Molecular diversity and distribution of eastern Atlantic and Mediterranean dogfishes *Squalus* highlight taxonomic issues in the genus

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Title (max. 120 ch): Molecular diversity and distribution of eastern Atlantic and Mediterranean dogfishes *Squalus* highlight taxonomic issues in the genus

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Running title (max. 45 ch): Eastern Atlantic and Mediterranean *Squalus*

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The alpha taxonomy of the globally-distributed shark genus *Squalus* has been under intense investigation recently and many new species have been described over the last decade. However, taxonomic uncertainty remains about several taxa. Without consistent nomenclature and the ability to reliably distinguish between the different *Squalus* species, basic data collection, downstream conservation and management efforts are seriously compromised. To aid in clarifying the taxonomic status of *Squalus* species in the eastern Atlantic and Mediterranean, we assessed species diversity at the molecular level and evaluated the consistency in species identification in the region. Samples from all nominal *Squalus* species recognized in the above regions were collected in an international effort and sequenced for regions of the mitochondrial COI and ND2 genes. These data were further analyzed alongside publicly available sequences, including 19 of the 26 *Squalus* species globally recognized, to compare the regional genus diversity with that found elsewhere. Our results confirm inconsistent species identification in the eastern Atlantic and Mediterranean *Squalus*, particularly concerning *S. blainville* and *S. megalops*, and reinforce the need to revise the status of *S. megalops* and *S. mitsukurii* as they may include several distinct species distributed around the world. The status of *S. blainville* is also discussed in light of the current findings and its problematic taxonomic history.

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Introduction

The taxonomy of elasmobranchs (Class Chondrichthyes: Subclass Elasmobranchii) has generally been understudied and poor baseline data on species identification persists, particularly for some groups (e.g. *Apristurus* and *Squalus*; Ebert & Stehmann 2013). Fundamental problems in accurately identifying and classifying species have hampered the collection of robust biological and ecological data. This situation is of particular concern in elasmobranchs taken as targets or as by-catch in several fisheries around the globe, since their highly conserved life history strategies make them extremely vulnerable to overexploitation (Musick *et al.* 2000). Data on abundance and range are critical in assessments of extinction risk and figures concerning fisheries exploitation and mortality are key for sustainable management. Therefore, the ability to identify and accurately distinguish species is of paramount importance, as species may decline or even disappear unnoticed.

The genus *Squalus* Linnaeus, 1758 is one of the most taxonomically problematic genera of sharks. This group, generally referred to as spurdogs or spiny dogfishes, includes approximately 26 species (*sensu* Eschmeyer *et al.* 2016) of small-sized squaloid sharks (<1.5 m of body size). The genus is globally-distributed, with species commonly found in the continental shelf and upper slope waters, as well as around oceanic islands and seamounts. Many species may be extremely abundant locally and are frequently caught in commercial fisheries around the world (Bonfil 1994; Walker 1998; Shotton 1999; Ferretti *et al.* 2005). However, the species diversity within the group is still poorly characterized. For instance, approximately 15 species have been described or resurrected in the last decade (e.g. Last *et al.* 2007a; Ebert *et al.* 2010; White & Iglésias 2011), particularly in the Indo-Pacific region. These recent taxonomic studies have doubled the number of valid species in the genus and have unveiled a considerable amount of “hidden” diversity in the group. As a result, half of the *Squalus* species are considered as Data Deficient according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2015). In addition, the uncertain taxonomic status of many other *Squalus* taxa has hampered the collection of adequate species-level information on the group, and hindered or even prevented conservation assessments of some heavily fished species (e.g. Cavanagh & Gibson 2007).

The alpha taxonomy of *Squalus* in the Atlantic Ocean *sensu lato* has been studied in the past, though mostly at a regional level (e.g. Bigelow & Schroeder 1948; Bass *et al.* 1976; Cadenat & Blache 1981; Muñoz- Chápuli & Ramos 1989). Five species of *Squalus* are currently reported for the Atlantic Ocean, namely *S. acanthias* Linnaeus, 1758, *S. blainville* (Risso, 1827), *S. cubensis* Howell Rivero, 1936, *S. megalops* (Macleay, 1881), and *S. mitsukurii* Jordan & Snyder, 1903.

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Regardless of current records of occurrence, many difficulties remain in accurately identifying the different species, particularly in the eastern Atlantic and Mediterranean regions (e.g. Muñoz-Chápuli & Ramos 1989, Marouani *et al.* 2011, Bonello *et al.* in press). One complicating issue has been the use of ambiguous diagnostic morphological traits to distinguish the different species (details in Garrick 1960; Muñoz-Chápuli & Ramos 1989; and Bonello *et al.* in press), exacerbated by the high morphological similarity among taxa. Furthermore, many nominal species have complicated taxonomic histories as a result of the ambiguity and lack of detail in the original species descriptions, the absence of type material, and multiple, often conflicting synonymy by different authors.

Given the number of problems with *Squalus* taxonomy and in morphological species identification in the eastern Atlantic and Mediterranean Sea, molecular genetic data can provide an alternative perspective on the alpha diversity of the dogfishes in these regions. Previous studies have shown that nucleotide sequences of the barcoding gene cytochrome oxidase I (COI) and of the NADH dehydrogenase subunit 2 (ND2) can provide a means to identify species of *Squalus* with a high degree of accuracy, and to pinpoint potentially undescribed taxa (e.g. Ward *et al.* 2005, 2007; Naylor *et al.* 2012a). For this purpose, a joint effort of several international elasmobranch researchers was aimed at uncovering the molecular diversity of *Squalus* and its distribution in the eastern Atlantic and Mediterranean. The results are contrasted with current assumptions of species diversity and distribution, and identify the most problematic taxa in regional species identification. Moreover, newly generated COI and ND2 sequence data from the eastern Atlantic and Mediterranean was compared to publicly available COI and ND2 sequence data on 19 of the 26 *Squalus* species to compare the regional species diversity with that found around the globe.

Material and methods

Tissue samples were obtained from fresh specimens (N=109) collected from the eastern Atlantic Ocean and Mediterranean Sea between 2009 and 2013 either during scientific research surveys, or from fisheries landings (Table S1). Additional tissue samples from *Squalus* specimens collected from other regions of the western Atlantic and Pacific Ocean (N=39) were also included in order to increase taxonomic and geographic coverage of the dataset (Table S1). Whole specimens were identified by the authors, and kept as voucher and/or photographed whenever possible. Tissue samples (e.g. muscle, fin clips) were preserved in 95% ethanol or in 20% dimethyl sulfoxide buffer saturated with NaCl (Seutin *et al.* 1991), and used for genomic DNA (gDNA) extraction using the Qiagen DNeasy Tissue kit (Qiagen, Valencia, CA, USA) or the

EasySpin Genomic DNA Tissue Kit (Citomed, Lisbon, Portugal) according to the manufacturers' instructions.

A 499 bp fragment of the COI gene (primers FishF2 5' TCGACTAATCATAAAGATATCGGCAC 3'; FishR1 5' TAGACTTCTGGGTGGCCAAAGAATCA 3'; Ward *et al.* 2005) and a 526 bp fragment of the ND2 gene (primers ND2_F 5' TTCCTCACACAAGCAACCGC- 3' and ND2_R 5' GATGGTGGCTGGGATGGC 3'; Veríssimo *et al.* 2010) were sequenced. Each fragment was amplified via the polymerase chain reaction (PCR) in 10 µl reactions including 5 µl of MyTaq™ HS Mix 2X (Bioline, London, U.K.), 0.4 µM of each primer, 3.2 µl of ultra-pure autoclaved water, and 1 µl of gDNA. PCR temperature conditions for the amplification of the COI and ND2 followed those outlined in Veríssimo *et al.* (2014) and Veríssimo *et al.* (2010), respectively. Amplicons were cleaned using ExoSAP-IT (USB) following the manufacturer's protocol, and sequenced in both directions at MacroGen Europe (Amsterdam, The Netherlands). The resulting DNA sequences were imported into Geneious Pro 5.4.6 (Biomatters Ltd, Auckland, New Zealand) and checked for quality and accuracy in nucleotide base assignment.

Additional nucleotide sequence data were obtained from the Barcode of Life project public database (COI: n=266; www.barcodinglife.org; Ratnasingham & Hebert, 2007), from the GenBank nucleotide database (COI: n=6; ND2: n=134; National Centre for Biotechnology Information, Bethesda, Maryland, U.S.A.; www.ncbi.nlm.nih.gov/), or directly from the authors of reference studies (i.e. Marouani *et al.* 2011) (Table S2). The above sequences were selected based on their association with previous and ongoing Barcode of Life projects for which voucher data are available (e.g. ELASMOMED, Cariani *et al.* unpublished data; Steinke *et al.* 2009; Mabrugaña *et al.* 2010), as well as with other studies dealing with *Squalus* taxa (e.g. Ward *et al.* 2007; Veríssimo *et al.* 2010; Marouani *et al.* 2011; White & Iglésias 2011; Naylor *et al.* 2012a; Straube *et al.* 2013; Bineesh *et al.* in press). All publicly available sequences were aligned with the newly generated data for each mtDNA gene separately, and the species names associated with each sequence were kept in the initial analyses. The species coverage and number of sequences publicly available differed between gene regions, so the two datasets are not equal. Sequence data from *Cirrhigaleus asper* (Merrett, 1973) and *Cirrhigaleus australis* White, Last & Stevens, 2007, species in the sister-genus of *Squalus* (but see Naylor *et al.* 2012b), were used as outgroups (GenBank Accession numbers: JF493199 and DQ108220 for COI, and JQ518974 and JQ519012 for ND2, respectively). To simplify the text and improve clarity, the designations *S. megalops* and *S. cf. megalops* will be considered equal hereon, as well as that of *S. mitsukurii* and *S. cf. mitsukurii*.

Nucleotide sequences from each mitochondrial gene region were aligned using the Geneious Pro 5.4.6 alignment algorithm with default parameters, and subsequently collapsed into unique haplotypes using the FaBox 1.41 online tool (Villesen 2007). Translation of the different haplotypes per gene region into the corresponding aminoacid sequences using the vertebrate mitochondrial genetic code was also performed in Geneious, and confirmed the absence of stop codons and of pseudogenes. The final alignment of unique haplotypes per gene region was used for phylogenetic reconstruction of molecular sequence relationships as detailed below.

Two phylogenetic reconstruction methods were applied to each of the two molecular datasets (i.e. COI and ND2), namely Maximum Likelihood (ML) and Bayesian Inference (BI). ML reconstruction was performed using PhyML online (<http://www.atgc-montpellier.fr/phyml/>; Guindon *et al.* 2010) with the automatic model selection option and default parameters of tree searching. The best model of sequence evolution was chosen based on the Akaike Information Criteria, and branch support was estimated with 1000 bootstrap replicates. BI reconstruction was performed with MrBayes 3.2 (Ronquist *et al.* 2012) using the model of sequence evolution selected as indicated above, two independent runs per dataset, and a 25% burn-in cutoff. Runs on the COI and ND2 datasets included a total of five and 15 million generations, respectively. Run convergence per dataset was confirmed by observing a mean standard deviation of split frequencies of <0.01 between runs, as indicated in the software manual. Also, additional convergence diagnostics included confirmation of effective sample sizes >200 for the combined parameter files calculated using Tracer version 1.6 (Rambaut *et al.* 2014). Generations sampled before convergence was attained were discarded as burn-in. Branch support values from the ML and BI trees will be expressed in percentages corresponding to the fraction of bootstrap replicates where that branch was reconstructed in the ML tree, and to the branch probability according to the BI method.

Based on the resulting clade reconstruction, the average Kimura-2-parameter genetic distances (K2P; Kimura 1980) as well as average *p*-distances were calculated between each pair of clades in MEGA 5.2 (Tamura *et al.* 2011; Tables S3 and S4). These genetics distances were used to infer the level of haplotype sequence divergence between the different clades and allow comparison with previous studies (e.g. Ward *et al.* 2007; Naylor *et al.* 2012a). However, given the concordance between genetic distances, only average *p*-distances will be referred in the text.

The geographic distribution of the different *Squalus* clades reconstructed for the eastern Atlantic and Mediterranean Sea was mapped using the geographical coordinates associated with each of the specimens sequenced, using RStudio version 3.2.1 (RStudio Team 2015) and the package *maps* version 3.0. This allowed for a regional perspective of species diversity distribution as well

as for comparison to current assumptions of *Squalus* species distribution in the above regions. Moreover, the distribution ranges of the major *Squalus* lineages identified here were also compared to previously defined marine provinces proposed by Briggs & Bowen (2012) to provide a global perspective of *Squalus* diversity distribution. The geographic coordinates of the specimens were superimposed on the distribution of annual sea-surface temperatures (SST) for the year 2015 in order to help visualize the distribution of *Squalus* lineages according to different ocean temperature zones. Data on the SST were downloaded from the NASA MODIS-Aqua database (<http://oceancolor.gsfc.nasa.gov/cgi/l3>, accessed on February 10, 2016). In cases where the geographical coordinates were not available, approximate coordinates were estimated whenever possible based on the general location provided for the sequence (if available; e.g. North-West Bay, Tasmania; Gulf of Maine, U.S.A.; Tables S1 and S2).

Results

Molecular diversity within Squalus

A total of 421 COI sequences and 254 ND2 sequences of *Squalus* were included in the analyses, representing 19 and 18 of the 26 species currently recognized, respectively, and covering all major oceans of the world (Table 1). Newly generated sequence data included 146 COI sequences and 120 ND2 sequences (Table S1), of which 106 and 101, respectively, were from specimens sampled in the eastern Atlantic and Mediterranean from all nominal *Squalus* species reported from these regions (i.e. *S. acanthias*, *S. blainville*, *S. megalops* and *S. mitsukurii*). Overall, 105 unique haplotypes were detected for the COI gene region differing in 107 variable nucleotide positions, whereas 165 unique haplotypes were found for the ND2 gene region differing in 154 variable nucleotide positions. All the newly generated COI and ND2 haplotype sequences are deposited in GenBank under Accession Nos. XXXX-XXXX and XXXX-XXXX, respectively (Table S1).

[Insert Table 1 & Fig. 1]

Phylogenetic reconstruction of COI and ND2 gene trees consistently clustered the *Squalus* sequences in three major lineages (I-III, Fig. 1) with high support values (>80%), except for lineage III for the ND2 tree. Clade composition within each of the major lineages was also consistent between gene regions and phylogenetic methods, although support values varied widely among clades and inter-clade relationships were largely unresolved. Sequences from eastern Atlantic and Mediterranean specimens spanned all three major lineages and clustered

into a total of four clades (Clades A-D, Fig. 1). The average *p*-distance among Clades A-D ranged between 2.2% and 7.8% for the COI and 3.0% and 7.4% for ND2 (Table 2).

[Insert Table 2]

The clearest result from the current analyses is the inconsistent identification of *Squalus* species along the Mediterranean and eastern Atlantic, especially in respect of *S. blainville* and *S. megalops* (Table 3). Specifically, specimens identified as *S. blainville* collected in the Mediterranean Sea and the northeastern Atlantic coasts off Portugal, Morocco and the Canary Islands clustered together with specimens identified as *S. megalops* from off Tunisia, Morocco, and the southeastern Atlantic coast off Angola, Namibia and South Africa (Clade B; Table 3). There are also several specimens originally identified as *S. acanthias* in the Mediterranean waters off the Balearic Islands, as well as around Crete, Cyprus and in the Aegean Sea, that also cluster in this clade.

[Insert Table 3]

In both the COI and ND2 trees, Clade B has low support values (<80%) but is consistently associated with three other clades from the western Pacific Ocean, namely *S. brevirostris* from Japan and Taiwan, *S. megalops* from Australia, and *S. raoulensis* from New Zealand (Fig. 1). The relationships among the four clades are not well resolved in the gene trees, with average *p*-distances between Clade B and the above clades ranging between 1.0% and 1.2% for COI, and between 1.2% and 1.8% for ND2 (Table S3 and S4). However, Clade B appears closest to *S. raoulensis*, and slightly more distant to the Australian *S. megalops* and to *S. brevirostris*. Fixed differences among the above clades were found at both gene regions (COI: 2-4; ND2: 4-7), suggesting long-term isolation among the different mitochondrial clades.

Further inconsistent use of the taxon names *S. blainville* and *S. megalops* is evident in Clade C from the COI tree, where a single individual from Tunisian waters identified as *S. blainville* by Marouani *et al.* (2011) clusters with sequences from specimens collected exclusively off tropical West Africa (i.e. Guinea-Bissau, Guinea-Conakry, and Gabon; Fig. 2) identified as *S. megalops* (Table 3). In the ND2 tree, the same specimens from central West Africa also cluster together in a well-supported clade ($\geq 80\%$). Clade C is well supported in both gene trees and regardless of phylogenetic method ($\geq 80\%$), and strongly divergent from Clade B (average *p*-distance: 6.8% for COI, 5.1% for ND2) despite the similar species identifications. It also differs from the remainder

clades in lineage III, showing average p -distances between 1.8% and 3.2% for COI, and between 2.4% and 5.1% for ND2 (Table S3 and S4).

Another finding from the current analysis is the existence of multiple clades with specimens identified as *S. mitsukurii*, including locations in the western (Uruguay, Brazil) and eastern South Atlantic (South Africa), Gulf of Mexico and off Hawaii (Fig. 1). The Hawaiian “mitsukurii” is consistently placed in association with *S. japonicus* from Taiwan, and *S. nasutus* from Indonesia and western Australia, forming a distinct group within lineage III with high support values ($\geq 80\%$). In turn, the Atlantic “mitsukurii” are placed in close association with *S. chloroculus* from southeastern Australia, and *S. montalbani* from Indonesia and southern and western Australia, albeit with low support values ($< 50\%$). Average p -distances between the Hawaiian and the Atlantic “mitsukurii” forms ranged between 1.4% and 2.0% for COI and 3.4% and 3.6% for ND2; in contrast, Clade D shows average p -distances from the remainder Atlantic “mitsukurii” between 0.2% - 0.8% for COI, and of 1.4% for ND2. Whether any of these forms represent *S. mitsukurii* as originally described remains unknown since no material from the type locality (Japan) was available for comparison; nonetheless, the results suggest they constitute separate taxa. Differentiation among the Atlantic “mitsukurii” forms is not clear in the current analysis as support for a Gulf of Mexico clade vs. a South African clade varies among gene regions and phylogenetic methods.

