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Coastal fish diversity of the Socotra Archipelago, Yemen

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Abstract

The Socotra Archipelago, located in the eastern Gulf of Aden, has a unique marine environment which combines tropical and ‘pseudo-temperate’ elements. Studies on the fish biogeography of the archipelago, partially framed in regional studies, have substantially outpaced critical elementary research on the archipelago’s fish diversity. The present study seeks to close this gap and identifies the Socotra Archipelago as a major hotspot of coastal fish diversity in the Indian Ocean.

The archipelago supports unique coastal fish assemblages which are predominantly composed of coral-associated (“reef”) species, in spite of the limited biogenic reef frameworks. A Preliminary Checklist comprises 682 species with confirmed records and a “Working List” includes an additional 51 records, totalling 733 faunal records in 108 families. The family Labridae is the most speciose, followed by Gobiidae, Pomacentridae, Serranidae and Chaetodontidae. The species richness of the archipelago is the highest when compared to adjacent Arabian ecoregions. The richness of the Acanthuridae, Chaetodontidae, Labridae, Pomacentridae and Pseudochromidae stand out as particularly high, and the richness of several families is as high as or higher than in the entire Red Sea. The total archipelagic richness is extrapolated at up to 875 species based on incidence-based richness models and expert opinion. Inshore fish inventories, covering 497 species, found between 14 and 132 species per site ($\bar{x} = 66$). Site diversity decreased across the archipelago from west to east and from north to south. Total fish diversity was highest around Socotra Island, followed by Abd al-Kuri & Kal Farun and Darsa & Samha. Occurrence frequencies were very unevenly distributed and dominated by *Pomacentrus caeruleus* and *Thalassoma lunare*, whilst many species were infrequent. The fish assemblages are dominated by species from the Indo-West Pacific and the north-western Indian Ocean. The assemblages are rich in rare species and hybrids, and include a low number of endemics (4–5), and a high number of species with far-reaching and Western Indian Ocean ranges.

Key words: Coastal fish assemblages; species inventory; richness modelling; diversity distribution; Socotra Archipelago

Introduction

The Socotra Archipelago (Yemen) in the northern Indian Ocean is recognized globally for its outstanding biodiversity and endemism, which justifies the designation of the entire island group as a UNESCO World Heritage Site in 2008 (Scholte *et al.* 2011; Van Damme & Banfield 2011; UNESCO web resource). Whilst the Socotra Archipelago’s public recognition as the “Galapagos of the Indian Ocean” (Sohlmann 2004) often alludes primarily to the diversity of its terrestrial ecosystems, the marine ecosystems are also highly diverse and unique (Cheung & DeVantier 2006).

History of ichthyological research in Socotra Archipelago

The archipelago lies at the centre of a region with relatively poorly-known coastal and marine fish faunas. In the late 19th century the Socotra Archipelago was the subject of a series of scientific expeditions, led by Balfour in 1880, by Riebeck and Schweinfurth in 1881, by Forbes and Ogilbie-Grant in 1897–1898, and by Paulay and Simony in 1898. Fishes were sampled for the first time on Socotra Island during the German expedition of Riebeck and Schweinfurth in 1881–1882, resulting in eight species being mentioned by Taschenberg (1883) without listing their names. Their collection was forgotten until part of it was rediscovered by the first author at the Zoological Museum in Hamburg (ZMH). The origin of these records from Socotra Archipelago can, however, not be reliably asserted (Krupp *et al.* 2006). Steindachner published more extensive studies, based on specimens collected by the Austrian Expedition to Socotra Archipelago and South Arabia of Paulay and Simony in 1898–1899. He listed 56 species of marine and brackish water fishes and described *Gerres socotranus* Steindachner and *Exocoetus socotranus* Steindachner as new to science (1902; also Steindachner 1903; and compare Lavergne *et al.* 2016).

The Oxford University Expedition of 1956 collected a small number of fishes, while the British R.A.F./Army Expeditions of 1964 and 1964–1965 and the combined R.A.F./Army/Civilian Expedition of 1967 did not contribute to the knowledge of the archipelago's fish fauna (Doe 1992; Wranik 1999). On 9 December 1957 the seminal ‘Xarifa-2 Expedition’ led by the famous Austrian SCUBA pioneer Hans Hass passed by Abdal-Kuri, the westernmost island of the archipelago, on its way to the Maldives. This brief visit resulted in an initial characterisation of the benthic communities (Scheer 1964; Scheer 1971) and a very small collection of fishes made by Wolfgang Klausewitz (Klausewitz 1958), who later on became a leading expert of the fishes of the Indian Ocean and the Red Sea. The specimens were deposited at the Senckenberg Museum of Nature, Frankfurt a.M.

