined and separated black upper caudal blotch and upper caudal fringe with upper caudal blotch not reaching the posterior margin of the upper caudal fin. In juvenile S. mitsukurii the upper caudal blotch is smaller and indistinct from the upper caudal fringe and the caudal bar is diagonal rather than triangular and does not reach the posterior edge of the lower caudal fin. In preservative: holotype similar, dark markings on fins faint but evident; caudal bar faint; broad, pale posterior margins on pectoral and pelvic fins well-defined. Eyes bright green in life (Figure 8C).

Size. Based on 197 Hawaii specimens surveyed, 156 females and 41 males (Daly-Engel et al. 2010; Cotton et al. 2011), the maximum observed length of females and males was 101 cm TL and 78 cm TL respectively. Cotton et al. (2011) reported that females reach maturity at ~64 cm TL and males reach maturity at ~47 cm TL.

Etymology. Derived from the type locality in the Hawaiian Archipelago

Vernacular. Hawaiian Spurdog
Figure 8. Images of the Hawaiian spurdog, *Squalus hawaiiensis*. A Lateral view of adult female *Squalus hawaiiensis*, drawing by R. McPhie. B Embryonic *Squalus hawaiiensis*, lateral and dorsal views, drawings by R. McPhie. C Embryonic *Squalus hawaiiensis*, dorsal view. Photo by RDG.

Discussion

We found marked genetic variation across 1,311 base pairs of mitochondrial DNA separating *Squalus hawaiiensis* from *Squalus mitsukurii* specimens collected from the Japanese type locality, as well as closely-related congeners from elsewhere in the Pacific (Figures 1, 2). Patterns of relatedness and inter- and intraspecific genetic distances
were comparable to other phylogenetic studies on *Squalus*, including species descriptions (Ward et al. 2005; Ward et al. 2007; Naylor et al. 2012). Our data show that *S. mitsukurii* from Japan and *S. hawaiiensis* are demonstrably distinct sister species (Figures 1, 2), most closely related to *S. japonicus* from Japan and *S. nasutus* from Australia. Morphological examination also distinguished *S. hawaiiensis* from these three species by a combination of differences in the trunk length (interdorsal distance), snout length, fin and fin spine lengths, and caudal coloration. We conclude that *S. hawaiiensis* represents a novel, previously-unidentified species. A holotype and paratypes a and b have been deposited into the Florida Museum of Natural History (FLMNH catalog numbers UF241161, UF241162, and UF241163; Table 3).

The holotype of *Squalus mitsukurii* was first listed from Misaki, Japan by Jordan and Snyder (1901) before being officially described two years later by Jordan and Fowler (1903), though as in the 1901 paper, the accompanying drawing was of *Squalus acanthias*. *Squalus mitsukurii* from Hawaii was referenced by Jordan & Evermann shortly thereafter in the publication “Shore Fishes of the Hawaiian Islands” (1905), with a copy of the misattributed illustration from 1903. Little scientific investigation has been done on *Squalus* from the Central Pacific since then, with the exception of a 1994 account of the rapid depletion of the dogfish stock around Hancock Seamount in the Northwestern Hawaiian Islands as a result of bycatch in the armorhead fishery (Wilson and Seki 1994), and a more recent investigation of age, growth, and reproduction (Cotton et al. 2011). In 2010, the authors found that *S. cf. mitsukurii* from Hawaii has the lowest rate of both multiple paternity and genetic diversity estimated in a shark population to date, indicating that this species might have a particularly low rebound potential in the face of fishing pressure (Simpfendorfer and Kyne 2009; Daly-Engel et al. 2010).

Because taxonomic descriptions that incorporate molecular data may use different marker types, study taxa, and methods of estimating divergence, it can be difficult to directly compare genetic distances among studies, or define a genetic threshold for speciation. But a lack of shared haplotypes, plus variation between species that is generally an order of magnitude higher than variation within species, is a consistent pattern reported in many elasmobranch species descriptions (Spies et al. 2006; Ward et al. 2007; Veríssimo et al. 2014; Daly-Engel et al. 2018; Pfleger et al. 2018). Among the four closely-related species we studied, average concatenated sequence divergence between species (1.045±0.183%) was nearly fourteen times the average within-species divergence (0.075±0.026), and therefore consistent with species-level differences reported for other elasmobranchs, including *Squalus* (Ward et al. 2007; Ebert et al. 2010; Viana et al. 2016).

In addition to being taxonomically unresolved, members of genus *Squalus* are often subject to high fishing pressure as bycatch in commercial trawl fisheries, sometimes resulting in severe population depletion (Wilson and Seki 1994; Graham et al. 2001; Kyne and Simpfendorfer 2007; Dulvy et al. 2014; Pfleger et al. 2018). Furthermore, their long reproductive intervals (12–24 months) and slow growth results in a low rate of replacement (Musick 1999; Musick and Ellis 2005; Cotton et al. 2011; Cotton and Grubbs 2015), compounding the depleting effect of fishing pressure. In general, *S. mitsukurii* is classified by the International Union for Conservation of Nature (IUCN)
as Data Deficient globally (Cavanagh et al. 2007), but life history parameters among *Squalus* species likely varies due to undiagnosed taxonomic variation. The combination of these variables may result in the extirpation or extinction of deep-water stocks and species before they are described by science, so taxonomic evaluation is of vital importance to ensure the survival of species that may not yet be managed as distinct evolutionary units. Further, though the barcoding gene, COI, has great utility for species identification, it may not provide sufficient resolution for diagnosing differences between organisms with low rates of molecular evolution, such as deep-water sharks. Because so many potential species remain unexamined, the name *S. mitsukurii* now represents a series of geographically distinct Evolutionary Significant Units (ESUs), each meriting its own taxonomic examination (Daly-Engel et al. Submitted).