Geographic distribution of Squalus diversity at the regional and global scales

The four clades detected in the eastern Atlantic and Mediterranean Sea show generally distinct distributions although some species co-occur in particular regions (Fig. 2). Clade A was found in the western Mediterranean Sea (e.g. Gulf of Lion) and in the Adriatic Sea, as well as in the eastern North Atlantic around the British Isles and off the west coast of South Africa. Clade B occurs throughout the Mediterranean Sea as well as in the eastern Atlantic, from Portugal to southwestern Morocco and the Canary Islands, as well as further south between Angola and South Africa. In contrast, Clade C was detected only in the western Mediterranean basin off Tunisia, and in the tropical West Africa, between Guinea-Bissau and Gabon. Finally, Clade D was detected only off the west coast of South Africa but may be part of a wider-distributed species pending future work on closely allied western Atlantic “*S. mitsukurii*” clades (Gulf of Mexico and eastern South America) and western Indian Ocean specimens (e.g. *S. megalops* from Mauritius; Fig. 1).

[Insert Fig. 2]

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The above geographic ranges of Clades A-D are in agreement with those of their respective lineages (I-III; Fig. 3), which show remarkable association with the distribution of distinct marine temperature zones (Table S5). Lineage I (includes Clade A) is found in the cold-temperate provinces around the world, including the eastern North Atlantic province, and extending into some warm-temperate provinces such as the Mediterranean section of the Lusitanian province and the Benguela province. Lineage II (includes Clade B) is found in warm-temperate waters (except around the cold-temperate Tasmanian province) and appears discontinuous under tropical conditions. In our study area, it is found in the Lusitanian and the Benguela provinces, extending into the tropical Agulhas Province off South Africa and possibly into the Tropical Eastern Atlantic province off Angola. Lineage III (includes Clades C-D) occurs across tropical and warm-temperate provinces around the globe. In particular, Clade C occurs in the western Mediterranean basin of the warm-temperate Lusitanian province and in the Tropical Eastern Atlantic, while Clade D was found only in the warm-temperate Benguela province and in the tropical Agulhas province. There were no records from the cold Arctic and Antarctic regions, or from the cold-temperate Sub-Antarctic and tropical Eastern Pacific regions. All lineages occur in the Atlantic and Pacific oceans, with the Indo-Pacific area harboring the largest number of known *Squalus*.

[Insert Fig. 3]

Discussion

Molecular diversity in Squalus and main taxonomic issues

The consistent topology recovered from both gene regions regarding the existence of three major *Squalus* lineages/groups are in agreement with previous molecular studies by Ward *et al.* (2007) and Naylor *et al.* (2012a). This subdivision within the genus appears consistent regardless of gene region, phylogenetic model selection and parameterization, and uneven/unequal taxon sampling schemes. The above subdivision is also largely concordant with the one proposed by Bigelow & Schroeder (1957) based on morphology, which has been widely accepted (though with some modifications; see Ebert *et al.* 2010). Clade composition within each lineage was also generally concordant with previous molecular and morphological studies (indicated above), aside from differences due to taxonomic ambiguity in species identification.

Regarding the eastern Atlantic and Mediterranean Sea, we detected four distinct *Squalus* clades of which one (Clade A) shows a worldwide distribution, two appear to be confined to the Atlantic basin (Clades B & C), and one possibly extends from the eastern South Atlantic into the western Indian Ocean (Clade D). Aside from Clade A, corresponding to *S. acanthias*, the identity of these clades is problematic and reflects the main issues associated with *Squalus* taxonomy in the eastern Atlantic and Mediterranean Sea. Our study confirms the ongoing misidentification of *Squalus* taxa in the eastern Atlantic and Mediterranean Sea (as well as elsewhere), and highlights the inconsistent use of the taxon names *S. blainville* and *S. megalops*. These names are often used interchangeably to designate the same species, although the former is predominantly used within the Mediterranean region, while the latter is largely applied to specimens from the eastern Atlantic. Conversely, our data also shows that *S. megalops* and *S. blainville* are both applied to designate each of two distinct species. Clearly, there is a great need for taxonomic clarification of these species. Previous studies have tried to address this issue by using morphological data to better distinguish them, and proposed a number of diagnostic traits to help in accurate species identification (e.g. Muñoz-Chápuli & Ramos 1989; Marouani *et al.* 2011). However, Bonello *et al.* (in press) report that all character states for most of these “diagnostic” traits were found on specimens belonging to one of the species, raising doubts of the usefulness and reliability of the “diagnostic” traits proposed earlier.

The current results also question the use of the name *S. megalops* to designate *Squalus* specimens from the eastern Atlantic and Mediterranean. The original description of *S. megalops* (Macleay 1881) was based on specimens collected off southeast Australia. Since then, several authors have proposed the species to be present in many different locations around the globe, including the eastern Atlantic and the Mediterranean Sea (Bigelow & Schroeder 1957; Bass *et al.* 1976; Cadenat & Blache 1981; Compagno 1984; Muñoz-Chápuli & Ramos 1989; Compagno *et al.* 2005). Currently, the species is assumed to belong to a complex of morphologically similar species in need of taxonomic re-evaluation (Cavanagh & Lisney 2003; Last *et al.* 2007b; Last & Stevens 2009; Ebert & Stehmann 2013). Our data support the species-complex scenario proposed for *S. megalops* and suggest that this species does not occur in the eastern Atlantic and Mediterranean waters. Based on current analyses, specimens of *S. megalops* from Australia (type locality) share no COI or ND2 haplotypes with eastern Atlantic and Mediterranean specimens identified as *S. megalops*. Moreover, the level of genetic differentiation between Clade B and the Australian *S. megalops* is similar or higher to that observed between Clade B and other species within lineage II (e.g. *S. raoulensis*). Overall, these observations strongly suggest that the Australian *S. megalops* and Clade B have been isolated for some time and have accumulated differences at the level seen between other species of the same lineage. Naylor *et*

al. (2012a) and Straube *et al.* (2013) also found that sequences from South African *S. megalops* did not cluster with the Australian counterpart. We therefore conclude that *S. megalops* should not be applied to specimens in the eastern Atlantic and Mediterranean Sea, as also proposed previously by Last & Stevens (2009). However, this leaves open the question as to which name should be used for Atlantic and Mediterranean specimens previously considered to be *S. megalops*.

Given the preferred usage of *S. blainville* in the Mediterranean Sea, it may be desirable in terms of nomenclatural stability to retain this name for specimens in Clade B. This would also be consistent with the type locality of *S. blainville* (i.e. Nice, France). Moreover, Serena (2005) states that this taxon (referred to as *S. blainville*) has a wider distribution and higher abundance within Mediterranean waters compared to *S. megalops*, which is considered rare. Our data is in agreement with this statement, showing Clade B to be widespread within the Mediterranean Sea in contrast to Clade C that was detected only off Tunisia. Clade C, which is clearly not related to *S. megalops* from Australian waters, includes a specimen from Tunisia identified as *S. blainville* by Marouani *et al.* (2011) and several other specimens from off tropical West Africa. The use of *S. blainville* by Marouani *et al.* (2011) follows Muñoz-Chápuli & Ramos (1989) who proposed that this species name should refer to specimens with low dorsal fins, short inner pectoral fin margins, tricuspid dermal denticles and hook-like clasper claws. This proposal sought to maintain stability with previous work by Bigelow & Schroeder (1948, 1957), who incorrectly concluded that *S. blainville* from the Mediterranean Sea were conspecific with *S. mitsukurii* from Japan and *S. fernandinus/fernandezianus* from Juan Fernandez Islands, based solely on adult denticle morphology. However, there has been little nomenclatural stability on the use of *S. blainville*, and several authors have used it to designate different morphotypes both within and outside the Mediterranean (e.g. Tortonese 1956; Bigelow & Schroeder 1948, 1957; Garrick 1960; Chen *et al.* 1979; Compagno 1984). The data presented here indicate that Bigelow & Schroeder (1948, 1957) were incorrect. Thus, we propose that *S. blainville* should be used to refer to specimens in Clade B, and that Clade C should be considered a new species and formally described as such. Also, a redescription of *S. blainville* is required to stabilize the name and facilitate accurate species identification.

Another important finding of the present analysis is the “hidden” species diversity within *S. mitsukurii*. Like *S. blainville* and *S. megalops*, *S. mitsukurii* has historically been viewed as a single wide-ranging species but recent studies have indicated that it may represent a large species-complex (Compagno 1984; Last *et al.* 2007b). Recent revision of *S. mitsukurii* in the Indo-Australian region resulted in the resurrection of *S. montalbani* (Philippines, Indonesia,

Australia) and *S. griffini* (New Zealand), and the description of *S. chloroculus* (Duffy & Last 2007; Last *et al.* 2007c). Our analysis shows distinct clades of specimens identified as *S. mitsukurii* from the Atlantic and Pacific oceans confirming the occurrence of different species at various locations around the world. Notwithstanding the absence of any comparative material from the type locality (i.e. Japan), it seems reasonable to assume that the Atlantic specimens (i.e. Clade D and nominal *S. mitsukurii* from the Gulf of Mexico and southwestern Atlantic) are unlikely to be the original *S. mitsukurii* given their separation from the type locality, and particularly compared to the level of speciation within lineage III apparent in the Pacific. In turn, specimens from the Gulf of Mexico and South Africa identified as *S. mitsukurii* may represent a different, and potentially undescribed, species of *Squalus*. Future studies objectively addressing the taxonomic status of the different clades under *S. mitsukurii* should be conducted at a global scale using a combination of morphology, molecular and life history data. These should also include representative samples from different locations where the species has been reported to occur, in addition to close relatives within lineage III to provide a reference for species-level delimitation.

Regional and global distribution of Squalus diversity

The distribution of *Squalus* diversity in the eastern Atlantic and Mediterranean Sea largely matches previous assumptions regarding species number (four species) and range, with the main differences residing in species identification. *Squalus* occurs continuously along the eastern Atlantic margin and throughout the Mediterranean Sea, with species replacing each other in different regions, as previously suggested by Cadenat & Blache (1981). For instance, Clade A occurs in the northern- and southern-most parts of the eastern Atlantic, being replaced by Clade B in the warm-temperate waters at mid-latitudes, and by Clade C in tropical waters at low latitudes. The great heterogeneity in climatic and hydrological conditions within the Mediterranean basin (Bianchi 2007; Spalding *et al.* 2012), as well as the great variability in environmental conditions off the South African west coast (Griffiths *et al.* 2010), possibly allow the co-existence of multiple *Squalus* species with apparently distinct environmental preferences (Clades A-C, and Clades A-B and D, respectively).

Considering the distribution of *Squalus* diversity at a global scale, the emerging pattern is that the three main lineages of *Squalus* occur in association with distinct but adjacent temperature zones; i.e. lineage I occurs mainly in cold-temperate waters (and is the only lineage occupying this zone); lineage II is found mainly in warm-temperate waters; and lineage III occupies tropical and warm-temperate waters. This scenario suggests that the early steps in the speciation of the genus may be due to ecological isolation according to habitat, a pattern proposed for many other

vertebrate groups (Streelman & Danley, 2003). Species within each *Squalus* lineage appear to have radiated within the same ecological space or that immediately adjacent (e.g. adjacent tropical vs. warm-temperate regions) perhaps in association with limited dispersal within (e.g. speciation within lineage III in the tropical Indo-Polynesian province) and across ecological space (speciation within lineage I and II of northern and southern hemisphere species).

Another interesting emerging feature from the global distribution of *Squalus* diversity is the unbalanced diversity levels among the three major mitochondrial lineages (Fig. 1): species diversity is lowest in the cold-temperate lineage I, with few but wide-ranging species (lineage I), and is highest in the warm-temperate and tropical lineage III. This pattern is in line with many previous studies indicating higher marine species diversity in tropical/low-latitude regions although the speciation mechanisms behind this pattern may be varied (reviewed in Bowen *et al.* 2013). The mechanisms behind the current pattern of species diversity distribution across lineages is beyond the scope of this paper, but fully resolved phylogenies using mitochondrial and nuclear markers may provide important clues on this topic.

Limitations

Comprehensive sampling of a globally-distributed shark genus is challenging and requires the combined effort of many international partners. This study makes use of a reasonably large, curated molecular dataset resulting from multiple previous studies in the genus, and compiles information from most of the *Squalus* species currently accepted. However, there are still limitations in the interpretation of the results and considerable gaps in our understating of the diversity and distribution within the genus.

Specifically, species delimitation using only mitochondrial markers may mask complex histories of isolation among allopatric taxa followed by secondary contact and mixing. This scenario would leave a trace of divergent mitochondrial haplotypes in the population/species, given maternal-inheritance without recombination of the mitochondrial genome, but homogeneous nuclear signatures because of recombination. This may be of particular relevance in the Indo-Pacific *Squalus* since the past fluctuations in sea-level and the complex bathymetry of the region may have concurred to create such complex histories of isolation and secondary contact of taxa. The situation in the eastern Atlantic and Mediterranean Sea appears less prone to the scenario described above since the potential suitable habitat, i.e. shelf and upper slope waters, would likely shift vertically along the coastline with fluctuating sea-levels and either contract or expand horizontally between glacial and interglacial periods, but not necessarily impose physical barriers

to individual dispersal. Moreover, the distinct mitochondrial clades detected here appear non-randomly distributed in space. Rather, they are associated with distinct temperature zones suggesting ecological isolation among clades rather than restricted dispersal as the mechanisms behind clade divergence.

Lineage sorting in conjunction with stochastic lineage extinction can also yield misleading inferences of species relationships and divergence levels if analyses are restricted to mitochondrial data alone. Effective population size for nuclear genes is substantially larger than for mitochondrial ones (4x larger if the sex ratio is 1:1). Consequently, loss of genetic variability in mtDNA is faster than for nuclear DNA when population sizes are small or where the population is fragmented (e.g. strong metapopulation structure; Grant & Leslie 1993). Observations of some nominal *Squalus* species show they are morphologically distinct but do not seem to exhibit similar molecular divergence levels (e.g. *S. graham* – *S. griffini*), while substantial molecular divergence exists within morphologically assumed cohesive species (e.g. *S. montalbani*). Data from nuclear markers would provide important contributions for robust species-clade delineation within *Squalus*, and future studies should aim to collect nuclear sequence data from across the genus diversity and distribution to confirm the results produced here. Likewise, further morphological analyses are greatly needed to identify reliable and accurate diagnostic traits to help distinguish the different species in the eastern Atlantic and Mediterranean, and most importantly Clades B and C.

Finally, the patterns of species/lineage distributions described above at both regional and global scales are preliminary since distribution ranges may change as more data become available or are incorporated from different sources. In particular, little data were available from the western South Atlantic waters although several *Squalus* species have been reported for this region (e.g. Sadowsky & Moreira 1981; Hazin *et al.* 2006; Oddone *et al.* 2010). One key issue limiting the availability of accurate presence data is the reliability of species identification. Nevertheless, the large-scale patterns of species distributions shown here, particularly at the lineage-level, appear non-random and are consistent with known biogeographic provinces and particular temperature zones. Further work is needed to confirm the current results and to improve the resolution at the species-level.

Conservation Implications

Based on the current results, the diversity of *Squalus* in the eastern Atlantic and Mediterranean Sea matches earlier observations regarding the number of species occurring in these regions (i.e.

four). However, the identity and geographic range of these taxa differ from current assumptions, aside from that of *S. acanthias* (i.e. Clade A). First, the data presented here suggest that *S. megalops* does not occur in these regions and support the notion that it may be restricted to Australian waters (Last *et al.* 2007a). Second, regardless of whether Clade B or Clade C is accepted as representing *S. blainville*, our data indicate that this species occurs within Mediterranean waters and in the eastern Atlantic but not outside the Atlantic basin as currently assumed. Third, our data also refutes the presence of *S. mitsukurii* in Atlantic waters, and instead points to the presence of previously undetected diversity. In conclusion, the distributions of several *Squalus* species within and outside the Atlantic *sensu lato* need to be re-evaluated in light of the current findings, and dedicated taxonomic efforts need to be spent in further taxonomic clarification prior to the adequate assessment of these species' conservation status.

The inconsistency in species identification showed here, particularly concerning Clades B and C, compromises the usefulness of data collected in previous studies on the biology and ecology of *S. blainville* and *S. megalops* from the eastern Atlantic and Mediterranean Sea. Regions of clade overlap are of particular concern and the Mediterranean Sea is an area where this problem is most acute, since specimens collected at a given location may be from different clades but treated as a single species. Empirical observations within South Africa also indicate that there is much confusion with the identification of *S. megalops* and *S. mitsukurii* among different workers, and particularly among fishery observers (R. Leslie, personal communication). Thus, there is a great need for taxonomic clarification of most eastern Atlantic and Mediterranean *Squalus* and in identifying reliable and unambiguous morphological traits to help in accurate and consistent species identification. Until that happens, it may useful to explicitly state the source of the used diagnostic traits and species designation for better correspondence among studies.

Concluding remarks

The aim of this paper was to clarify the diversity of *Squalus* species in the eastern Atlantic and Mediterranean, and to infer the consistency of species identification in these regions. To our knowledge, this study represents the most comprehensive molecular analysis of the genus *Squalus* so far, and clearly shows misidentification of Atlantic *Squalus*. The results also confirm many of the taxonomic uncertainties surrounding species delimitation, and pinpoint additional "hidden" diversity within the genus. The eastern Atlantic and Mediterranean represent some of the most intensively studied regions of the world's oceans; however, this wealth of information does not translate into a good understanding of the species diversity and raises additional concerns regarding accurate identification of elasmobranchs in other regions.