Between 1964 and the late 1980s, several Russian and German ship-based expeditions conducted oceanographic, biodiversity and fisheries surveys in the western Indian Ocean including the waters around Socotra Archipelago (Hariri & Shotah 1999; Manilo & Bogorodsky 2003). In 1964 the German research vessel ‘Meteor’ collected fish specimens in deep waters south-west of the Socotra Archipelago within the framework of the International Indian Ocean Programme (IIOP), which are mostly deposited at the Zoological Museum Hamburg (ZMH; Kotthaus 1967), and in 1988–1989 the Russian research vessel ‘Vityaz’ made extensive deep water and deep sea collections around the archipelago (Manilo & Bogorodsky 2003; Weigmann *et al.* 2013), which are mainly deposited at the Shirshov Institute of Oceanography in Moscow (Bogorodsky pers. obs.). Based on these collections several species were described as new to science, including *Plectranthias intermedius* (Kotthaus, 1973) and *Pseudophichthys macroporos* Kotthaus, 1968, and two named after Socotra: *Ariosoma sokotranum* Karmovskaya, 1991 and *Gymnothorax sokotrensis* Kotthaus, 1968. Recently, new elasmobranch species and additional distributional data were identified in these collections. The deep-sea shark *Planonasus parini* was described by Weigmann *et al.* (2013) and the deep-sea shark *Apristurus breviventralis* was described by Kawauchi *et al.* (2014). The distribution range of *Pristiophorus nancyae* Ebert & Cailliet, 2011 was extended to the Gulf of Aden and Socotra Archipelago by Weigmann *et al.* (2014) and another deep-water skate *Okamejei ornata* was described by Weigmann *et al.* (2015). Deep-dwelling species are only considered in the present account of the coastal fishes of the Socotra Archipelago if they are known to possibly also occur at depths above 200 m, i.e. *Pseudophichthys macroporos*, *Gymnothorax sokotrensis* and *Plectranthias intermedius*.

Although scientific interest in the Socotra Archipelago resurred in 1970s in the former South Yemen, fish diversity and ecology had not been studied specifically and ichthyological research focussed predominantly on fisheries. Scientific efforts gained significant momentum from 1996 onwards during the project ‘Conservation and Sustainable Use of Socotra Archipelago’ (usually abbreviated as the ‘Socotra Biodiversity Project’, SBP), led by the United Nations Development Programme (UNDP) and the Environment Protection Authority of Yemen (EPA) (Cheung & DeVantier 2006). The scientific results achieved by the ‘Marine Habitat, Biodiversity and Fisheries Surveys’ (MBS) within the framework of the SBP substantially improved the understanding of the marine ecosystems, biota and fisheries of the archipelago. Altogether more than 600 marine and coastal sites were surveyed, the coastal and marine biodiversity and biotopes were inventoried, inshore biological assemblages were studied and mapped, and the lobster, demersal and shark fisheries were assessed. Additionally, a fishery management plan and a conservation management zoning plan were developed, a GIS database was set up and biological and fisheries monitoring systems were established. A total of 43 specialised reports were prepared during this project by an international team of more than 30 scientists (Krupp *et al.* 2002).

Kemp was the first to assess inshore fish assemblages of the island group, specifically in a preparatory study

for the SBP in 1996. He reported 215 species based on visual records and provided an initial regional zoogeographical analysis derived from distribution data of four families (Kemp 1998; compare also Kemp 2000b). During the SBP bioinventories and quantitative fish community surveys were completed between 1999 and 2002 using underwater visual census techniques, photography and sampling, and led by the first author of this paper. Fish assemblages were found to be species rich by regional comparison and included unique reef fish assemblages in spite of the lack of biogenic reef formation (Zajonz *et al.* 2000; Zajonz & Khalaf 2002; Zajonz & Saeed 2002).