**Conclusions**

Morphological and genetic differences indicate that the dogfish shark in Hawaii represents a novel species, designated here as *Squalus hawaiiensis*, the Hawaiian spurdog shark, named for the type location. Further, *Squalus mitsukurii* in Japan is subject to taxonomic confusion even among experts, and may comprise multiple distinct species, one of which likely includes the holotype. There, thorough morphological and genetic examination is warranted to elucidate the subtle differences between co-occurring populations that are morphologically indistinguishable but genetically unique. Given the number of previously-cryptic species identified in the *S. mitsukurii* complex alone, analysis of other populations will likely yield further identification of cryptic diversity within the genus *Squalus*.

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Description of a new deep-water dogfish shark from Hawaii...

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Appendix I

Demographic data for specimens used in this study. ID numbers refer to those used in Figure 1; GenBank Accession numbers are listed by gene (ND2/CO1); CSIRO = Commonwealth Scientific and Industrial Research Organisation Marine & Atmospheric Research (Hobart, Tasmania).

| ID #   | Squalus species | GenBank Accession #s | Source               | Collector/identifier | Origin                                | Latitude | Longitude  | Collection date | Depth (m) | Sex | TL (mm) |
|--------|-----------------|----------------------|----------------------|----------------------|---------------------------------------|----------|------------|----------------|-----------|-----|---------|
| Sna021 | nasutus         | MG654959.1/MK005141  | CSIRO                | P. Last & W. White    | West Australia, W of Shark Bay        | 25.0635  | 112.1483E  | 23 Apr 2006     | 340       |     |         |
| Sna022 |                 | MG654960.1/MK005140  | CSIRO                | W. White              | West Australia, W of Leander Point     | 29.3100  | 113.9467E  | 06 Feb 1991     | 505       |     |         |
| Sja049 |                 | MG654922.1/MK005129  | CSIRO                | W. White              | Taiwan, Tashi fish market, near I-Lan (NE coast) |         |            | 24 May 2005     |           |     |         |
| Sja050 |                 | MG654923.1/MK012557  | CSIRO                | W. White              | Taiwan, Tashi fish market, near I-Lan (NE coast) |         |            | 23 May 2005     |           |     |         |
| Sja051 | japonicus       | MG654924.1/MK005128  | CSIRO                | P. Last               | Taiwan, Tashi fish market, near I-Lan (NE coast) |         |            | 23 May 2005     |           |     |         |
| Sja074 |                 | MG654925.1/MK005130  | A. Veríssimo         | N. Straube            | Suruga Bay, Japan                     |          |            |               |           |     |         |
| Sja075 |                 | MG654926.1/MK005127  | A. Veríssimo         | N. Straube            | Suruga Bay, Japan                     |          |            |               |           |     |         |
| Sja121 |                 | MG654927.1/MG792167.1| A. Yamaguchi         | Sho Tanaka            | Suruga Bay, Japan                     |          |            | May 5 2011      | F 945     |     |         |
| Sja123 |                 | MG654928.1/MG792169.1| A. Yamaguchi         | Sho Tanaka            | Suruga Bay, Japan                     |          |            | 21 Mar 2007     | F 885     |     |         |
| Sja124 |                 | MG654929.1/MG792170.1| A. Yamaguchi         | Sho Tanaka            | Suruga Bay, Japan                     |          |            | 24 Apr 2009     | M 774     |     |         |
| Smi120 | mitukurii       | MG654933.1/MG792166.1| A. Yamaguchi         | Sho Tanaka            | Suruga Bay, Japan                     |          |            | 21 Mar 2007     | M 778     |     |         |
| Smi122 |                 | MG654934.1/MG792168.1| A. Yamaguchi         | Sho Tanaka            | Suruga Bay, Japan                     |          |            | 10 May 2011     | F 1096    |     |         |
| Sha090 | hawaiiensis     | MG654906.1/MK005139  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4916N | 157.7525W  | 17 Aug 2015     | 360       | F  | 58.4    |
| Sha091 |                 | MG654907.1/MK005138  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4916N | 157.7525W  | 17 Aug 2015     | 360       | F  | 64.8    |
| Sha093 |                 | MG654908.1/MK005136  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4916N | 157.7525W  | 17 Aug 2015     | 360       | F  | 63.5    |
| Sha114 |                 | MG654909.1/MK005131  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4983N | 157.7310W  | 29 Jan 2016     | 305       | M  | 60.8    |
| Sha115 |                 | MG654910.1/MK005135  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4983N | 157.7310W  | 29 Jan 2016     | 305       | M  | 57.5    |
| Sha116 |                 | MG654911.1/MK005134  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4983N | 157.7310W  | 29 Jan 2016     | 305       | M  | 75.1    |
| Sha117 |                 | MG654912.1/MK005133  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4983N | 157.7310W  | 29 Jan 2016     | 305       | M  | 48.8    |
| Sha118 |                 | MG654913.1/MK005132  | J.M. Anderson        | J.M. Anderson         | Kaneohe Bay, Oahu, Hawaii             | 21.4983N | 157.7310W  | 29 Jan 2016     | 305       | M  | 55.5    |