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Fig. 1. A-B Phylogenetic trees of *Squalus* based on nucleotide sequences from specimens sampled worldwide. –A. Tree based on COI sequences. –B Tree based on ND2 sequences. Clades detected in the eastern Atlantic and Mediterranean (Clades A – C) are highlighted in black or marked with a black arrow (Clade D). Branch support values are indicated for ML/BI only when >80%. Absence or * indicates values <80%.

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Fig. 2. Distribution of *Squalus* specimens from the eastern Atlantic and Mediterranean Sea, according to the reconstructed molecular clades. Grey circles – Clade A; white squares – Clade B; black diamonds – Clade C; black triangles – Clade D.

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Fig. 3. Distribution of the three main *Squalus* lineages worldwide: grey circles – lineage I; white squares – lineage II; black triangles – lineage III.

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A)

ZSC: for review purposes only please do not distribute

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Lineage I

Lineage II

Lineage III

Lineage I

Lineage II

Lineage III

ZSC submitted manuscript

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Table 1 List of *Squalus* species and the corresponding number of sequences of the COI and ND2 mitochondrial genes used in the current analysis (number of new sequences indicated in parentheses). Origin of the sampled specimens per species is also indicated. Note: the Mediterranean Sea and the Gulf of Mexico are included in the Atlantic. *Squalus* cf. *megalops* are included in *S. megalops*, and *S. cf. mitsukurii* are included in *S. mitsukurii*.

	COI	ND2	Origin
<i>S. acanthias</i>	175(30)	87(29)	Atlantic & Pacific
<i>S. albifrons</i>	4	1	
<i>S. blainville</i>	31(16)	12(12)	Atlantic
<i>S. brevirostris</i>	6	4	Pacific
<i>S. cf. fernandezianus</i>	1(1)		Pacific
<i>S. chloroculus</i>	6	1	Indo-Pacific
<i>S. crassispinus</i>	2	1	Indian
<i>S. cubensis</i>	22	1	Atlantic
<i>S. edmundsi</i>	14	1	Indo-Pacific
<i>S. formosus</i>	1	6	Pacific
<i>S. grahami</i>	6	1	Pacific
<i>S. griffini</i>	3(3)	4(4)	Pacific
<i>S. hemipinnis</i>	6		Indo-Pacific
<i>S. japonicus</i>	4	4	Pacific
<i>S. megalops</i>	64(59)	57(55)	Atlantic, Indian & Pacific
<i>S. mitsukurii</i>	19(17)	18(17)	Atlantic, Indian & Pacific
<i>S. montalbani</i>	18(11)	4	Indo-Pacific
<i>S. nasutus</i>	7	1	Pacific
<i>S. raoulensis</i>	4(4)	3(3)	Pacific
<i>Squalus</i> sp.	5(5)	1	Atlantic & Pacific
<i>Squalus</i> sp. A	6		Indian
<i>S. suckleyi</i>	17	47	Pacific
Total	421	254	

Table 2 Average genetic *p*-distances between *Squalus* clades occurring in the eastern Atlantic and Mediterranean (Clade A-D). Upper diagonal: values based on ND2 haplotypes; lower diagonal: values based on COI haplotypes.

	Clade A	Clade B	Clade C	Clade D
Clade A		0.074	0.065	0.065
Clade B	0.078		0.051	0.054
Clade C	0.073	0.068		0.030
Clade D	0.074	0.069	0.022	

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Table 3 Total number of specimens sampled in the eastern Atlantic and Mediterranean whose sequences cluster in Clades A-D (COI and ND2 combined), according to their original species identification. *Squalus* cf. *megalops* are included in *S. megalops*, and *S. cf. mitsukurii* are included in *S. mitsukurii*.

	Clade A	Clade B	Clade C	Clade D
<i>S. acanthias</i>	208	26		
<i>S. blainville</i>		33	1	
<i>S. megalops</i>		46	14	
<i>S. mitsukurii</i>				9
<i>Squalus</i> sp.				1
Total	208	105	15	10

Table S1 - Newly collected specimens of *Squalus*, including information on original species identification

Sample ID	Collector/Contributor	Whole voucher availability
MB85_15403	Ana Veríssimo	YES
MB85_15404	Ana Veríssimo	YES
MB85_15405	Ana Veríssimo	YES
MB85_15406	Ana Veríssimo	YES
MB85_15407	Ana Veríssimo	YES
MB85_15408	Ana Veríssimo	YES
MB85_15409	Ana Veríssimo	YES
MB85_15410	Ana Veríssimo	YES
MB85_15411	Ana Veríssimo	YES
MB85_15412	Ana Veríssimo	YES
MB85_15413	Ana Veríssimo	YES
MB85_15414	Ana Veríssimo	YES
MB85_15415	Ana Veríssimo	YES
MB85_15416	Ana Veríssimo	YES
MB85_15417	Ana Veríssimo	YES
05-01-05	Ana Veríssimo	NO
05-01-32	Ana Veríssimo	NO
05-01-45	Ana Veríssimo	NO
05-01-40	Ana Veríssimo	NO
05-01-48	Ana Veríssimo	NO
05-01-07	Ana Veríssimo	NO
348	Ana Veríssimo	NO
349	Ana Veríssimo	NO
350	Ana Veríssimo	NO
351	Ana Veríssimo	NO
352	Ana Veríssimo	NO
30.27	Andrew Griffiths	NO
30.28	Andrew Griffiths	NO
36.24	Andrew Griffiths	NO
36.26	Andrew Griffiths	NO
36.27	Andrew Griffiths	NO
36.28	Andrew Griffiths	NO
36.29	Andrew Griffiths	NO
47.27	Andrew Griffiths	NO
47.28	Andrew Griffiths	NO
47.29	Andrew Griffiths	NO
47.30	Andrew Griffiths	NO
47.31	Andrew Griffiths	NO
47.32	Andrew Griffiths	NO
47.33	Andrew Griffiths	NO
47.34	Andrew Griffiths	NO
47.35	Andrew Griffiths	NO
47.36	Andrew Griffiths	NO
47.37	Andrew Griffiths	NO
47.38	Andrew Griffiths	NO
BSeret_F	Bernard Séret	NO
BSeret_M	Bernard Séret	NO
4	Clinton Duffy	NO

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3	5	Clinton Duffy	NO
4	6	Clinton Duffy	NO
5	7	Clinton Duffy	NO
6	MA655697	Clinton Duffy	NO
7	MA655698	Clinton Duffy	NO
8	MA655737	Clinton Duffy	NO
9	ANG-NAM1	Diana Zaera-Perez	NO
10	ANG-NAM2	Diana Zaera-Perez	NO
11	ANG-NAM3	Diana Zaera-Perez	NO
12	ANG-NAM4	Diana Zaera-Perez	NO
13	ANG-NAM5	Diana Zaera-Perez	NO
14	ANG-NAM6	Diana Zaera-Perez	NO
15	ANG-NAM7	Diana Zaera-Perez	NO
16	ANG-NAM8	Diana Zaera-Perez	NO
17	ANG-NAM10	Diana Zaera-Perez	NO
18	ANG-NAM11	Diana Zaera-Perez	NO
19	ANG-NAM13	Diana Zaera-Perez	NO
20	ANG-NAM14	Diana Zaera-Perez	NO
21	ANG-NAM15	Diana Zaera-Perez	NO
22	ANG-NAM17	Diana Zaera-Perez	NO
23	ANG-NAM18	Diana Zaera-Perez	NO
24	ANG-NAM19	Diana Zaera-Perez	NO
25	ANG-NAM21	Diana Zaera-Perez	NO
26	ANG-NAM22	Diana Zaera-Perez	NO
27	ANG-NAM23	Diana Zaera-Perez	NO
28	ANG-NAM24	Diana Zaera-Perez	NO
29	ANG-NAM25	Diana Zaera-Perez	NO
30	ANG-NAM28	Diana Zaera-Perez	NO
31	ANG-NAM9	Diana Zaera-Perez	NO
32	ANG20A	Diana Zaera-Perez	NO
33	ANG21A	Diana Zaera-Perez	NO
34	ANG27A	Diana Zaera-Perez	NO
35	ANG28A	Diana Zaera-Perez	NO
36	ANG29A	Diana Zaera-Perez	NO
37	ANG30A	Diana Zaera-Perez	NO
38	ANG34A	Diana Zaera-Perez	NO
39	ANG35A	Diana Zaera-Perez	NO
40	ANG36A	Diana Zaera-Perez	NO
41	ANG37A	Diana Zaera-Perez	NO
42	ANG38A	Diana Zaera-Perez	NO
43	ANG39A	Diana Zaera-Perez	NO
44	ANG40A	Diana Zaera-Perez	NO
45	GEN 11	Diana Zaera-Perez	NO
46	GEN 12	Diana Zaera-Perez	NO
47	GB1	Diana Zaera-Perez	NO
48	GB12	Diana Zaera-Perez	NO
49	GB2	Diana Zaera-Perez	NO
50	GB3	Diana Zaera-Perez	NO
51	GB4	Diana Zaera-Perez	NO
52	GB5	Diana Zaera-Perez	NO
53	GBI1	Diana Zaera-Perez	NO
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4	GBI2	Diana Zaera-Perez	NO
5	GBI3	Diana Zaera-Perez	NO
6	GBI4	Diana Zaera-Perez	NO
7	GCK1	Diana Zaera-Perez	NO
8	GCK2	Diana Zaera-Perez	NO
9	GCK3	Diana Zaera-Perez	NO
10	GCK4	Diana Zaera-Perez	NO
11	Greece_22	Ioannis Batzakas	NO
12	Greece_23	Ioannis Batzakas	NO
13	Greece_21	Ioannis Batzakas	NO
14	GoLionLL010312	Joan Navarro	NO
15	GoLionLL101111_1	Joan Navarro	NO
16	GoLionPS280212	Joan Navarro	NO
17			
18	Crete3	Panagiotis Grigoriou/Aspasia Sterioti	YES
19	Crete2	Panagiotis Grigoriou/Aspasia Sterioti	YES
20	Crete1	Panagiotis Grigoriou/Aspasia Sterioti	YES
21	323	Rob Leslie	NO
22	281	Rob Leslie	NO
23	282	Rob Leslie	NO
24	283	Rob Leslie	NO
25	284	Rob Leslie	NO
26	285	Rob Leslie	NO
27	286	Rob Leslie	NO
28	302	Rob Leslie	NO
29	304	Rob Leslie	NO
30	305	Rob Leslie	NO
31	306	Rob Leslie	NO
32	324	Rob Leslie	NO
33	325	Rob Leslie	NO
34	326	Rob Leslie	NO
35			
36	BPS-0470	Samuel Iglésias	NO
37	BPS-0471	Samuel Iglésias	NO
38	BPS-2212	Samuel Iglésias	NO
39	BPS-2213	Samuel Iglésias	NO
40	Saca5	Sebastian Hernández	NO
41	Saca7	Sebastian Hernández	NO
42	Sferran	Sebastian Hernández	NO
43	Smega1	Sebastian Hernández	NO
44	Smega2	Sebastian Hernández	NO
45	Sgriff	Sebastian Hernández	NO
46	Smontal1	Sebastian Hernández	NO
47	Smontal10	Sebastian Hernández	NO
48	Smontal11	Sebastian Hernández	NO
49	Smontal2	Sebastian Hernández	NO
50	Smontal3	Sebastian Hernández	NO
51	Smontal4	Sebastian Hernández	NO
52	Smontal5	Sebastian Hernández	NO
53	Smontal6	Sebastian Hernández	NO
54	Smontal7	Sebastian Hernández	NO
55	Smontal8	Sebastian Hernández	NO
56	Smontal9	Sebastian Hernández	NO
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Sraoul	Sebastian Hernández	NO
S_sp5_1	Sebastian Hernández	NO
S_sp5_2	Sebastian Hernández	NO
S_sp5_3	Sebastian Hernández	NO
S_sp5_4	Sebastian Hernández	NO
S_sp5_5	Sebastian Hernández	NO

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, sampling location (latitude, longitude and depth in meters), and biological information (sex, total length in

Storing Institution	Station	Original species identification	Collection date	Sex
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	M
MUHNAC - Lisbon		Squalus blainville	15/11/2013	M
MUHNAC - Lisbon		Squalus blainville	15/11/2013	M
MUHNAC - Lisbon		Squalus blainville	15/11/2013	M
MUHNAC - Lisbon		Squalus blainville	15/11/2013	M
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
MUHNAC - Lisbon		Squalus blainville	15/11/2013	F
	1	Squalus mitsukurii	2005	M
	1	Squalus mitsukurii	2005	M
	1	Squalus mitsukurii	2005	M
	1	Squalus mitsukurii	2005	M
	1	Squalus mitsukurii	2005	M
	1	Squalus mitsukurii	2005	M
		Squalus mitsukurii	22/9/2005	M
		Squalus mitsukurii	22/9/2005	F
		Squalus mitsukurii	22/9/2005	F
		Squalus mitsukurii	22/9/2005	F
		Squalus mitsukurii	22/9/2005	F
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	1/6/2010	F
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	1/6/2010	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
MEDITS		Squalus acanthias	7/7/2011	M
		Squalus megalops	19/11/2013	M
		Squalus megalops	21/11/2013	M
	2450-3	Squalus griffini	16/07/2007	M

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3		2450-3	Squalus griffini	16/07/2007	F
4		2436-8	Squalus griffini	6/3/2007	F
5		2455-23	Squalus griffini		M
6					
7	Auckland Museum		Squalus raoulensis	24/5/2011	
8	Auckland Museum		Squalus raoulensis	24/5/2011	
9	Auckland Museum		Squalus raoulensis	24/5/2011	
10		47	Squalus megalops	4/8/2011	F
11		51	Squalus megalops	4/8/2011	F
12		40	Squalus megalops	4/8/2011	F
13		40	Squalus megalops	4/8/2011	F
14		94	Squalus megalops	4/8/2011	F
15		73	Squalus megalops	4/8/2011	M
16		82	Squalus megalops	4/8/2011	M
17		61	Squalus megalops	4/8/2011	M
18		47	Squalus megalops	4/8/2011	F
19		90	Squalus megalops	4/8/2011	M
20		73	Squalus megalops	4/8/2011	M
21		61	Squalus megalops	4/8/2011	M
22		73	Squalus megalops	4/8/2011	M
23		82	Squalus megalops	4/8/2011	M
24		51	Squalus megalops	4/8/2011	F
25		51	Squalus megalops	4/8/2011	M
26		51	Squalus megalops	4/8/2011	F
27		61	Squalus megalops	4/8/2011	M
28		47	Squalus megalops	4/8/2011	F
29		51	Squalus megalops	4/8/2011	M
30		61	Squalus megalops	4/8/2011	M
31		51	Squalus megalops	4/8/2011	F
32		82	Squalus megalops	4/8/2011	M
33		79	Squalus megalops	4/5/2012	F
34		32	Squalus megalops	4/5/2012	M
35		76	Squalus megalops	4/5/2012	F
36		79	Squalus megalops	4/5/2012	F
37		79	Squalus megalops	4/5/2012	F
38		79	Squalus megalops	4/5/2012	F
39		79	Squalus megalops	4/5/2012	F
40		79	Squalus megalops	4/5/2012	F
41		79	Squalus megalops	4/5/2012	M
42		79	Squalus megalops	4/5/2012	M
43		79	Squalus megalops	4/5/2012	M
44		79	Squalus megalops	4/5/2012	M
45		79	Squalus megalops	4/5/2012	M
46		79	Squalus megalops	4/5/2012	M
47		79	Squalus megalops	4/5/2012	M
48		79	Squalus megalops	4/5/2012	M
49		trap	Squalus megalops	4/7/2010	F
50		trap	Squalus megalops	4/7/2010	F
51		3	Squalus megalops	4/6/2010	M
52		18	Squalus megalops	4/6/2010	M
53		3	Squalus megalops	4/6/2010	M
54		3	Squalus megalops	4/6/2010	M
55		3	Squalus megalops	4/6/2010	M
56		3	Squalus megalops	4/6/2010	M
57		3	Squalus megalops	4/6/2010	F
58		32	Squalus megalops	4/10/2010	M
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32	<i>Squalus megalops</i>	4/10/2010	M
48	<i>Squalus megalops</i>	4/10/2010	F
32	<i>Squalus megalops</i>	4/10/2010	M
10	<i>Squalus megalops</i>	4/10/2010	M
21	<i>Squalus megalops</i>	4/10/2010	M
21	<i>Squalus megalops</i>	4/10/2010	M
	<i>Squalus megalops</i>	4/10/2010	M
	<i>Squalus acanthias</i>	17/6/2013	M
	<i>Squalus acanthias</i>	17/6/2013	F
	<i>Squalus acanthias</i>	17/6/2013	F
	<i>Squalus acanthias</i>	3/1/2012	M
	<i>Squalus acanthias</i>	10/11/2011	F
	<i>Squalus acanthias</i>	28/2/2012	M
	<i>Squalus acanthias</i>	11/4/2013	F
	<i>Squalus acanthias</i>	27/11/2008	F
	<i>Squalus acanthias</i>	27/11/2008	F
A31480	<i>Squalus acanthias</i>	10/2/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31368	<i>Squalus cf. megalops</i>	17/1/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
A31480	<i>Squalus cf. mitsukurii</i>	10/2/2011	
	<i>Squalus blainville</i>		
	<i>Squalus blainville</i>		
	<i>Squalus blainville</i>		
	<i>Squalus blainville</i>		
	<i>Squalus acanthias</i>		
	<i>Squalus acanthias</i>		
	<i>Squalus cf. fernandezianus</i>		
	<i>Squalus cf. megalops</i>		
	<i>Squalus cf. megalops</i>		
	<i>Squalus griffini</i>		
	<i>Squalus montalbani</i>		
	<i>Squalus montalbani</i>		
	<i>Squalus montalbani</i>		
	<i>Squalus montalbani</i>		
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	<i>Squalus montalbani</i>		

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Squalus raoulensis
Squalus sp
Squalus sp
Squalus sp
Squalus sp
Squalus sp

Review Copy

1 cm, total weight in grams), genetic markers sequenced and corresponding genetic clade and lineage.