After the completion of the SBP in 2002 the first author and various collaborators have continued investigating Socotra Archipelago's inshore and estuarine fish assemblages. Gill & Zajonz (2003) were the first to describe a new species of fish, *Halidesmus socotraensis*, from the islands for more than a century, which was followed by a study of pseudochromine and pseudoplesiopine dottyback fishes, including the descriptions of *Pseudochromis chrysospilus* and *P. socotraensis* by Gill & Zajonz (2011).

From 2008 to 2015 a follow-on research programme was supported through the Senckenberg Biodiversity and Climate Research Centre (SBiK-F) covering fish biology and fisheries at large, and to a certain extent also reef and estuarine ecology. Some of the results from these studies have already been published or submitted e.g. Lavergne *et al.* (2014) and Lavergne *et al.* (2016). The study of Lavergne *et al.* (2013), and the MSc dissertations of M.S. Aideed (2013) and M. Martin (2014) primarily relate to trophic ecology, biomass and fishery-based social-ecological systems. Various additional papers by several of the present authors are currently in preparation and relate directly to the present faunistic account, including a revised biogeography of the coastal fish assemblages of the island group (Zajonz *et al.* submitted), a new blenniid fish of the genus *Ecsenius* McCulloch from the Socotra Archipelago (by Springer *et al.*), reports of putative new hybrids from a Southern Arabian Hybrid Zone (by Zajonz *et al.*), and new records of species with very extensive ranges of dispersal (by Zajonz *et al.*). A limited number of other fish studies from the Socotra Archipelago were also completed during this period e.g. DiBattista *et al.* (2015a) on seven hybrids of reef fish, and Ali *et al.* (2016) on fish feeding ecology.

Studies related to the Socotra Archipelago include Randall & DiBattista (2013), who described the damselfish *Chromis fieldi* from the Indian Ocean, synonymising *inter alia* the earlier record of *C. dimidiatus* (Klunzinger) by Zajonz *et al.* (2000), a species now considered restricted to the Red Sea, and designated type specimens from Socotra Archipelago, collected by these authors. The last coastal species described as new to science from Socotran waters are *Carcharhinus humani* White & Weigmann, 2014 based on individuals collected in 1988 by the R.V. 'Vityaz' from 41–43 m depth, and *Pempheris zjonzi* Randall & Victor, 2015. The latter species was described based on specimens collected by Zajonz and Khalaf during the SBP in 1999. Recent studies of the contemporary marine biogeography of the Arabian region by DiBattista *et al.* (2016b) and of the origin of Red Sea endemics by DiBattista *et al.* (2016a) used unpublished and outdated faunistic data from the Socotra Archipelago by several of the present authors (Zajonz *et al.* 2000). Recent studies of the cosmopolitan butterfly fish *Chaetodon auriga* (Forsskål) by Di Battista *et al.* (2015b) and of the phylogeography, population structure and evolution of the subgenus *Corallochaetodon* by Waldrop *et al.* (2016), i.e. of *Chaetodon trifasciatus* Park and *C. melapterus* Guichenot reflected on populations of these species inhabiting the Socotra Archipelago. A recent study by Fernandez-Silva *et al.* (2015) on the phylogeography of *Mulloidichthys flavolineatus* (Lacepède) had implications on the taxonomic status of the population at the Socotra Archipelago, and resulted in a paper (Fernandez-Silva *et al.* 2016) differentiating the populations in the north-western Indian Ocean at subspecies level as *M. flavolineatus flavicaudus* Fernandez-Silva & Randall from those living elsewhere in the Indo-West Pacific based on genetic and morphological characters, and showing the presence of the subspecies in Socotra Archipelago based on photographic evidence. A study on seascape genetics of clownfishes from the Arabian Peninsula (Saenz-Agudelo *et al.* 2015) reflected on populations and hybrids of *Amphiprion bicinctus* Rüppell and *A. omanensis* Allen & Mee from Socotra Archipelago based on DiBattista *et al.* (2015a). DiBattista *et al.* (2017) most recently identified a crypto-genetic lineage of *Lutjanus kasmira* encompassing populations on Socotra Island and Oman. None of the studies published since Zajonz & Khalaf (2002) presented faunal lists or updated the fish species inventory of the archipelago.

The study by Lavergne *et al.* (2016) documented and analysed estuarine and lagoonal fish diversity and fish assemblage structure at Socotra Island (13 sites, including 11 'temporarily open/closed estuaries', TOCEs) and three selected comparative sites at the Gulf of Aden coast of Yemen, based on surveys conducted in 1999 and 2000, and from 2007 to 2009. A total of 65 species in 32 families were recorded from Socotra Archipelago and 20 species in 17 families from the Hadhramout coast of mainland Yemen. Twenty-one species represented new faunal records

for Socotra Archipelago. The fish species richness of estuaries and lagoons of Socotra Island totalled 76 species if Steindachner's historical records were included. Rarefaction and extrapolation analyses suggested that the actual fish species richness of Socotra Island's estuaries might be even higher. Mugilidae and Gobiidae were the most species-rich families followed by Lutjanidae, Gerreidae and Sparidae. Five species dominated the occurrence and abundance frequencies: *Terapon jarbua* (Forsskål), *Hyporhamphus sindensis* (Regan), *Aphanianus dispar* (Rüppell), *Ambassis dussumieri* Cuvier and *Planiliza macrolepis* (Smith). Observed and rarefied species richness showed a higher average fish diversity of Socotra Island's estuaries than found on the mainland. It was also comparatively high relative to, for example, species inventories of well-researched and much larger coastal estuaries in southern Africa (Harrison & Whitfield 1995; Harrison 2005).

Field research by international scientists at the archipelago has been hampered by unrest in mainland Yemen since 2011, and became virtually impossible as of 2015. Even the work by national researchers became severely constrained as a result of logistic and financial issues. For these reasons, the execution of the SBiK-F research programme has unfortunately remained fragmentary. One of its original aims, to—*inter alia*—compile a near-complete fish species inventory, to document all records by samples and photographs and to produce an annotated checklist of the coastal fish assemblages of the Socotra Archipelago, could not be achieved. Given the repeated and continuing obstacles posed by the political and security situation in the country, it has not been possible to complete this checklist as yet. At the same time, the crises are having adverse effects on environmental management (EPA Socotra pers. comm., Zajonz *et al.* pers. obs.).

The main aim of this paper is to characterize the diversity of the coastal fishes of the Socotra Archipelago. Its objectives are (a) to summarize the current faunistic and taxonomic information on the coastal fish assemblages of the Socotra Archipelago and to compile a preliminary species inventory, (b) to present a basic analysis of the diversity and distribution of the coastal fish assemblages, including an extrapolation of its total fish diversity, and (c) to facilitate targeted, follow-on studies and support ongoing conservation management efforts.

Published literature was considered in the text of this paper until submission whereas taxonomic and faunistic information could only be considered in the diversity and distributional analyses if published before March 2015. This paper corresponds to a parallel paper on the distributional biogeography of the fishes of Socotra Archipelago (Zajonz *et al.* submitted). The compilation of the joint distributional datasets had to be concluded at a certain stage in order to allow the statistical analyses of both papers to fully correspond to one another. Nomenclatural and taxonomic information published after March 2015 was still considered in the FL 2017 (Annex 1–2).

Study area

The Socotra Archipelago lies in the north-western corner of the Indian Ocean between 53°0'E and 54°35'E and 12°5'N and 12°43'N at the junction between the Gulf of Aden and the Arabian Sea (Fig. 1). The archipelago includes the main island of Socotra, three smaller islands Darsa, Samha, Abd al-Kuri and two islets Sabuniya and Kal Farun. The western-most island Abd al-Kuri is separated from mainland Africa (Somalia) by the Socotra Passage, a narrow strip of water only 95 km wide, and the eastern tip of Socotra Island is separated by 330 km from the nearest point at mainland Arabia (Yemen, Ras Fartak). The main island of Socotra has an east-west extension of 134 km and a total area of approximately 3,550 km² and is the second largest island in the western Indian Ocean after Madagascar (Klaus & Turner 2004; Cheung & DeVantier 2006).

Oceanic conditions around the island group are highly variable due to the seasonally reversing current system driven by the alternating monsoon seasons in the northern Indian Ocean that creates a huge, complex upwelling system during the summer monsoon (Kemp 1998; Fleitmann *et al.* 2004; Klaus & Turner 2004; Fleitmann *et al.* 2007; Scholte & De Geest 2010; van Rispensberg *et al.* 2013). During the weaker, wet north-east monsoon (November–February) the dominant Somali Current travels southwards along the coast of mainland Africa. With the onset of the more forceful dry summer or south-west monsoon (May–September), the surface flow of the Somali Current is reversed from southward to northward (Fig. 2). The reversed Somali Current, in combination with the south-west monsoon winds, drives the formation of two distinct nutrient enriched upwelling systems along the coast of Somalia and the south-eastern Arabian coast of Yemen and Oman (Wyrtiki 1973; Schott *et al.* 1990; Fischer *et al.* 1996; Schott & Fischer 2000; Frattoni *et al.* 2006).