Maturity stage	Total length (cm)	Weight (g)	Latitude	Longitude	Depth (m)
Mature	610		39.647	-9.302	
Immature	515		39.647	-9.302	
Mature	615		39.647	-9.302	
Mature	464		39.647	-9.302	
Mature	516		39.647	-9.302	
Mature	600		39.647	-9.302	
Mature	469		39.647	-9.302	
Mature	467		39.647	-9.302	
Mature	598		39.647	-9.302	
Mature	706		39.647	-9.302	
Mature	678		39.647	-9.302	
Mature	676		39.647	-9.302	
Mature	731		39.647	-9.302	
Mature	644		39.647	-9.302	
Mature	711		39.647	-9.302	
Mature	580		26.771	-84.859	514
Mature	580		26.771	-84.859	514
Mature	610		26.771	-84.859	514
Mature	605		26.771	-84.859	514
Mature	655		26.771	-84.859	514
Mature	595		26.771	-84.859	514
Immature	427	315	21.730	-158.140	
Immature	452	353	21.730	-158.140	
maturing	655	1148	21.730	-158.140	
maturing	672	1205	21.730	-158.140	
Immature	504	495	21.730	-158.140	
	570		39.910	3.570	<700
	294		39.910	3.570	<700
	325		39.910	3.570	<700
	313		39.910	3.570	<700
	492		39.910	3.570	<700
	433		39.910	3.570	<700
	361		39.910	3.570	<700
	520	600	34.925	33.862	
	555	820	34.925	33.862	
	485	504	34.925	33.862	
	523	750	34.925	33.862	
	550	850	34.925	33.862	
	510	650	34.925	33.862	
	490	600	34.925	33.862	
	550	800	34.925	33.862	
	560	900	34.925	33.862	
	510	620	34.925	33.862	
	500	620	34.925	33.862	
	511	620	34.925	33.862	
Immature	485				
Immature	505				
	890		-42.483	170.416	473

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3	809		-42.483	170.416	473
4	797		-36.313	176.168	400
5	617		-41.285	170.843	386
6			-30.510	-178.620	240
7			-30.510	-178.620	240
8			-30.510	-178.590	237
9	560	840	-15.372	11.949	115
10	498	670	-16.207	11.604	72
11	551	860	-14.046	12.251	143
12	465	450	-14.046	12.251	143
13	523	660	-18.339	11.642	153.5
14	385	250	-17.002	11.369	174
15	410	320	-17.212	11.480	150
16	426	380	-16.646	11.400	124
17	612	1300	-15.372	11.949	115
18	440	440	-17.867	11.741	63.5
19	453	400	-17.002	11.369	174
20	451	430	-16.646	11.400	124
21	434	370	-17.002	11.369	174
22	410	325	-17.212	11.480	150
23	438	400	-16.207	11.604	72
24	426	360	-16.207	11.604	72
25	441	430	-16.207	11.604	72
26	430	380	-16.646	11.400	124
27	583	940	-15.372	11.949	115
28	430	380	-16.207	11.604	72
29	421	380	-16.646	11.400	124
30	490	560	-16.207	11.604	72
31	411	308	-17.212	11.480	150
32	528		-16.534	11.415	116
33	466		-10.291	13.066	117
34	531		-16.271	11.517	106
35	528		-16.534	11.415	116
36	576		-16.534	11.415	116
37	576		-16.534	11.415	116
38	460		-16.534	11.415	116
39	426		-16.534	11.415	116
40	426		-16.534	11.415	116
41	531		-16.534	11.415	116
42	531		-16.534	11.415	116
43	424		-16.534	11.415	116
44	424		-16.534	11.415	116
45	628	1600	-15.011	60.146	288
46	701	2150	-15.011	60.146	288
47	654	1150	0.019	8.911	134
48	622	1100	-3.007	9.487	156.5
49	655	1250	0.019	8.911	134
50	416	350	0.019	8.911	134
51	422	350	0.019	8.911	134
52	356	220	0.019	8.911	134
53	680	900	10.099	-16.609	168
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3		700	1300	10.099	-16.609
4		841	2250	10.920	-17.211
5		660	1050	10.099	-16.609
6		670	1250	9.047	-15.105
7		670	1350	9.318	-15.859
8		680	1200	9.318	-15.859
9		640	1050	9.318	-15.859
10		510	541	38.956	26.482
11		525	570	38.956	26.482
12		650	1250	38.956	26.482
13		365	162	42.530	3.580
14		296		42.530	3.580
15	Immature	755	1454	42.750	4.190
16		605	1920	35.450	25.594
17	Mature	590	790	34.873	26.030
18	Mature	720	1260	34.873	26.030
19	Mature			-30.694	15.539
20				-35.547	19.519
21				-35.547	19.519
22				-35.547	19.519
23				-35.547	19.519
24				-35.547	19.519
25				-35.547	19.519
26				-35.547	19.519
27				-35.547	19.519
28				-30.694	15.539
29				-30.694	15.539
30				-30.694	15.539
31				-30.694	15.539
32				-30.694	15.539
33				-30.694	15.539
34				-30.694	15.539
35				-30.694	15.539
36		230		28.146	-14.739
37		380		28.146	-14.739
38		500		42.527	10.025
39		700		42.527	10.025
40					
41					
42				-33.827	-80.734
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Latitude and longitude values in italic red were estimated based on information from the exact sampling site.

Country	Region	Exact site	Markers
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI & ND2
Portugal	Eastern Atlantic	off Figueira da Foz	ND2
Portugal	Eastern Atlantic	off Figueira da Foz	ND2
Portugal	Eastern Atlantic	off Figueira da Foz	ND2
Portugal	Eastern Atlantic	off Figueira da Foz	COI
Portugal	Eastern Atlantic	off Figueira da Foz	COI
	Gulf of Mexico		COI & ND2
	Gulf of Mexico		COI & ND2
	Gulf of Mexico		COI & ND2
	Gulf of Mexico		COI & ND2
	Gulf of Mexico		COI & ND2
	Gulf of Mexico		COI & ND2
USA	Central Pacific	Hawaii	ND2
USA	Central Pacific	Hawaii	COI & ND2
USA	Central Pacific	Hawaii	COI
USA	Central Pacific	Hawaii	COI & ND2
USA	Central Pacific	Hawaii	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Spain	Mediterranean	Mallorca, Baearic Islands	COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		COI & ND2
Cyprus	Mediterranean		ND2
Morocco	Eastern Atlantic	Agadir fish market	COI & ND2
Morocco	Eastern Atlantic	Agadir fish market	COI & ND2
New Zealand	Pacific	Hokitika Canyon, West Coast, South Island	ND2

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3	New Zealand	Western Pacific	Hokitika Canyon, West Coast, South Island	COI & ND2
4	New Zealand	Western Pacific	East of Great barrier Island, NE North Island	COI & ND2
5	New Zealand	Western Pacific	off Karamea Bight, northwestern South Island	ND2
6	New Zealand	Western Pacific	Kermadec Islands,NZ	COI & ND2
7	New Zealand	Western Pacific	Kermadec Islands,NZ	COI & ND2
8	New Zealand	Western Pacific	Kermadec Islands,NZ	COI & ND2
9	Angola	Eastern Atlantic		COI & ND2
10	Angola	Eastern Atlantic		COI
11	Angola	Eastern Atlantic		COI & ND2
12	Angola	Eastern Atlantic		COI & ND2
13	Namibia	Eastern Atlantic		COI & ND2
14	Angola	Eastern Atlantic		COI & ND2
15	Angola	Eastern Atlantic		COI & ND2
16	Angola	Eastern Atlantic		COI & ND2
17	Angola	Eastern Atlantic		COI & ND2
18	Angola	Eastern Atlantic		COI & ND2
19	Angola	Eastern Atlantic		COI & ND2
20	Namibia	Eastern Atlantic		COI & ND2
21	Angola	Eastern Atlantic		COI & ND2
22	Angola	Eastern Atlantic		COI & ND2
23	Angola	Eastern Atlantic		COI & ND2
24	Angola	Eastern Atlantic		COI & ND2
25	Angola	Eastern Atlantic		COI & ND2
26	Angola	Eastern Atlantic		COI & ND2
27	Angola	Eastern Atlantic		COI & ND2
28	Angola	Eastern Atlantic		COI & ND2
29	Angola	Eastern Atlantic		COI & ND2
30	Angola	Eastern Atlantic		COI & ND2
31	Angola	Eastern Atlantic		COI & ND2
32	Angola	Eastern Atlantic		COI & ND2
33	Angola	Eastern Atlantic		COI & ND2
34	Angola	Eastern Atlantic		COI & ND2
35	Angola	Eastern Atlantic		COI & ND2
36	Angola	Eastern Atlantic		COI & ND2
37	Angola	Eastern Atlantic		COI & ND2
38	Angola	Eastern Atlantic		COI
39	Angola	Eastern Atlantic		COI & ND2
40	Angola	Eastern Atlantic		COI
41	Angola	Eastern Atlantic		COI & ND2
42	Angola	Eastern Atlantic		COI & ND2
43	Angola	Eastern Atlantic		COI & ND2
44	Angola	Eastern Atlantic		COI & ND2
45	Angola	Eastern Atlantic		COI & ND2
46	Angola	Eastern Atlantic		COI & ND2
47	Angola	Eastern Atlantic		COI & ND2
48	Angola	Eastern Atlantic		COI & ND2
49	Mauritius	Western Indian		COI & ND2
50	Mauritius	Western Indian		COI & ND2
51	Gabon	Eastern Atlantic		ND2
52	Gabon	Eastern Atlantic		COI & ND2
53	Gabon	Eastern Atlantic		ND2
54	Gabon	Eastern Atlantic		COI & ND2
55	Gabon	Eastern Atlantic		COI & ND2
56	Gabon	Eastern Atlantic		COI & ND2
57	Gabon	Eastern Atlantic		COI & ND2
58	Guinea-Bissau	Eastern Atlantic		COI & ND2
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3	Guinea-Bissau	Eastern Atlantic		COI & ND2
4	Guinea-Bissau	Eastern Atlantic		COI & ND2
5	Guinea-Bissau	Eastern Atlantic		COI & ND2
6	Guinea-Conakri	Eastern Atlantic		COI & ND2
7	Guinea-Conakri	Eastern Atlantic		COI & ND2
8	Guinea-Conakri	Eastern Atlantic		COI & ND2
9	Guinea-Conakri	Eastern Atlantic		COI & ND2
10	Guinea-Conakri	Eastern Atlantic		ND2
11	Greece	Mediterranean	South of Lesvos	COI & ND2
12	Greece	Mediterranean	South of Lesvos	COI & ND2
13	Greece	Mediterranean	South of Lesvos	COI & ND2
14	France	Mediterranean	Gulf of Lion	COI & ND2
15	France	Mediterranean	Gulf of Lion	COI & ND2
16	France	Mediterranean	Gulf of Lion	COI & ND2
17	Greece	Mediterranean	Crete	COI & ND2
18	Greece	Mediterranean	Crete	COI & ND2
19	Greece	Mediterranean	Crete	COI & ND2
20	South Africa	Eastern Atlantic		COI & ND2
21	South Africa	Eastern Atlantic		COI
22	South Africa	Eastern Atlantic		COI & ND2
23	South Africa	Eastern Atlantic		COI & ND2
24	South Africa	Eastern Atlantic		COI
25	South Africa	Eastern Atlantic		COI & ND2
26	South Africa	Eastern Atlantic		COI & ND2
27	South Africa	Eastern Atlantic		COI & ND2
28	South Africa	Eastern Atlantic		COI & ND2
29	South Africa	Eastern Atlantic		COI & ND2
30	South Africa	Eastern Atlantic		COI & ND2
31	South Africa	Eastern Atlantic		COI & ND2
32	South Africa	Eastern Atlantic		COI & ND2
33	South Africa	Eastern Atlantic		COI & ND2
34	South Africa	Eastern Atlantic		COI & ND2
35	Spain	Eastern Atlantic	Canary Islands	COI
36	Spain	Eastern Atlantic	Canary Islands?	COI
37	France	Mediterranean	Corsica	COI
38	France	Mediterranean	Corsica	COI
39		Pacific		COI
40		Pacific		COI
41	Chile	Eastern Pacific	Juan Fernández Island	COI
42		Pacific		COI
43		Pacific		COI
44		Pacific		COI
45		Pacific		COI
46		Pacific		COI
47		Pacific		COI
48		Pacific		COI
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50		Pacific		COI
51		Pacific		COI
52		Pacific		COI
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Genetic clade	Genetic lineage	COI_Accession	ND2_Accession
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
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Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
Clade B	II		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (GoM/Uruguay)	III		
S. mitsukurii (Hawaii)	III		
S. mitsukurii (Hawaii)	III		
S. mitsukurii (Hawaii)	III		
S. mitsukurii (Hawaii)	III		
Clade B	II		
Clade B	II		
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Clade B	II		
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Clade B	II		
Clade B	II		
Clade B	II		
S. griffini	III		

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3	S. griffini	III
4	S. griffini	III
5	S. griffini	III
6	S. raoulensis	II
7	S. raoulensis	II
8	S. raoulensis	II
9	Clade B	II
10	Clade B	II
11	Clade B	II
12	Clade B	II
13	Clade B	II
14	Clade B	II
15	Clade B	II
16	Clade B	II
17	Clade B	II
18	Clade B	II
19	Clade B	II
20	Clade B	II
21	Clade B	II
22	Clade B	II
23	Clade B	II
24	Clade B	II
25	Clade B	II
26	Clade B	II
27	Clade B	II
28	Clade B	II
29	Clade B	II
30	Clade B	II
31	Clade B	II
32	Clade B	II
33	Clade B	II
34	Clade B	II
35	Clade B	II
36	Clade B	II
37	Clade B	II
38	Clade B	II
39	Clade B	II
40	Clade B	II
41	Clade B	II
42	Clade B	II
43	Clade B	II
44	Clade B	II
45	Clade B	II
46	Clade B	II
47	Clade B	II
48	Clade B	II
49	S. cf. megalops (Mauritius)	III
50	S. cf. megalops (Mauritius)	III
51	Clade C	III
52	Clade C	III
53	Clade C	III
54	Clade C	III
55	Clade C	III
56	Clade C	III
57	Clade C	III
58	Clade C	III
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3	Clade C	III
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7	Clade C	III
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9	Clade C	III
10	Clade C	III
11	Clade B	II
12	Clade B	II
13	Clade B	II
14	Clade A	I
15	Clade A	I
16	Clade A	I
17	Clade B	II
18	Clade B	II
19	Clade B	II
20	Clade A	I
21	Clade B	II
22	Clade B	II
23	Clade B	II
24	Clade B	II
25	Clade B	II
26	Clade B	II
27	Clade B	II
28	Clade D	III
29	Clade D	III
30	Clade D	III
31	Clade D	III
32	Clade D	III
33	Clade D	III
34	Clade D	III
35	Clade D	III
36	Clade B	II
37	Clade B	II
38	Clade B	II
39	Clade B	II
40	Clade A	I
41	Clade A	I
42	Squalus sp. (Juan Fernández Is.)	III
43	S. megalops	II
44	S. raoulensis	II
45	S. griffini	III
46	S. montalbani	III
47	S. chloroculus	III
48	S. nasutus	III
49	S. montalbani	III
50	S. montalbani	III
51	S. montalbani	III
52	S. montalbani	III
53	S. montalbani	III
54	S. montalbani	III
55	S. montalbani	III
56	S. montalbani	III
57	S. montalbani	III
58	S. montalbani	III
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S. raoulensis	II
S. montalbani	III
S. montalbani	III
S. montalbani	III
S. montalbani	III
S. montalbani	III

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Table S2 - Sequences downloaded from publicly available databases, including information on sequence

Database (& reference)	Sequence ID	Original species identification	Latitude	Longitude
BOLD:AAA1547	ELAME211-09	Squalus acanthias	44.816	12.769
BOLD:AAA1547	ELAME235-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME237-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME238-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME239-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME240-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME241-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME242-09	Squalus acanthias	45.166	13.159
BOLD:AAA1547	ELAME251-09	Squalus acanthias	43.864	13.643
BOLD:AAA1547	ELAME252-09	Squalus acanthias	43.864	13.643
BOLD:AAA1547	ELAME255-09	Squalus acanthias	44.557	13.683
BOLD:AAA1547	ELAME256-09	Squalus acanthias	44.557	13.683
BOLD:AAA1547	ELAME257-09	Squalus acanthias	44.557	13.683
BOLD:AAA1547	ELAME258-09	Squalus acanthias	44.557	13.683
BOLD:AAA1547	ELAME259-09	Squalus acanthias	44.832	13.221
BOLD:AAA1547	ELAME260-09	Squalus acanthias	43.677	13.555
BOLD:AAA1547	ELAME263-09	Squalus acanthias	44.633	14.134
BOLD:AAA1547	ELAME265-09	Squalus acanthias	44.323	13.799
BOLD:AAA1547	ELAME266-09	Squalus acanthias	44.100	13.643
BOLD:AAA1547	ELAME267-09	Squalus acanthias	44.100	13.643
BOLD:AAA1547	ELAME268-09	Squalus acanthias	44.356	12.999
BOLD:AAA1547	ELAME269-09	Squalus acanthias	44.356	12.999
BOLD:AAA1547	ELAME271-09	Squalus acanthias	44.322	14.112
BOLD:AAA1547	ELAME273-09	Squalus acanthias	44.322	14.112
BOLD:AAA1547	ELAME274-09	Squalus acanthias	44.223	14.112
BOLD:AAA1547	ELAME275-09	Squalus acanthias	44.322	14.112
BOLD:AAA1547	ELAME276-09	Squalus acanthias	44.322	14.112
BOLD:AAA1547	ELAME277-09	Squalus acanthias	44.322	14.112
BOLD:AAA1547	ELAME279-09	Squalus acanthias	43.877	13.798
BOLD:AAA1547	ELAME280-09	Squalus acanthias	43.886	13.666
BOLD:AAA1547	ELAME291-09	Squalus acanthias	44.926	14.587
BOLD:AAA1547	ELAME292-09	Squalus acanthias	43.926	14.587
BOLD:AAA1547	ELAME302-09	Squalus acanthias	44.322	14.000
BOLD:AAA1547	ELAME303-09	Squalus acanthias	44.322	14.000
BOLD:AAA1547	ELAME304-09	Squalus acanthias	44.322	14.000
BOLD:AAA1547	ELAME311-09	Squalus acanthias	44.755	12.988
BOLD:AAA1547	ELAME315-09	Squalus acanthias	44.210	13.654
BOLD:AAA1547	ELAME317-09	Squalus acanthias	44.210	13.654
BOLD:AAA1547	ELAME318-09	Squalus acanthias	44.210	13.654
BOLD:AAA1547	ELAME319-09	Squalus acanthias	44.210	13.654
BOLD:AAA1547	ELAME358-09	Squalus acanthias	45.485	13.385
BOLD:AAA1547	ELAME359-09	Squalus acanthias	44.241	13.383
BOLD:AAA1547	ELAME360-09	Squalus acanthias	44.241	13.383
BOLD:AAA1547	ELAME361-09	Squalus acanthias	44.241	13.383
BOLD:AAA1547	ELAME362-09	Squalus acanthias	44.241	13.383
BOLD:AAA1547	ELAME363-09	Squalus acanthias	44.241	13.383
BOLD:AAA1547	ELAME364-09	Squalus acanthias	44.338	13.027
BOLD:AAA1547	ELAME366-09	Squalus acanthias	44.338	13.027