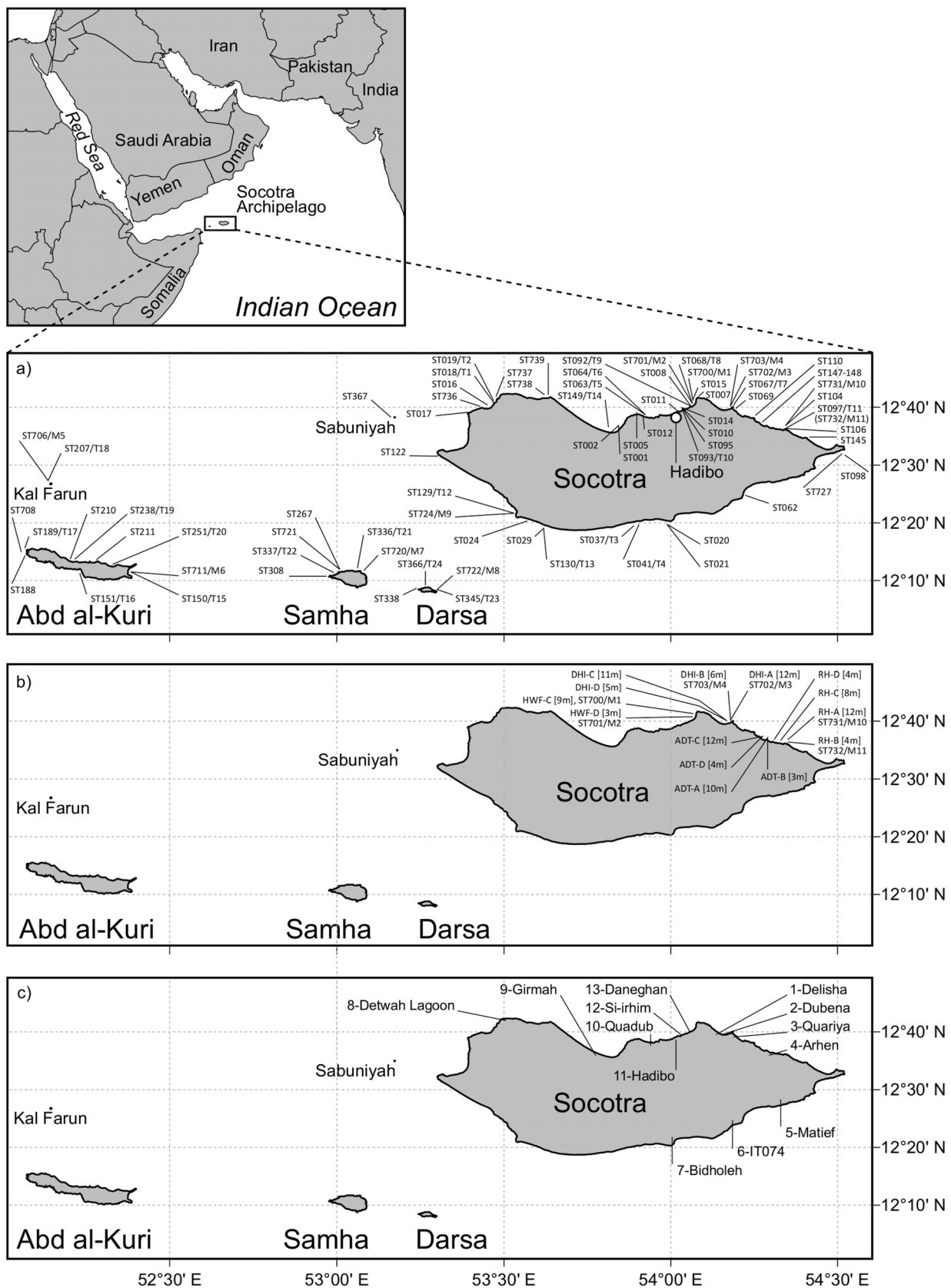


FIGURE 1. Overview map of the Socotra Archipelago, showing its geographic location in the Indian Ocean; with: (a) 74 subtidal Fish Inventory Sites (FIS) of 1999 and 2000, which include transect sites (/T) and ecological monitoring sites (/M) (Zajonz & Khalaf 2002; Zajonz & Saeed 2002); (b) 14 fish biomass monitoring sites from 2007 to 2014 (Zajonz *et al.* 2016); and (c) 13 main estuarine and lagoon survey sites from 1999 to 2009 (Lavergne 2012; Lavergne *et al.* 2016).

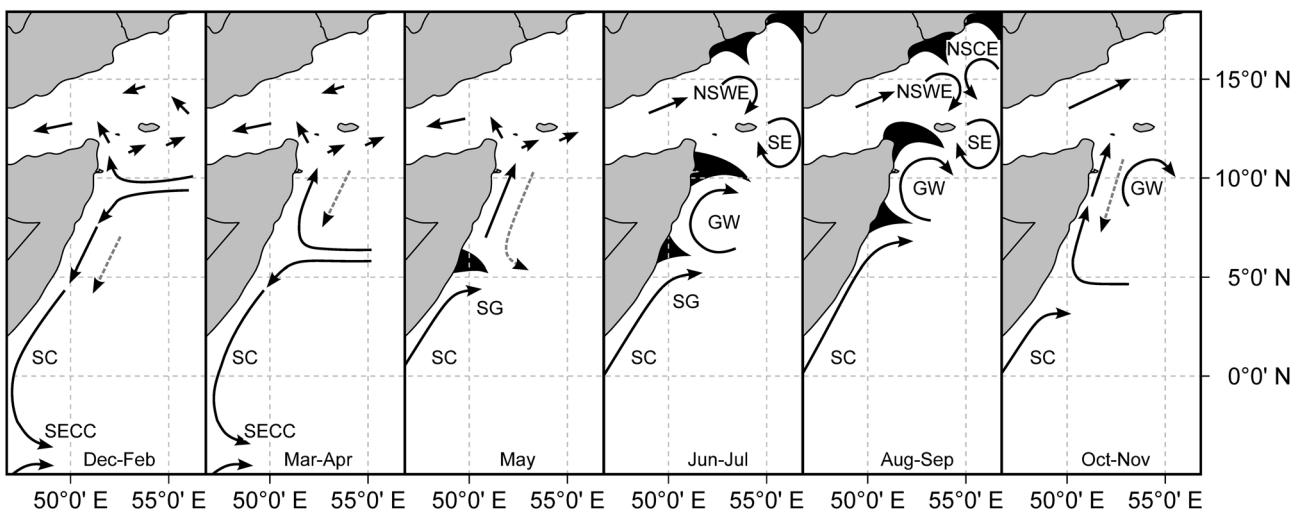


FIGURE 2. Schematic diagram illustrating the seasonal variation of the major oceanographic currents and circulatory features in the northern Indian Ocean and Gulf of Aden region (modified from Klaus & Turner 2004, compiled and adapted from several sources). Black arrows indicate surface currents (0–100 m), dashed arrows indicate subsurface currents (100–400 m depth) when they are in opposition to surface currents. Black shaded areas indicate the area of seasonal cold-water upwelling. Abbreviations: South Equatorial Counter Current (SECC), Somali Current (SC), Southern Gyre (SG), Great Whirl (GW), Socotra Eddy (SE), North Socotra Warm Eddy (NSWE), and North Socotra Cold Eddy (NSCE).

Remotely-sensed chlorophyll-a concentrations reveal seasonal patterns with an increase in productivity from annual minima in April–May (warmest months, prior to onset of the summer monsoon) to annual maxima in August–September (coolest months) (Klaus & Turner 2004). *In-situ* records show that primary productivity more than triples between the winter (0.5–0.8 g C/m²/day) and the summer monsoon (3 g C/m²/day). Average chlorophyll-a concentrations vary between 0.5–5.0 mg/m³ (Veldhuis *et al.* 1997), with maxima of 15 mg/m³ in sheltered locations (Baars *et al.* 1998). Decadal averages (2003 to 2012) of mean monthly Chl-a values at 19 sites around the archipelago show minima before the summer monsoon in April (0.206 mg/m³) and May (0.145 mg/m³) and maxima in July (1,153 mg/m³) and September (1,279 mg/m³) (Zajonz *et al.* 2016). The high primary productivity driven by the monsoonal oceanographic dynamics provide the basis for the unique productivity levels also in higher trophic categories (Zajonz *et al.* 2016), as also stated by Hariri *et al.* (2002) “*The north-eastern part of the Gulf of Aden and the area south of Socotra are among the most productive marine areas in the world, with productivity levels comparable to those off the coasts of Peru and West Africa*”. The resulting fish biomass is exploited by a large and productive fishery (IFAD 2010; Zajonz *et al.* 2016).