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3	BOLD:AAA1547	ELAME368-09	Squalus acanthias	44.618	12.772
4	BOLD:AAA1547	ELAME369-09	Squalus acanthias	44.618	12.772
5	BOLD:AAA1547	ELAME370-09	Squalus acanthias	44.618	12.772
6	BOLD:AAA1547	ELAME371-09	Squalus acanthias	44.618	12.772
7	BOLD:AAA1547	ELAME372-09	Squalus acanthias	44.618	12.772
8	BOLD:AAA1547	ELAME373-09	Squalus acanthias	44.618	12.770
9	BOLD:AAA1547	ELAME374-09	Squalus acanthias	44.618	12.772
10	BOLD:AAA1547	ELAME375-09	Squalus acanthias	44.012	14.446
11	BOLD:AAA1547	ELAME376-09	Squalus acanthias	44.012	14.446
12	BOLD:AAA1547	ELAME377-09	Squalus acanthias	43.938	14.471
13	BOLD:AAA1547	ELAME378-09	Squalus acanthias	43.938	14.471
14	BOLD:AAA1547	ELAME379-09	Squalus acanthias	43.938	14.471
15	BOLD:AAA1547	ELAME380-09	Squalus acanthias	43.938	14.446
16	BOLD:AAA1547	ELAME381-09	Squalus acanthias	43.938	14.471
17	BOLD:AAA1547	ELAME382-09	Squalus acanthias	43.938	14.471
18	BOLD:AAA1547	ELAME384-09	Squalus acanthias	44.768	12.846
19	BOLD:AAA1547	ELAME385-09	Squalus acanthias	44.768	12.846
20	BOLD:AAA1547	ELAME386-09	Squalus acanthias	44.468	13.285
21	BOLD:AAA1547	ELAME387-09	Squalus acanthias	44.468	13.285
22	BOLD:AAA1547	ELAME388-09	Squalus acanthias	44.741	13.391
23	BOLD:AAA1547	ELAME389-09	Squalus acanthias	45.118	12.655
24	BOLD:AAA1547	ELAME391-09	Squalus acanthias	43.938	14.591
25	BOLD:AAA1547	ELAME393-09	Squalus acanthias	43.938	14.591
26	BOLD:AAA1547	ELAME394-09	Squalus acanthias	43.938	14.591
27	BOLD:AAA1547	ELAME395-09	Squalus acanthias	43.851	14.508
28	BOLD:AAA1547	ELAME396-09	Squalus acanthias	44.151	14.351
29	BOLD:AAA1547	ELAME397-09	Squalus acanthias	44.446	12.618
30	BOLD:AAA1547	ELAME399-09	Squalus acanthias	44.200	13.037
31	BOLD:AAA1547	ELAME401-09	Squalus acanthias	44.200	13.037
32	BOLD:AAA1547	ELAME403-09	Squalus acanthias	44.200	13.037
33	BOLD:AAA1547	ELAME405-09	Squalus acanthias	44.200	13.037
34	BOLD:AAA1547	ELAME407-09	Squalus acanthias	43.666	13.334
35	BOLD:AAA1547	ELAME408-09	Squalus acanthias	43.666	13.334
36	BOLD:AAA1547	ELAME410-09	Squalus acanthias	43.666	13.334
37	BOLD:AAA1547	ELAME411-09	Squalus acanthias	43.666	13.334
38	BOLD:AAA1547	ELAME413-09	Squalus acanthias	43.666	13.334
39	BOLD:AAA1547	ELAME415-09	Squalus acanthias	43.666	13.334
40	BOLD:AAA1547	ELAME417-09	Squalus acanthias	43.666	13.334
41	BOLD:AAA1547	ELAME418-09	Squalus acanthias	43.666	13.334
42	BOLD:AAA1547	ELAME420-09	Squalus acanthias	45.358	13.180
43	BOLD:AAA1547	ELAME422-09	Squalus acanthias	45.358	13.180
44	BOLD:AAA1547	ELAME424-09	Squalus acanthias	45.358	13.180
45	BOLD:AAA1547	ELAME426-09	Squalus acanthias	45.358	13.180
46	BOLD:AAA1547	ELAME428-09	Squalus acanthias	45.358	13.180
47	BOLD:AAA1547	ELAME431-09	Squalus acanthias	45.358	13.180
48	BOLD:AAA1547	ELAME432-09	Squalus acanthias	45.358	13.180
49	BOLD:AAA1547	ELAME435-09	Squalus acanthias	45.358	13.180
50	BOLD:AAA1547	ELAME436-09	Squalus acanthias	45.080	13.160
51	BOLD:AAA1547	ELAME438-09	Squalus acanthias	45.080	13.160
52	BOLD:AAA1547	ELAME440-09	Squalus acanthias	45.080	13.160
53	BOLD:AAA1547	ELAME442-09	Squalus acanthias	45.080	13.160
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3	BOLD:AAA1547	ELAME444-09	Squalus acanthias	45.080	13.160
4	BOLD:AAA1547	ELAME446-09	Squalus acanthias	45.080	13.160
5	BOLD:AAA1547	ELAME448-09	Squalus acanthias	43.770	14.285
6	BOLD:AAA1547	ELAME449-09	Squalus acanthias	43.666	13.334
7	BOLD:AAA1547	ELAME450-09	Squalus acanthias	43.666	13.334
8	BOLD:AAA1547	ELAME451-09	Squalus acanthias	43.666	13.334
9	BOLD:AAA1547	ELAME452-09	Squalus acanthias	43.666	13.334
10	BOLD:AAA1547	ELAME453-09	Squalus acanthias	44.983	13.201
11	BOLD:AAA1547	ELAME454-09	Squalus acanthias	45.093	13.071
12	BOLD:AAA1547	ELAME455-09	Squalus acanthias	45.300	13.162
13	BOLD:AAA1547	ELAME457-09	Squalus acanthias	44.991	12.972
14	BOLD:AAA1547	ELAME458-09	Squalus acanthias	44.991	12.972
15	BOLD:AAA1547	ELAME459-09	Squalus acanthias	44.871	12.901
16	BOLD:AAA1547	ELAME460-09	Squalus acanthias	44.871	12.901
17	BOLD:AAA1547	ELAME461-09	Squalus acanthias	44.871	12.901
18	BOLD:AAA1547	ELAME462-09	Squalus acanthias	43.850	13.030
19	BOLD:AAA1547	ELAME484-09	Squalus blainville	34.354	33.126
20	BOLD:AAA1550	ELAME505-09	Squalus blainville	34.360	33.181
21	BOLD:AAA1550	ELAME508-09	Squalus blainville	34.361	33.149
22	BOLD:AAA1550	ELAME509-09	Squalus blainville	34.361	33.149
23	BOLD:AAA1550	ELAME510-09	Squalus blainville	34.361	33.149
24	BOLD:AAA1550	ELAME521-09	Squalus blainville	37.314	11.866
25	BOLD:AAA1550	ELAME522-09	Squalus blainville	37.314	11.866
26	BOLD:AAA1550	ELAME523-09	Squalus blainville	37.314	11.866
27	BOLD:AAA1550	ELAME524-09	Squalus blainville	37.314	11.866
28	BOLD:AAA1550	ELAME586-09	Squalus blainville	43.228	9.650
29	BOLD:AAA1550	ELAME587-09	Squalus blainville	43.228	9.650
30	BOLD:AAA1550	ELAME588-09	Squalus blainville	43.228	9.650
31	BOLD:AAA1550	ELAME589-09	Squalus blainville	43.228	9.650
32	BOLD:AAA1550	ELAME590-09	Squalus blainville	43.228	9.650
33	BOLD:AAA1547	FOA083-04	Squalus acanthias	-42.700	148.400
34	BOLD:AAA1547	FOA084-04	Squalus acanthias	-42.667	148.433
35	BOLD:AAA1547	FOA085-04	Squalus acanthias	-42.830	147.550
36	BOLD:AAA1547	FOA086-04	Squalus acanthias	-43.082	147.310
37	BOLD:AAA1547	FOA087-04	Squalus acanthias	-43.167	147.250
38	BOLD:AAA1547	FOAE100-06	Squalus acanthias	43.190	-68.310
39	BOLD:AAA1547	FOAE101-06	Squalus acanthias	43.190	-68.310
40	BOLD:AAA1547	FOAE102-06	Squalus acanthias	43.190	-68.310
41	BOLD:AAA1547	FOAE103-06	Squalus acanthias	43.190	-68.310
42	BOLD:AAA1547	FOAE104-06	Squalus acanthias	43.190	-68.310
43	BOLD:AAA1547	FOAE105-06	Squalus acanthias	-38.633	-73.983
44	BOLD:AAA1547	FOAE106-06	Squalus acanthias	-38.633	-73.983
45	BOLD:AAA1547	FOAE107-06	Squalus acanthias	-38.633	-73.983
46	BOLD:AAA1547	FOAE108-06	Squalus acanthias	-38.633	-73.983
47	BOLD:AAA1547	FOAE109-06	Squalus acanthias	-38.633	-73.983
48	BOLD:AAA1547	FOAE110-06	Squalus acanthias	49.070	-8.250
49	BOLD:AAA1547	FOAE111-06	Squalus acanthias	49.070	-8.250
50	BOLD:AAA1547	FOAE112-06	Squalus acanthias	49.070	-8.250
51	BOLD:AAA1547	FOAE113-06	Squalus acanthias	49.070	-8.250
52	BOLD:AAB2934	FOA030-04	Squalus albifrons	-32.983	152.233
53	BOLD:AAB2934	FOA108-04	Squalus albifrons	-33.617	151.917
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3	BOLD:AAB2934	FOA109-04	Squalus albifrons	-33.617	151.917
4	BOLD:AAB2934	FOA110-04	Squalus albifrons	-33.467	152.000
5	BOLD:AAA1550	FOAE072-06	Squalus brevirostris		
6	BOLD:AAA1550	FOAE074-06	Squalus brevirostris		
7	BOLD:AAA1550	FOAF119-07	Squalus brevirostris	31.483	130.033
8	BOLD:AAA1550	FOAF120-07	Squalus brevirostris	31.483	130.033
9	BOLD:AAA1550	FOAF121-07	Squalus brevirostris	31.483	130.033
10	BOLD:AAA1550	FOAF122-07	Squalus brevirostris	31.417	130.183
11	BOLD:AAB2934	FOA097-04	Squalus chloroculus	-33.420	129.917
12	BOLD:AAB2934	FOA098-04	Squalus chloroculus	-33.720	129.817
13	BOLD:AAB2934	FOA099-04	Squalus chloroculus	-33.720	129.817
14	BOLD:AAB2934	FOA100-04	Squalus chloroculus		
15	BOLD:AAB2934	FOA101-04	Squalus chloroculus	-33.433	152.100
16	BOLD:AAB2934	FOAD654-05	Squalus chloroculus	-42.167	144.750
17	BOLD:AAB2934	FOA116-04	Squalus crassispinus	-19.100	117.017
18	BOLD:AAB2934	FOA117-04	Squalus crassispinus	-19.100	117.017
19	BOLD:AAB2934	FOA102-04	Squalus edmundsi	-31.950	115.133
20	BOLD:AAB2934	FOA103-04	Squalus edmundsi	-31.717	114.967
21	BOLD:AAB2934	FOA104-04	Squalus edmundsi	-31.717	114.967
22	BOLD:AAB2934	FOA105-04	Squalus edmundsi	-31.717	114.967
23	BOLD:AAB2934	FOA111-04	Squalus edmundsi	-32.333	115.000
24	BOLD:AAB2934	FOA112-04	Squalus edmundsi	-32.333	115.000
25	BOLD:AAB2934	FOA113-04	Squalus edmundsi	-32.333	115.000
26	BOLD:AAB2934	FOA114-04	Squalus edmundsi		
27	BOLD:AAB2934	FOA115-04	Squalus edmundsi		
28	BOLD:AAB2934	FOAE075-06	Squalus edmundsi	-8.750	115.167
29	BOLD:AAB2934	FOAE076-06	Squalus edmundsi	-8.750	115.167
30	BOLD:AAB2934	FOAE078-06	Squalus edmundsi	-8.750	116.583
31	BOLD:AAB2934	FOAE079-06	Squalus edmundsi	-8.750	116.583
32	BOLD:AAB2934	FOAE388-06	Squalus edmundsi	-8.750	116.583
33	BOLD:AAB2934	FOA094-04	Squalus grahami	-33.433	152.100
34	BOLD:AAB2934	FOA120-04	Squalus grahami	-33.533	152.000
35	BOLD:AAB2934	FOA121-04	Squalus grahami	-33.533	152.000
36	BOLD:AAB2934	FOA122-04	Squalus grahami	-33.533	152.000
37	BOLD:AAB2934	FOA123-04	Squalus grahami	-33.533	152.000
38	BOLD:AAB2934	FOA124-04	Squalus grahami	-33.433	152.100
39	BOLD:AAB2934	FOAE090-06	Squalus hemipinnis	-8.750	115.167
40	BOLD:AAB2934	FOAE091-06	Squalus hemipinnis	-8.750	115.167
41	BOLD:AAB2934	FOAE092-06	Squalus hemipinnis	-8.750	115.167
42	BOLD:AAB2934	FOAE093-06	Squalus hemipinnis	-8.750	115.167
43	BOLD:AAB2934	FOAE094-06	Squalus hemipinnis	-8.750	115.167
44	BOLD:AAB2934	FOAE389-06	Squalus hemipinnis	-8.750	116.583
45	BOLD:AAB2934	FOAE080-06	Squalus japonicus		
46	BOLD:AAB2934	FOAE081-06	Squalus japonicus		
47	BOLD:AAB2934	FOAE083-06	Squalus japonicus		
48	BOLD:AAB2934	FOAE084-06	Squalus japonicus		
49	BOLD:AAA1550	FOA088-04	Squalus megalops	-38.717	148.267
50	BOLD:AAA1550	FOA090-04	Squalus megalops	-38.717	148.267
51	BOLD:AAA1550	FOA091-04	Squalus megalops	-38.717	148.267
52	BOLD:AAA1550	FOA092-04	Squalus megalops	-38.500	148.417
53	BOLD:AAB2934	FOA093-04	Squalus montalbani	-33.433	152.100
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3	BOLD:AAB2934	FOA095-04	Squalus montalbani	-33.433	152.100
4	BOLD:AAB2934	FOA096-04	Squalus montalbani	-33.433	152.100
5	BOLD:AAB2934	FOA106-04	Squalus montalbani	-32.000	114.917
6	BOLD:AAB2934	FOAE087-06	Squalus montalbani	-8.750	115.167
7	BOLD:AAB2934	FOAE088-06	Squalus montalbani	-8.750	115.167
8	BOLD:AAB2934	FOAE089-06	Squalus montalbani	-7.020	106.470
9	BOLD:AAB2934	FOA118-04	Squalus nasutus		
10	BOLD:AAB2934	FOA119-04	Squalus nasutus		
11	BOLD:AAB2934	FOAE095-06	Squalus nasutus	-8.750	115.167
12	BOLD:AAB2934	FOAE096-06	Squalus nasutus	-8.750	115.167
13	BOLD:AAB2934	FOAE097-06	Squalus nasutus	-7.667	109.000
14	BOLD:AAB2934	FOAE098-06	Squalus nasutus	-7.667	109.000
15	BOLD:AAB2934	FOAE099-06	Squalus nasutus	-7.667	109.000
16	BOLD:AAA1547	FOAE115-06	Squalus suckleyi	47.730	-122.470
17	BOLD:AAA1547	FOAE116-06	Squalus suckleyi	47.730	-122.470
18	BOLD:AAA1547	FOAE117-06	Squalus suckleyi	47.730	-122.470
19	BOLD:AAA1547	FOAE118-06	Squalus suckleyi	47.730	-122.470
20	BOLD:AAA1547	FOAE119-06	Squalus suckleyi	47.730	-122.470
21	BOLD:AAA1547	FOAE120-06	Squalus suckleyi	44.730	146.230
22	BOLD:AAA1547	FOAE121-06	Squalus suckleyi	44.730	146.230
23	BOLD:AAA1547	FOAE122-06	Squalus suckleyi	44.730	146.230
24	BOLD:AAA1547	FARG199-06	Squalus acanthias	-46.471	-66.369
25	BOLD:AAA1547	FARG201-06	Squalus acanthias	-46.471	-66.369
26	BOLD:AAA1547	FARG202-06	Squalus acanthias	-46.471	-66.369
27	BOLD:AAA1547	FARG203-06	Squalus acanthias	-46.471	-66.369
28	BOLD:AAA1547	FARG204-06	Squalus acanthias	-45.343	-61.545
29	BOLD:AAA1547	FARG205-06	Squalus acanthias	-45.343	-61.545
30	BOLD:AAA1547	FARG227-06	Squalus acanthias	-44.407	-61.308
31	BOLD:AAA1547	FARG228-06	Squalus acanthias	-44.407	-61.308
32	BOLD:AAA1547	FARG254-06	Squalus acanthias	-41.580	-58.540
33	BOLD:AAA1547	FARG255-06	Squalus acanthias	-41.580	-58.540
34	BOLD:AAA1547	FARG334-07	Squalus acanthias	-34.570	-52.260
35	BOLD:AAB2934	FARG333-07	Squalus mitsukurii	-34.570	-52.260
36	BOLD:AAB2934	FARG335-07	Squalus mitsukurii	-34.570	-52.260
37	BOLD:AAA1550	GMSHK028-11	Squalus cubensis	29.310	-86.495
38	BOLD:AAA1550	GMSHK032-11	Squalus cubensis	29.136	-86.590
39	BOLD:AAA1550	GMSHK047-11	Squalus cubensis	29.137	-86.957
40	BOLD:AAA1550	GMSHK048-11	Squalus cubensis	29.137	-86.957
41	BOLD:AAA1550	GMSHK051-11	Squalus cubensis	29.142	-86.116
42	BOLD:AAA1550	GMSHK052-11	Squalus cubensis	29.141	-86.117
43	BOLD:AAA1550	GMSHK053-11	Squalus cubensis	29.135	-85.959
44	BOLD:AAA1550	GMSHK180-12	Squalus cubensis		
45	BOLD:AAA1550	GMSHK185-12	Squalus cubensis		
46	BOLD:AAA1550	GMSHK186-12	Squalus cubensis		
47	BOLD:AAA1550	GMSHK187-12	Squalus cubensis		
48	BOLD:AAA1550	GMSHK189-12	Squalus cubensis		
49	BOLD:AAA1550	GMSHK197-12	Squalus cubensis		
50	BOLD:AAA1550	GMSHK209-12	Squalus cubensis		
51	BOLD:AAA1550	GMSHK248-12	Squalus cubensis		
52	BOLD:AAA1550	GMSHK249-12	Squalus cubensis		
53	BOLD:AAA1550	GMSHK250-12	Squalus cubensis		
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3	BOLD:AAA1550	GMSHK251-12	<i>Squalus cubensis</i>		
4	BOLD:AAA1550	GMSHK252-12	<i>Squalus cubensis</i>		
5	BOLD:AAA1550	GMSHK253-12	<i>Squalus cubensis</i>		
6	BOLD:AAA1550	GMSHK268-12	<i>Squalus cubensis</i>		
7	BOLD:AAA1550	GMSHK282-12	<i>Squalus cubensis</i>		
8	BOLD:AAA1547	TZFPB051-05	<i>Squalus suckleyi</i>	48.810	-125.250
9	BOLD:AAA1547	TZFPB114-05	<i>Squalus suckleyi</i>	48.850	-125.150
10	BOLD:AAA1547	TZFPB141-05	<i>Squalus suckleyi</i>	48.900	-125.030
11	BOLD:AAA1547	TZFPB168-05	<i>Squalus suckleyi</i>	48.930	-125.440
12	BOLD:AAA1547	TZFPB465-06	<i>Squalus suckleyi</i>		
13	BOLD:AAA1547	TZFPB536-06	<i>Squalus suckleyi</i>		
14	BOLD:AAA1547	TZFPB559-06	<i>Squalus suckleyi</i>		
15	BOLD:AAA1547	TZFPB567-06	<i>Squalus suckleyi</i>		
16	BOLD:AAA1547	TZFPB580-06	<i>Squalus suckleyi</i>		
17	GenBank	KF899758	<i>Squalus</i> sp. A		
18	GenBank	KF899759	<i>Squalus</i> sp. A		
19	GenBank	KF899760	<i>Squalus</i> sp. A		
20	GenBank	KF899761	<i>Squalus</i> sp. A		
21	GenBank	KF899762	<i>Squalus</i> sp. A		
22	GenBank	KF899763	<i>Squalus</i> sp. A		
23	GenBank	EF539330	<i>Squalus formosus</i>		
24		BW6237	<i>Squalus megalops</i>	34.267	10.515
25		BW6236	<i>Squalus blainville</i>	33.967	10.515
26	GenBank	JQ035532	<i>S. acanthias</i>	37.090	-74.830
27	GenBank	JQ035533	<i>S. acanthias</i>	52.371	-5.871
28	GenBank	JQ035534	<i>S. acanthias</i>	-47.488	-63.089
29	GenBank	JQ035535	<i>S. acanthias</i>	-47.168	-62.082
30	GenBank	JQ035536	<i>S. acanthias</i>	-46.396	-61.509
31	GenBank	JQ035537	<i>S. acanthias</i>	-46.396	-61.509
32	GenBank	JQ035538	<i>S. acanthias</i>	-43.054	-174.200
33	GenBank	JQ035539	<i>S. acanthias</i>	-43.573	-176.460
34	GenBank	JQ035540	<i>S. acanthias</i>	-46.506	-62.563
35	GenBank	JQ035541	<i>S. acanthias</i>	54.617	-10.579
36	GenBank	JQ035542	<i>S. acanthias</i>	-43.550	-176.394
37	GenBank	JQ035543	<i>S. acanthias</i>	-46.203	-64.152
38	GenBank	JQ035544	<i>S. acanthias</i>	-46.219	-65.120
39	GenBank	JQ035545	<i>S. acanthias</i>	-43.573	-176.460
40	GenBank	JQ035546	<i>S. acanthias</i>	-43.054	-174.200
41	GenBank	JQ035547	<i>S. acanthias</i>	54.758	-10.416
42	GenBank	JQ035548	<i>S. suckleyi</i>	36.679	-121.879
43	GenBank	JQ035549	<i>S. suckleyi</i>	36.963	-121.879
44	GenBank	JQ035550	<i>S. suckleyi</i>	36.781	-121.897
45	GenBank	JQ035551	<i>S. suckleyi</i>	36.673	-122.008
46	GenBank	JQ035552	<i>S. suckleyi</i>	47.816	-125.686
47	GenBank	JQ035553	<i>S. suckleyi</i>	41.637	140.690
48	GenBank	JQ035554	<i>S. suckleyi</i>	36.698	-121.820
49	GenBank	JQ035555	<i>S. suckleyi</i>	36.720	-121.832
50	GenBank	JQ035556	<i>S. suckleyi</i>	36.677	-122.005
51	GenBank	JQ035557	<i>S. suckleyi</i>	36.679	-121.879
52	GenBank	JQ035558	<i>S. suckleyi</i>	41.637	140.690
53	GenBank	JQ035559	<i>S. suckleyi</i>	36.963	-121.879
54					
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2					
3	GenBank	JQ035560	<i>S. suckleyi</i>	41.637	140.690
4	GenBank	JQ035561	<i>S. suckleyi</i>	36.781	-121.897
5	GenBank	JQ035562	<i>S. suckleyi</i>	36.673	-122.008
6	GenBank	JQ035563	<i>S. suckleyi</i>	36.698	-121.820
7	GenBank	JQ035564	<i>S. suckleyi</i>	36.720	-121.832
8	GenBank	JQ035565	<i>S. suckleyi</i>	36.677	-122.005
9	GenBank	JQ035566	<i>S. suckleyi</i>	36.679	-121.879
10	GenBank	JQ035567	<i>S. suckleyi</i>	41.637	140.690
11	GenBank	JQ035568	<i>S. suckleyi</i>	36.963	-121.879
12	GenBank	JQ035569	<i>S. acanthias</i>	-42.112	-73.037
13	GenBank	JQ035570	<i>S. acanthias</i>	-42.112	-73.037
14	GenBank	JQ035571	<i>S. acanthias</i>	-42.112	-73.037
15	GenBank	JQ035572	<i>S. acanthias</i>	-42.112	-73.037
16	GenBank	JQ035573	<i>S. acanthias</i>	55.349	-9.837
17	GenBank	JQ035574	<i>S. acanthias</i>	54.463	-8.891
18	GenBank	JQ035575	<i>S. acanthias</i>	54.484	-9.457
19	GenBank	JQ035576	<i>S. acanthias</i>	54.179	-10.684
20	GenBank	JQ035577	<i>S. acanthias</i>	53.701	-11.337
21	GenBank	JQ035578	<i>S. acanthias</i>	53.924	-11.204
22	GenBank	JQ035579	<i>S. acanthias</i>	53.802	-11.078
23	GenBank	JQ035580	<i>S. acanthias</i>	53.706	-10.880
24	GenBank	JQ035581	<i>S. acanthias</i>	53.104	-9.896
25	GenBank	JQ035582	<i>S. acanthias</i>	53.072	-10.187
26	GenBank	JQ035583	<i>S. acanthias</i>	52.899	-10.440
27	GenBank	JQ035584	<i>S. suckleyi</i>	41.637	140.690
28	GenBank	JQ035585	<i>S. suckleyi</i>	41.637	140.690
29	GenBank	JQ035586	<i>S. suckleyi</i>	41.637	140.690
30	GenBank	JQ035587	<i>S. suckleyi</i>	41.637	140.690
31	GenBank	JQ035588	<i>S. suckleyi</i>	41.637	140.690
32	GenBank	JQ035589	<i>S. suckleyi</i>	41.637	140.690
33	GenBank	JQ035590	<i>S. suckleyi</i>	41.637	140.690
34	GenBank	JQ035591	<i>S. suckleyi</i>	41.637	140.690
35	GenBank	JQ035592	<i>S. suckleyi</i>	41.637	140.690
36	GenBank	JQ035593	<i>S. suckleyi</i>	41.637	140.690
37	GenBank	JQ035594	<i>S. suckleyi</i>	41.637	140.690
38	GenBank	JQ035595	<i>S. suckleyi</i>	41.637	140.690
39	GenBank	JQ035596	<i>S. acanthias</i>	-43.203	-174.093
40	GenBank	JQ035597	<i>S. acanthias</i>	-43.550	-176.394
41	GenBank	JQ035598	<i>S. acanthias</i>	-44.034	-173.583
42	GenBank	JQ035599	<i>S. acanthias</i>	-43.550	-176.394
43	GenBank	JQ035600	<i>S. acanthias</i>	-43.203	-174.093
44	GenBank	JQ035601	<i>S. acanthias</i>	-43.573	-176.460
45	GenBank	JQ035602	<i>S. acanthias</i>	-44.034	-173.583
46	GenBank	JQ035603	<i>S. acanthias</i>	-43.054	-174.200
47	GenBank	JQ035604	<i>S. acanthias</i>	-44.034	-173.583
48	GenBank	JQ035605	<i>S. suckleyi</i>	44.062	-124.726
49	GenBank	JQ035606	<i>S. suckleyi</i>	47.816	-125.686
50	GenBank	JQ035607	<i>S. suckleyi</i>	44.062	-124.726
51	GenBank	JQ035608	<i>S. acanthias</i>	40.963	-71.520
52	GenBank	JQ035609	<i>S. acanthias</i>	52.217	-6.076
53	GenBank	JQ035610	<i>S. acanthias</i>	52.189	-5.608
54					
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2					
3	GenBank	JQ035611	<i>S. acanthias</i>	52.312	-4.258
4	GenBank	JQ035612	<i>S. acanthias</i>	52.949	-4.856
5	GenBank	JQ035613	<i>S. acanthias</i>	52.945	-5.377
6	GenBank	JQ035614	<i>S. acanthias</i>	40.963	-71.520
7	GenBank	JQ035615	<i>S. acanthias</i>	53.797	-4.760
8	GenBank	JQ035616	<i>S. acanthias</i>	51.252	-6.540
9	GenBank	JQ035617	<i>S. acanthias</i>	40.963	-71.520
10	GenBank	JQ035618	<i>S. acanthias</i>	40.963	-71.520
11	GenBank	JQ035619	<i>S. acanthias</i>	40.963	-71.520
12	GenBank	JQ035620	<i>S. acanthias</i>	40.963	-71.520
13	GenBank	JQ035621	<i>S. acanthias</i>	40.963	-71.520
14	GenBank	JQ035622	<i>S. acanthias</i>	40.963	-71.520
15	GenBank	JQ035623	<i>S. acanthias</i>	40.963	-71.520
16	GenBank	JQ035624	<i>S. acanthias</i>	40.963	-71.520
17	GenBank	JQ035625	<i>S. acanthias</i>	36.870	-75.740
18	GenBank	JQ035626	<i>S. acanthias</i>	37.090	-74.830
19	GenBank	JQ035627	<i>S. acanthias</i>	36.870	-75.740
20	GenBank	JQ035628	<i>S. acanthias</i>	37.090	-74.830
21	GenBank	JQ035629	<i>S. suckleyi</i>	47.816	-125.686
22	GenBank	JQ035630	<i>S. suckleyi</i>	44.062	-124.726
23	GenBank	JQ035631	<i>S. suckleyi</i>	47.816	-125.686
24	GenBank	JQ035632	<i>S. suckleyi</i>	44.062	-124.726
25	GenBank	JQ035633	<i>S. suckleyi</i>	47.816	-125.686
26	GenBank	JQ035634	<i>S. suckleyi</i>	44.062	-124.726
27	GenBank	JQ519005	<i>Squalus albifrons</i>		
28	GenBank	JQ519115	<i>Squalus brevirostris</i>		
29	GenBank	JQ518979	<i>Squalus cf. megalops</i>	-36.518	21.202
30	GenBank	JQ518980	<i>Squalus cf. mitsukurii</i>	-34.519	25.408
31	GenBank	JQ519006	<i>Squalus chloroculus</i>		
32	GenBank	JQ519002	<i>Squalus crassispinus</i>		
33	GenBank	JQ518976	<i>Squalus cubensis</i>		
34	GenBank	JQ518996	<i>Squalus edmundsi</i>		
35	GenBank	JQ519175	<i>Squalus formosus</i>		
36	GenBank	JQ519000	<i>Squalus grahami</i>		
37	GenBank	JQ519174	<i>Squalus japonicus</i>		
38	GenBank	JQ519053	<i>Squalus megalops</i>		
39	GenBank	JQ519001	<i>Squalus montalbani</i>		
40	GenBank	JQ519038	<i>Squalus nasutus</i>		
41	GenBank	JQ518975	<i>Squalus sp.</i>		
42	GenBank	JQ518977	<i>Squalus suckleyi</i>	59.832	-148.531
43	GenBank	JQ518978	<i>Squalus suckleyi</i>		
44	GenBank	KF927970	<i>Squalus brevirostris</i>		
45	GenBank	KF927971	<i>Squalus brevirostris</i>		
46	GenBank	KF927972	<i>Squalus brevirostris</i>		
47	GenBank	KF927973	<i>Squalus formosus</i>		
48	GenBank	KF927974	<i>Squalus formosus</i>		
49	GenBank	KF927975	<i>Squalus formosus</i>		
50	GenBank	KF927976	<i>Squalus formosus</i>		
51	GenBank	KF927977	<i>Squalus formosus</i>		
52	GenBank	KF927978	<i>Squalus japonicus</i>		
53	GenBank	KF927979	<i>Squalus japonicus</i>		
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GenBank	KF927980	<i>Squalus japonicus</i>
GenBank	KF927981	<i>Squalus montalbani</i>
GenBank	KF927982	<i>Squalus montalbani</i>
GenBank	KF927983	<i>Squalus montalbani</i>

Review Copy

1				
2				
3	reference/identification, original species identification, sampling location (latitude, longitude a			
4				
5				
6	Depth (m)	Country	Source	Marker
7	30.6	Italy	ELASMOMED	COI
8	33.5	Croatia	ELASMOMED	COI
9	33.5	Croatia	ELASMOMED	COI
10	33.5	Croatia	ELASMOMED	COI
11	33.5	Croatia	ELASMOMED	COI
12	33.5	Croatia	ELASMOMED	COI
13	33.5	Croatia	ELASMOMED	COI
14	33.5	Croatia	ELASMOMED	COI
15		Italy	ELASMOMED	COI
16		Italy	ELASMOMED	COI
17		Croatia	ELASMOMED	COI
18		Croatia	ELASMOMED	COI
19		Croatia	ELASMOMED	COI
20		Croatia	ELASMOMED	COI
21		Croatia	ELASMOMED	COI
22		Croatia	ELASMOMED	COI
23		Italy	ELASMOMED	COI
24		Croatia	ELASMOMED	COI
25		Croatia	ELASMOMED	COI
26		Italy	ELASMOMED	COI
27		Italy	ELASMOMED	COI
28		Italy	ELASMOMED	COI
29		Italy	ELASMOMED	COI
30		Croatia	ELASMOMED	COI
31		Croatia	ELASMOMED	COI
32		Croatia	ELASMOMED	COI
33		Croatia	ELASMOMED	COI
34		Croatia	ELASMOMED	COI
35		Croatia	ELASMOMED	COI
36		Croatia	ELASMOMED	COI
37		Italy	ELASMOMED	COI
38		Italy	ELASMOMED	COI
39		Croatia	ELASMOMED	COI
40		Croatia	ELASMOMED	COI
41		Croatia	ELASMOMED	COI
42		Croatia	ELASMOMED	COI
43		Croatia	ELASMOMED	COI
44		Croatia	ELASMOMED	COI
45		Italy	ELASMOMED	COI
46		Croatia	ELASMOMED	COI
47		Croatia	ELASMOMED	COI
48		Croatia	ELASMOMED	COI
49		Croatia	ELASMOMED	COI
50	60.4	Croatia	ELASMOMED	COI
51	60.4	Italy	ELASMOMED	COI
52	60.4	Italy	ELASMOMED	COI
53	60.4	Italy	ELASMOMED	COI
54	60	Italy	ELASMOMED	COI
55	46.1	Italy	ELASMOMED	COI
56	46.1	Italy	ELASMOMED	COI
57	45.6	Italy	ELASMOMED	COI
58				
59				
60				

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2				
3	34.5	Italy	ELASMOMED	COI
4	34.5	Italy	ELASMOMED	COI
5	34.5	Italy	ELASMOMED	COI
6	34.5	Italy	ELASMOMED	COI
7	34.5	Italy	ELASMOMED	COI
8	34.5	Italy	ELASMOMED	COI
9	31.4	Italy	ELASMOMED	COI
10	70	Italy	ELASMOMED	COI
11	70	Croatia	ELASMOMED	COI
12	73.3	Croatia	ELASMOMED	COI
13	73.3	Croatia	ELASMOMED	COI
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17	73.3	Croatia	ELASMOMED	COI
18	73.3	Croatia	ELASMOMED	COI
19	73.3	Croatia	ELASMOMED	COI
20	33.7	Italy	ELASMOMED	COI
21	48.6	Italy	ELASMOMED	COI
22	48.6	Croatia	ELASMOMED	COI
23	48.2	Croatia	ELASMOMED	COI
24	42.01	Croatia	ELASMOMED	COI
25	26.6	Italy	ELASMOMED	COI
26	70	Croatia	ELASMOMED	COI
27	70	Croatia	ELASMOMED	COI
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29	73.9	Croatia	ELASMOMED	COI
30	70.7	Croatia	ELASMOMED	COI
31	28.8	Italy	ELASMOMED	COI
32	51	Italy	ELASMOMED	COI
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35	51	Italy	ELASMOMED	COI
36	51	Italy	ELASMOMED	COI
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38	38.8	Italy	ELASMOMED	COI
39	38.8	Italy	ELASMOMED	COI
40	38	Italy	ELASMOMED	COI
41	31.2	Italy	ELASMOMED	COI
42	25.9	Italy	ELASMOMED	COI
43	25.9	Italy	ELASMOMED	COI
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45	29.7	Croatia	ELASMOMED	COI
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57	36	Croatia	ELASMOMED	COI
58	36	Croatia	ELASMOMED	COI
59				
60				

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2				
3	36	Croatia	ELASMOMED	COI
4	36	Croatia	ELASMOMED	COI
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13	33.3	Croatia	ELASMOMED	COI
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18	31	Italy	ELASMOMED	COI
19		Italy	ELASMOMED	COI
20				
21	600	Cyprus	ELASMOMED	COI
22	615	Cyprus	ELASMOMED	COI
23	615	Cyprus	ELASMOMED	COI
24	615	Cyprus	ELASMOMED	COI
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27	125	Italy	ELASMOMED	COI
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36	509	Australia	Last et al. 2007	COI
37	535	Australia	Last et al. 2007	COI
38		Australia	Last et al. 2007	COI
39		Australia	Last et al. 2007	COI
40	20	Australia	Last et al. 2007	COI
41		United States	Last et al. 2007	COI
42		United States	Last et al. 2007	COI
43		United States	Last et al. 2007	COI
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46		Chile	Last et al. 2007	COI
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52		United Kingdom	Last et al. 2007	COI
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55		United Kingdom	Last et al. 2007	COI
56	135	Australia	Last et al. 2007	COI
57	331	Australia	Last et al. 2007	COI
58				
59				
60				

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2				
3	331	Australia	Last et al. 2007	COI
4	230	Australia	Last et al. 2007	COI
5		Taiwan	Last et al. 2007	COI
6		Taiwan	Last et al. 2007	COI
7				
8	150	Japan	Last et al. 2007	COI
9	150	Japan	Last et al. 2007	COI
10	150	Japan	Last et al. 2007	COI
11	27	Japan	Last et al. 2007	COI
12	514	Australia	Last et al. 2007	COI
13	1150	Australia	Last et al. 2007	COI
14	1150	Australia	Last et al. 2007	COI
15		Australia	Last et al. 2007	COI
16	383	Australia	Last et al. 2007	COI
17	460	Australia	Last et al. 2007	COI
18	187	Australia	Last et al. 2007	COI
19	187	Australia	Last et al. 2007	COI
20	850	Australia	Last et al. 2007	COI
21	485	Australia	Last et al. 2007	COI
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28		Australia	Last et al. 2007	COI
29		Australia	Last et al. 2007	COI
30	60	Indonesia	Last et al. 2007	COI
31	60	Indonesia	Last et al. 2007	COI
32		Indonesia	Last et al. 2007	COI
33		Indonesia	Last et al. 2007	COI
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36	383	Australia	Last et al. 2007	COI
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40	329	Australia	Last et al. 2007	COI
41	383	Australia	Last et al. 2007	COI
42	90	Indonesia	Last et al. 2007	COI
43	90	Indonesia	Last et al. 2007	COI
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48		Indonesia	Last et al. 2007	COI
49		Taiwan	Last et al. 2007	COI
50		Taiwan	Last et al. 2007	COI
51		Taiwan	Last et al. 2007	COI
52		Taiwan	Last et al. 2007	COI
53	87	Australia	Last et al. 2007	COI
54	87	Australia	Last et al. 2007	COI
55	87	Australia	Last et al. 2007	COI
56	220	Australia	Last et al. 2007	COI
57	383	Australia	Last et al. 2007	COI
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3	383	Australia	Last et al. 2007	COI
4	383	Australia	Last et al. 2007	COI
5	640	Australia	Last et al. 2007	COI
6	60	Indonesia	Last et al. 2007	COI
7	60	Indonesia	Last et al. 2007	COI
8		Indonesia	Last et al. 2007	COI
9		Indonesia	Last et al. 2007	COI
10		Australia	Last et al. 2007	COI
11		Australia	Last et al. 2007	COI
12		Indonesia	Last et al. 2007	COI
13		Indonesia	Last et al. 2007	COI
14		Indonesia	Last et al. 2007	COI
15		Indonesia	Last et al. 2007	COI
16		Indonesia	Last et al. 2007	COI
17		Indonesia	Last et al. 2007	COI
18		United States	Last et al. 2007	COI
19		United States	Last et al. 2007	COI
20		United States	Last et al. 2007	COI
21		United States	Last et al. 2007	COI
22		United States	Last et al. 2007	COI
23		Japan	Last et al. 2007	COI
24		Japan	Last et al. 2007	COI
25		Japan	Last et al. 2007	COI
26	60	Argentina	Mabragaña et al. 2011	COI
27	60	Argentina	Mabragaña et al. 2011	COI
28	60	Argentina	Mabragaña et al. 2011	COI
29	60	Argentina	Mabragaña et al. 2011	COI
30	104	Argentina	Mabragaña et al. 2011	COI
31	104	Argentina	Mabragaña et al. 2011	COI
32	102	Argentina	Mabragaña et al. 2011	COI
33	102	Argentina	Mabragaña et al. 2011	COI
34	85	Argentina	Mabragaña et al. 2011	COI
35	85	Argentina	Mabragaña et al. 2011	COI
36	120	Uruguay	Mabragaña et al. 2011	COI
37	120	Uruguay	Mabragaña et al. 2011	COI
38	120	Uruguay	Mabragaña et al. 2011	COI
39		United States		COI
40		United States		COI
41		United States		COI
42		United States		COI
43		United States		COI
44		United States		COI
45		United States		COI
46		United States		COI
47		United States		COI
48	250	Gulf of Mexico		COI
49	250	Gulf of Mexico		COI
50	250	Gulf of Mexico		COI
51	250	Gulf of Mexico		COI
52		Gulf of Mexico		COI
53		Gulf of Mexico		COI
54		Gulf of Mexico		COI
55	1000	Gulf of Mexico		COI
56	1000	Gulf of Mexico		COI
57	1000	Gulf of Mexico		COI
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3	1000	Gulf of Mexico		COI
4	1000	Gulf of Mexico		COI
5	1000	Gulf of Mexico		COI
6	800	Gulf of Mexico		COI
7		Gulf of Mexico		COI
8	57	Canada	Steinke et al. 2009	COI
9	110.5	Canada	Steinke et al. 2009	COI
10	145	Canada	Steinke et al. 2009	COI
11	51	Canada	Steinke et al. 2009	COI
12		Canada	Steinke et al. 2009	COI
13		Canada	Steinke et al. 2009	COI
14		Canada	Steinke et al. 2009	COI
15		Canada	Steinke et al. 2009	COI
16		Canada	Steinke et al. 2009	COI
17		Canada	Steinke et al. 2009	COI
18		Canada	Steinke et al. 2009	COI
19		India	Bineesh et al. 2016	COI
20		India	Bineesh et al. 2016	COI
21		India	Bineesh et al. 2016	COI
22		India	Bineesh et al. 2016	COI
23		India	Bineesh et al. 2016	COI
24		India	Bineesh et al. 2016	COI
25		Taiwan	White & Iglésias 2011	COI
26		Tunisia	Marouani et al. 2011	COI
27		Tunisia	Marouani et al. 2011	COI
28	60	Virginia, USA	Veríssimo et al. 2010	ND2
29		United Kingdom	Veríssimo et al. 2010	ND2
30	109	Argentina	Veríssimo et al. 2010	ND2
31	128	Argentina	Veríssimo et al. 2010	ND2
32	128	Argentina	Veríssimo et al. 2010	ND2
33	115	Argentina	Veríssimo et al. 2010	ND2
34	748	New Zealand	Veríssimo et al. 2010	ND2
35	518	New Zealand	Veríssimo et al. 2010	ND2
36	109	Argentina	Veríssimo et al. 2010	ND2
37		Ireland	Veríssimo et al. 2010	ND2
38	489	New Zealand	Veríssimo et al. 2010	ND2
39	93	Argentina	Veríssimo et al. 2010	ND2
40	98	Argentina	Veríssimo et al. 2010	ND2
41	518	New Zealand	Veríssimo et al. 2010	ND2
42	748	New Zealand	Veríssimo et al. 2010	ND2
43		Ireland	Veríssimo et al. 2010	ND2
44	69	California, USA	Veríssimo et al. 2010	ND2
45	102	California, USA	Veríssimo et al. 2010	ND2
46	150	California, USA	Veríssimo et al. 2010	ND2
47		California, USA	Veríssimo et al. 2010	ND2
48		Washington/Oregon, USA	Veríssimo et al. 2010	ND2
49	100	Japan	Veríssimo et al. 2010	ND2
50		California, USA	Veríssimo et al. 2010	ND2
51		California, USA	Veríssimo et al. 2010	ND2
52		California, USA	Veríssimo et al. 2010	ND2
53	69	California, USA	Veríssimo et al. 2010	ND2
54	100	Japan	Veríssimo et al. 2010	ND2
55	102	California, USA	Veríssimo et al. 2010	ND2
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4	100	Japan	Verissimo et al. 2010	ND2
5	150	California, USA	Verissimo et al. 2010	ND2
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13	51	Chile	Verissimo et al. 2010	ND2
14	51	Chile	Verissimo et al. 2010	ND2
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16	51	Chile	Verissimo et al. 2010	ND2
17		Ireland	Verissimo et al. 2010	ND2
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51		Washington/Oregon, USA	Verissimo et al. 2010	ND2
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54	41	Massachusetts, USA	Verissimo et al. 2010	ND2
55		United Kingdom	Verissimo et al. 2010	ND2
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	41	Massachusetts, USA	Verissimo et al. 2010	ND2
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		Washington/Oregon, USA	Verissimo et al. 2010	ND2
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		Washington/Oregon, USA	Verissimo et al. 2010	ND2
		Australia	Naylor et al. 2012	ND2
		Japan	Naylor et al. 2012	ND2
	184	South Africa	Naylor et al. 2012	ND2
	344	South Africa	Naylor et al. 2012	ND2
		Australia	Naylor et al. 2012	ND2
		Australia	Naylor et al. 2012	ND2
		Jamaica	Naylor et al. 2012	ND2
		Australia	Naylor et al. 2012	ND2
		Taiwan	Naylor et al. 2012	ND2
		Australia	Naylor et al. 2012	ND2
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		Brazil	Naylor et al. 2012	ND2
		Alaska	Naylor et al. 2012	ND2
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		Taiwan	Straube et al. 2013	ND2
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56	S. albifrons	III
57	S. albifrons	III
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3	<i>S. albifrons</i>	III
4	<i>S. albifrons</i>	III
5	<i>S. brevirostris</i>	II
6	<i>S. brevirostris</i>	II
7	<i>S. brevirostris</i>	II
8	<i>S. brevirostris</i>	II
9	<i>S. brevirostris</i>	II
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11	<i>S. brevirostris</i>	II
12	<i>S. chloroculus</i>	III
13	<i>S. chloroculus</i>	III
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16	<i>S. chloroculus</i>	III
17	<i>S. chloroculus</i>	III
18	<i>S. chloroculus</i>	III
19	<i>S. crassispinus</i>	III
20	<i>S. crassispinus</i>	III
21	<i>S. edmundsi</i>	III
22	<i>S. edmundsi</i>	III
23	<i>S. edmundsi</i>	III
24	<i>S. edmundsi</i>	III
25	<i>S. edmundsi</i>	III
26	<i>S. edmundsi</i>	III
27	<i>S. edmundsi</i>	III
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32	<i>S. edmundsi</i>	III
33	<i>S. edmundsi</i>	III
34	<i>S. edmundsi</i>	III
35	<i>S. edmundsi</i>	III
36	<i>S. grahami</i>	III
37	<i>S. grahami</i>	III
38	<i>S. grahami</i>	III
39	<i>S. grahami</i>	III
40	<i>S. grahami</i>	III
41	<i>S. grahami</i>	III
42	<i>S. hemipinnis</i>	III
43	<i>S. hemipinnis</i>	III
44	<i>S. hemipinnis</i>	III
45	<i>S. hemipinnis</i>	III
46	<i>S. hemipinnis</i>	III
47	<i>S. hemipinnis</i>	III
48	<i>S. hemipinnis</i>	III
49	<i>S. japonicus</i>	III
50	<i>S. japonicus</i>	III
51	<i>S. japonicus</i>	III
52	<i>S. japonicus</i>	III
53	<i>S. megalops</i>	II
54	<i>S. megalops</i>	II
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56	<i>S. megalops</i>	II
57	<i>S. megalops</i>	II
58	<i>S. montalbani</i>	III
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3	<i>S. montalbani</i>	III
4	<i>S. montalbani</i>	III
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9	<i>S. montalbani</i>	III
10	<i>S. nasutus</i>	III
11	<i>S. nasutus</i>	III
12	<i>S. nasutus</i>	III
13	<i>S. nasutus</i>	III
14	<i>S. nasutus</i>	III
15	<i>S. nasutus</i>	III
16	<i>S. nasutus</i>	III
17	<i>S. suckleyi</i>	I
18	<i>S. suckleyi</i>	I
19	<i>S. suckleyi</i>	I
20	<i>S. suckleyi</i>	I
21	<i>S. suckleyi</i>	I
22	<i>S. suckleyi</i>	I
23	<i>S. suckleyi</i>	I
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37	Clade A	I
38	<i>S. mitsukurii</i> (GoM/Uruguay)	III
39	Clade D	III
40	<i>S. cubensis</i>	II
41	<i>S. cubensis</i>	II
42	<i>S. cubensis</i>	II
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53	<i>S. cubensis</i>	II
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57	<i>S. cubensis</i>	II
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4	S. cubensis	II
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6	S. cubensis	II
7	S. cubensis	II
8	S. cubensis	II
9	S. suckleyi	I
10	S. suckleyi	I
11	S. suckleyi	I
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15	S. suckleyi	I
16	S. suckleyi	I
17	S. suckleyi	I
18	S. suckleyi	I
19	Squalus sp. A	III
20	Squalus sp. A	III
21	Squalus sp. A	III
22	Squalus sp. A	III
23	Squalus sp. A	III
24	Squalus sp. A	III
25	Squalus formosus	III
26	Clade B	II
27	Clade C	III
28	Clade A	I
29	Clade A	I
30	Clade A	I
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32	Clade A	I
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37	S. suckleyi	I
38	S. suckleyi	I
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46	S. suckleyi	I
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19	Clade A	I
20	Clade A	I
21	Clade A	I
22	Clade A	I
23	S. suckleyi	I
24	S. suckleyi	I
25	S. suckleyi	I
26	S. suckleyi	I
27	S. suckleyi	I
28	S. suckleyi	I
29	S. albifrons	III
30	S. brevirostris	II
31	Clade B	II
32	Clade D	III
33	S. chloroculus	III
34	S. crassispinus	III
35	S. cf. mitsukurii (GoM)	III
36	S. edmundsi	III
37	S. formosus	III
38	S. grahami	III
39	S. japonicus	III
40	S. megalops	II
41	S. montalbani	III
42	S. nasutus	III
43	Clade D	III
44	S. suckleyi	I
45	S. suckleyi	I
46	S. brevirostris	II
47	S. brevirostris	II
48	S. brevirostris	II
49	S. formosus	III
50	S. formosus	III
51	S. formosus	III
52	S. formosus	III
53	S. formosus	III
54	S. formosus	III
55	S. japonicus	III
56	S. japonicus	III
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S. japonicus	III
S. montalbani	III
S. montalbani	III
S. montalbani	III

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ociated with each sequence (COI or ND2) and corresponding genetic clade and lineage.

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Table S3 – Average genetic distances among COI haplotype pairs between the different gei

<u>COI</u>	Clade A	<i>S. suckleyi</i>	Clade B	<i>S. brevirostris</i>
LINEAGE I				
Clade A		0.01	0.078	0.080
<i>S. suckleyi</i>	0.011		0.075	0.074
LINEAGE II				
Clade B	0.084	0.080		0.012
<i>S. brevirostris</i>	0.087	0.079	0.012	
<i>S. cubensis</i>	0.082	0.074	0.021	0.021
<i>S. megalops</i>	0.088	0.080	0.011	0.014
<i>S. raoulensis</i>	0.086	0.078	0.010	0.011
LINEAGE III				
Clade C	0.078	0.070	0.072	0.072
Clade D	0.079	0.071	0.073	0.072
<i>S. albifrons</i>	0.074	0.066	0.066	0.067
<i>S. chloroculus</i>	0.080	0.072	0.071	0.069
<i>S. crassispinus</i>	0.070	0.066	0.082	0.081
<i>S. edmundsi</i>	0.074	0.071	0.072	0.071
<i>S. formosus</i>	0.081	0.073	0.073	0.073
<i>S. grahami</i>	0.079	0.071	0.064	0.065
<i>S. griffini</i>	0.079	0.071	0.064	0.065
<i>S. hemipinnis</i>	0.078	0.074	0.072	0.072
<i>S. japonicus</i>	0.081	0.072	0.071	0.071
<i>S. mitsukurii</i> (GoM/Uruguay)	0.074	0.066	0.066	0.065
<i>S. mitsukurii</i> (Uruguay)	0.077	0.069	0.070	0.070
<i>S. mitsukurii</i> (Hawaii)	0.079	0.070	0.075	0.074
<i>S. montalbani</i>	0.082	0.074	0.075	0.074
<i>S. nasutus</i>	0.082	0.073	0.071	0.072
<i>Squalus</i> sp. A	0.096	0.088	0.079	0.080
<i>Squalus</i> sp. (Juan Fern.)	0.079	0.071	0.073	0.074
<i>S. cf. megalops</i> (Mau1)	0.074	0.066	0.068	0.067
<i>S. cf. megalops</i> (Mau2)	0.079	0.071	0.070	0.072

Above diagonal - Average *p*- distances based on the number of base differences per site

Below diagonal - Average K2P genetic distances based on the number of base substitutio

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netic clades. Upper diagonal: average distances; lower diagonal: average K2P-distances.

S. cubensis	S. megalops	S. raoulensis	Clade C	Clade D	S. albifrons	S. chloroculus
0.077	0.082	0.08	0.073	0.074	0.070	0.075
0.07	0.075	0.073	0.066	0.067	0.063	0.068
0.021	0.011	0.010	0.068	0.069	0.063	0.067
0.021	0.013	0.011	0.068	0.068	0.063	0.065
	0.019	0.017	0.065	0.065	0.062	0.064
0.019		0.011	0.066	0.070	0.061	0.068
0.018	0.011		0.065	0.066	0.060	0.063
0.069	0.069	0.068		0.022	0.020	0.025
0.069	0.074	0.070	0.023		0.018	0.009
0.065	0.064	0.063	0.020	0.018		0.021
0.068	0.072	0.066	0.026	0.009	0.021	
0.076	0.083	0.079	0.027	0.020	0.027	0.026
0.067	0.072	0.068	0.023	0.017	0.019	0.020
0.072	0.068	0.070	0.023	0.020	0.006	0.024
0.061	0.065	0.061	0.018	0.012	0.014	0.017
0.061	0.065	0.061	0.023	0.016	0.018	0.021
0.069	0.073	0.069	0.019	0.017	0.015	0.020
0.068	0.070	0.067	0.021	0.017	0.017	0.021
0.065	0.066	0.063	0.022	0.008	0.022	0.014
0.066	0.071	0.067	0.020	0.002	0.016	0.007
0.071	0.075	0.072	0.027	0.016	0.022	0.021
0.067	0.076	0.073	0.026	0.009	0.021	0.014
0.068	0.071	0.068	0.023	0.021	0.023	0.026
0.081	0.080	0.076	0.033	0.019	0.030	0.025
0.070	0.074	0.070	0.018	0.008	0.018	0.013
0.064	0.070	0.065	0.025	0.006	0.016	0.011
0.066	0.071	0.067	0.023	0.004	0.018	0.009

from averaging over all sequence pairs between groups.
ns per site from averaging over all sequence pairs between groups.

	<i>S. crassispinus</i>	<i>S. edmundsi</i>	<i>S. formosus</i>	<i>S. grahami</i>	<i>S. griffini</i>	<i>S. hemipinnis</i>	<i>S. japonicus</i>
1							
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8							
9	0.066	0.070	0.076	0.074	0.074	0.073	0.076
10	0.063	0.067	0.069	0.067	0.067	0.070	0.068
11							
12							
13	0.077	0.068	0.069	0.061	0.061	0.068	0.067
14	0.076	0.067	0.069	0.061	0.061	0.068	0.067
15	0.072	0.064	0.068	0.058	0.058	0.065	0.064
16	0.078	0.068	0.065	0.062	0.062	0.069	0.067
17	0.074	0.065	0.066	0.058	0.058	0.065	0.064
18							
19							
20							
21	0.026	0.022	0.022	0.018	0.022	0.019	0.021
22	0.020	0.016	0.020	0.012	0.016	0.017	0.017
23	0.026	0.018	0.006	0.014	0.018	0.015	0.017
24	0.025	0.019	0.023	0.017	0.021	0.020	0.021
25		0.024	0.028	0.020	0.024	0.025	0.025
26							
27	0.024		0.02	0.016	0.020	0.007	0.019
28	0.029	0.021		0.016	0.020	0.017	0.015
29	0.020	0.017	0.016		0.004	0.013	0.013
30	0.025	0.020	0.020	0.004		0.017	0.017
31	0.026	0.007	0.017	0.013	0.017		0.014
32	0.026	0.020	0.015	0.013	0.017	0.014	
33	0.023	0.019	0.024	0.016	0.020	0.021	0.021
34	0.018	0.015	0.018	0.010	0.014	0.015	0.015
35	0.025	0.021	0.020	0.016	0.020	0.019	0.005
36	0.024	0.020	0.019	0.015	0.019	0.020	0.016
37	0.029	0.026	0.022	0.017	0.021	0.020	0.006
38	0.036	0.032	0.032	0.024	0.028	0.027	0.029
39	0.020	0.021	0.020	0.012	0.016	0.017	0.017
40	0.023	0.019	0.023	0.014	0.018	0.019	0.019
41	0.020	0.017	0.020	0.012	0.016	0.017	0.017
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S. mitsukurii(GoM/Uruguay)	S. mitsukurii(Uruguay)	S. mitsukurii (Hawaii)	S. montalbani
	0.070	0.072	0.074
	0.063	0.065	0.066
			0.077
			0.070
	0.063	0.067	0.071
	0.062	0.066	0.070
	0.062	0.063	0.067
	0.063	0.068	0.071
	0.060	0.064	0.068
			0.069
	0.022	0.020	0.026
	0.008	0.002	0.016
	0.022	0.016	0.022
	0.013	0.007	0.021
	0.023	0.018	0.024
	0.018	0.014	0.020
	0.024	0.018	0.020
	0.016	0.010	0.016
	0.020	0.014	0.020
	0.021	0.015	0.019
	0.021	0.015	0.019
		0.006	0.005
			0.020
			0.013
0.006			0.014
0.020	0.014		0.007
0.013	0.007	0.016	0.016
0.022	0.019	0.009	0.021
0.024	0.017	0.032	0.024
0.013	0.006	0.020	0.012
0.011	0.004	0.018	0.011
0.008	0.002	0.016	0.008

	S. nasutus	Squalus sp. A	Squalus sp. (Juan Fern.)	S. cf. megalops (Mau1)	S. cf. megalops (Mau2)
1					
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9	0.077	0.089	0.074	0.070	0.074
10	0.069	0.082	0.067	0.063	0.067
11					
12					
13	0.068	0.074	0.069	0.065	0.067
14	0.068	0.075	0.069	0.064	0.068
15	0.065	0.076	0.066	0.061	0.063
16	0.067	0.076	0.070	0.067	0.068
17	0.065	0.072	0.066	0.062	0.064
18					
19					
20					
21	0.023	0.032	0.018	0.024	0.022
22	0.021	0.019	0.008	0.006	0.004
23	0.023	0.029	0.018	0.016	0.018
24	0.026	0.024	0.013	0.011	0.009
25	0.029	0.035	0.020	0.022	0.020
26	0.025	0.031	0.020	0.018	0.016
27	0.021	0.031	0.020	0.022	0.020
28	0.017	0.023	0.012	0.014	0.012
29	0.021	0.027	0.016	0.018	0.016
30	0.020	0.026	0.017	0.019	0.017
31	0.006	0.028	0.017	0.019	0.017
32	0.021	0.023	0.012	0.010	0.008
33	0.019	0.017	0.006	0.004	0.002
34	0.009	0.031	0.020	0.018	0.016
35	0.020	0.023	0.012	0.011	0.008
36		0.03	0.021	0.023	0.021
37	0.031		0.019	0.021	0.019
38	0.021	0.019		0.010	0.008
39	0.023	0.021	0.010		0.006
40	0.021	0.019	0.008	0.006	
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Table S4 – Average genetic distances among ND2 haplotype pairs between the different genet

<u>ND2</u>	Clade A	<i>S. suckleyi</i>	Clade B	<i>S. brevirostris</i>
LINEAGE I				
Clade A		0.019	0.074	0.077
<i>S. suckleyi</i>	0.019		0.077	0.080
LINEAGE II				
Clade B	0.080	0.084		0.018
<i>S. brevirostris</i>	0.082	0.086	0.018	
<i>S. megalops</i>	0.073	0.076	0.018	0.015
<i>S. raoulensis</i>	0.075	0.078	0.012	0.013
LINEAGE III				
Clade C	0.069	0.073	0.054	0.059
Clade D	0.069	0.076	0.057	0.057
<i>S. albifrons</i>	0.073	0.076	0.067	0.069
<i>S. chloroculus</i>	0.069	0.071	0.055	0.055
<i>S. crassispinus</i>	0.058	0.069	0.059	0.067
<i>S. edmundsi</i>	0.084	0.091	0.069	0.071
<i>S. formosus</i>	0.076	0.084	0.083	0.083
<i>S. grahami</i>	0.069	0.071	0.049	0.050
<i>S. griffini</i>	0.071	0.070	0.051	0.052
<i>S. japonicus</i>	0.075	0.078	0.055	0.056
<i>S. mitsukurii</i> (GoM/Jamaica)	0.067	0.070	0.050	0.050
<i>S. mitsukurii</i> (Hawaii)	0.077	0.080	0.053	0.054
<i>S. montalbani</i>	0.072	0.075	0.055	0.054
<i>S. nasutus</i>	0.075	0.078	0.051	0.056
<i>Squalus</i> sp. (Brazil)	0.070	0.074	0.053	0.053
<i>S. cf. megalops</i> (Mau1)	0.069	0.076	0.055	0.055
<i>S. cf. megalops</i> (Mau2)	0.067	0.070	0.049	0.048

Above diagonal - Average *p*- distances based on the number of base differences per site from
Below diagonal - Average K2P genetic distances based on the number of base substitutions per

ic clades. Upper diagonal: average distances; lower diagonal: average K2P-distances.

S. megalops	S. raoulensis	Clade C	Clade D	S. albifrons	S. chloroculus
0.068	0.070	0.065	0.065	0.068	0.064
0.071	0.073	0.069	0.071	0.071	0.066
0.018	0.012	0.051	0.054	0.064	0.053
0.015	0.013	0.056	0.054	0.065	0.052
	0.013	0.052	0.051	0.061	0.050
0.013		0.054	0.053	0.063	0.051
0.055	0.057		0.030	0.024	0.029
0.054	0.056	0.031		0.038	0.017
0.065	0.067	0.024	0.039		0.038
0.052	0.054	0.030	0.017	0.039	
0.060	0.062	0.036	0.035	0.043	0.039
0.066	0.069	0.054	0.039	0.050	0.048
0.080	0.082	0.043	0.050	0.030	0.050
0.046	0.048	0.030	0.025	0.039	0.019
0.048	0.050	0.032	0.027	0.041	0.021
0.052	0.058	0.036	0.039	0.046	0.037
0.047	0.049	0.029	0.014	0.038	0.016
0.050	0.056	0.034	0.037	0.044	0.035
0.051	0.053	0.029	0.018	0.039	0.016
0.052	0.054	0.032	0.035	0.037	0.033
0.050	0.052	0.023	0.012	0.033	0.013
0.052	0.054	0.034	0.017	0.044	0.015
0.046	0.048	0.028	0.012	0.037	0.013

n averaging over all sequence pairs between groups.

per site from averaging over all sequence pairs between groups.

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S. crassispinus	S. edmundsi	S. formosus	S. grahami	S. griffini	S. japonicus
0.055	0.078	0.071	0.064	0.066	0.070
0.065	0.084	0.078	0.067	0.065	0.073
0.056	0.065	0.077	0.047	0.049	0.053
0.063	0.067	0.077	0.048	0.050	0.053
0.057	0.063	0.075	0.044	0.046	0.050
0.059	0.065	0.077	0.046	0.048	0.055
0.035	0.051	0.042	0.029	0.031	0.035
0.034	0.038	0.048	0.025	0.027	0.038
0.042	0.048	0.029	0.038	0.040	0.044
0.038	0.046	0.048	0.019	0.021	0.036
	0.055	0.048	0.038	0.040	0.036
0.058		0.064	0.046	0.048	0.059
0.050	0.068		0.048	0.050	0.058
0.039	0.047	0.050		0.002	0.029
0.041	0.050	0.052	0.002		0.030
0.037	0.062	0.061	0.029	0.031	
0.039	0.041	0.049	0.023	0.025	0.037
0.035	0.060	0.059	0.027	0.029	0.006
0.039	0.047	0.050	0.020	0.022	0.033
0.033	0.054	0.052	0.029	0.031	0.012
0.037	0.041	0.044	0.021	0.023	0.035
0.044	0.048	0.055	0.027	0.029	0.042
0.037	0.041	0.048	0.021	0.023	0.035

	S. mitsukurii (GoM/Jamaica)	S. mitsukurii (Hawaii)	S. montalbani	S. nasutus	Squalus sp. (Brazil)
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9	0.063	0.072	0.067	0.070	0.066
10	0.065	0.074	0.070	0.072	0.069
11					
12					
13	0.048	0.051	0.052	0.049	0.050
14	0.047	0.051	0.051	0.053	0.050
15	0.045	0.048	0.049	0.050	0.048
16	0.047	0.053	0.051	0.051	0.050
17					
18					
19	0.029	0.033	0.029	0.031	0.023
20	0.014	0.036	0.018	0.034	0.011
21	0.037	0.042	0.037	0.036	0.032
22	0.016	0.034	0.016	0.032	0.013
23	0.037	0.034	0.037	0.032	0.036
24	0.040	0.057	0.045	0.051	0.040
25	0.047	0.056	0.048	0.050	0.043
26	0.023	0.027	0.020	0.029	0.021
27	0.025	0.029	0.022	0.030	0.023
28	0.035	0.006	0.032	0.011	0.034
29		0.034	0.017	0.031	0.010
30	0.035		0.030	0.010	0.032
31	0.017	0.031		0.028	0.014
32	0.032	0.010	0.029		0.030
33	0.010	0.033	0.014	0.031	
34	0.012	0.035	0.020	0.037	0.014
35	0.007	0.029	0.014	0.031	0.008
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S. cf. megalops (Mau1) S. cf. megalops (Mau2)

0.064	0.062
0.071	0.065
0.053	0.047
0.052	0.046
0.050	0.044
0.051	0.046
0.033	0.027
0.017	0.011
0.042	0.036
0.015	0.013
0.042	0.036
0.046	0.040
0.052	0.046
0.027	0.021
0.029	0.023
0.040	0.034
0.012	0.006
0.034	0.029
0.020	0.014
0.036	0.030
0.013	0.008
	0.006
0.006	

Table S5 – Distribution of *Squalus* specimens along the different marine provinces

Marine Regions	Marine Provinces	Lineage I
COLD		
Arctic Region		
Antarctic Region		
COLD-TEMPERATE		
Eastern Atlantic Region		X
Eastern North Pacific Region	Aleutian	X
	Oregon	X
New Zealand-Australian Region	Tasmania	X
	New Zealand	X
	Antipodes	
South American Region	Southern Chile	X
	Tierra del Fuego	X
	Southern Argentina	X
	Falkland Islands	
Sub-Antarctic Region	South Georgia	
	Bouvet	
	Crozet	
	Prince Edward	
	Kerguelen	
	Macquarie	
Western Atlantic Region		X
Western North Pacific Region	Oriental	X
	Kurile	
	Okhotsk	X
WARM-TEMPERATE		
Eastern Atlantic Region	Lusitania	X
	Black Sea	
	Caspian	
	Aral	
	Benguela	X
	Tristan-Gough	
	Amsterdam-St Paul	
Eastern Pacific Region	California	
	Peru-Chilean	
	Juan Fernández	
Western Atlantic Region	Carolina (& Northern GoM)	
	Argentinian	
Western Pacific Region	Sino-Japanese	
	Auckland	
	Kermadec	

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		Southeastern Australian
		Southwestern Australian
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	TROPICAL	
	Eastern Atlantic Region	Tropical Eastern Atlantic
		St. Helena
		Ascension
		Agulhas
	Eastern Pacific Region	Cortez
		Panamanian
		Galapagos
	Tropical Indo-West Pacific Region	Western Indian Ocean
		Red Sea
		Indo-Polynesian
		Hawaiian
		Marquesas
		Easter Island
	Western Atlantic Region	Caribbean
	<hr/>	

Lineage II	Lineage III
0.00	0.00
0.01	0.01
0.02	0.02
0.03	0.03
0.04	0.04
0.05	0.05
0.06	0.06
0.07	0.07
0.08	0.08
0.09	0.09
0.10	0.10
0.11	0.11
0.12	0.12
0.13	0.13
0.14	0.14
0.15	0.15
0.16	0.16
0.17	0.17
0.18	0.18
0.19	0.19
0.20	0.20
0.21	0.21
0.22	0.22
0.23	0.23
0.24	0.24
0.25	0.25
0.26	0.26
0.27	0.27
0.28	0.28
0.29	0.29
0.30	0.30
0.31	0.31
0.32	0.32
0.33	0.33
0.34	0.34
0.35	0.35
0.36	0.36
0.37	0.37
0.38	0.38
0.39	0.39
0.40	0.40
0.41	0.41
0.42	0.42
0.43	0.43
0.44	0.44
0.45	0.45
0.46	0.46
0.47	0.47
0.48	0.48
0.49	0.49
0.50	0.50
0.51	0.51
0.52	0.52
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0.67	0.67
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0.71	0.71
0.72	0.72
0.73	0.73
0.74	0.74
0.75	0.75
0.76	0.76
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0.81	0.81
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0.88	0.88
0.89	0.89
0.90	0.90
0.91	0.91
0.92	0.92
0.93	0.93
0.94	0.94
0.95	0.95
0.96	0.96
0.97	0.97
0.98	0.98
0.99	0.99
1.00	1.00

X	X
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X	X
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Review Copy

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