The seasonally variable oceanographic dynamics and upwelling systems also influence the spatial and temporal distribution and composition of the benthic communities and associated fish assemblages (Zajonz & Khalaf 2002; Schils & Coppejans 2003a; DeVantier *et al.* 2004; Klaus & Turner 2004). Moreover, the oceanographic dynamics position the islands at the crossroads between the regional ocean currents, a setting that has implications for the dispersal and genetic connectivity of marine organisms, and patterns of marine diversity and biogeography in the wider northern and western Indian Ocean (e.g. Kemp 1998; Zajonz *et al.* 2000; Zajonz & Khalaf 2002; Schils & Coppejans 2003b; DeVantier *et al.* 2004; Schils 2006; DiBattista *et al.* 2015a; DiBattista *et al.* 2016b; Zajonz *et al.* 2016; Zajonz *et al.* submitted).

The shallow inshore benthic habitats in the Socotra Archipelago support highly heterogeneous benthic communities reflecting the variable environmental conditions and different levels of exposure to these conditions. The biotope types found range from soft sediment and sandy habitats with seagrass beds to rocky habitats with encrusting communities composed of turf algae, macroalgae and sponges, mixed macroalgal and hard and soft coral communities, and highly diverse hard coral dominated communities (Klaus & Turner 2004). Biogenic reef framework development is constrained by the marginal ‘pseudo-temperate’ (Klaus & Turner 2004) conditions, and reefs are generally located in the lee of headlands or within embayments sheltered from direct exposure to monsoonal forces. Coral-dominated communities are usually found growing directly on rock substrate and coral cover and diversity is high, with some 253 scleractinian species (58 genera, 16 families) having been recorded to

date. Macroalgae-dominated assemblages are also diverse in terms of assemblage types and species richness. They cover a substantial part of the inshore areas particularly on the south coast of Socotra Island, a result of its exposure to the south-west monsoon and upwelling (Schils 2002; DeVantier *et al.* 2004; Klaus & Turner 2004). The south coast assemblages show a lower affinity with the (sub-)tropical Indian Ocean flora and harbour many disjunctly distributed species, whereas those at northern coasts support more species commonly known from the tropical Indian Ocean (Schils 2002; Schils & Coppejans 2003a, 2003b).

The main island of Socotra has about 30 estuaries and one lagoon which vary greatly in their morphology, freshwater and seawater inputs and ecological conditions, whereas no such ecosystems are found on the other islands. The monsoon seasons contribute to creating marked seasonal changes in drainage flows, salinity and temperature regimes and thus, in combination with the local topography, very variable and heterogeneous estuarine environments. Most estuaries are separated from the sea by berms of gravel or sand and only get temporarily connected to the sea after flash floods or by storm surges representing TOCEs (Klaus & Turner 2004; Lavergne 2012; Lavergne *et al.* 2013; Lavergne *et al.* 2016).

Materials and methods

From 1998 to 2002, under the auspices of the Environmental Protection Authority, Yemen, the Senckenberg Research Institute and Museum of Nature, Frankfurt, conducted the MBS in the framework of the SBP (Krupp *et al.* 2002). The majority of the data presented herein were recorded during these studies by Zajonz, Krupp and Saeed following the seminal precursor study conducted by Kemp in 1996 (Kemp 1998). Faunistic information of the fisheries surveys of the SBP (e.g. Hariri & Yusif 1999; Saeed 2000; Nichols 2001; Mohsen 2002) were reviewed and considered as well. Major subsequent field studies included fish monitoring surveys led by Zajonz and Saeed in 2003 and 2007, estuarine studies led by Lavergne, Zajonz and Krupp from 2007 to 2011, and fish biomass monitoring and fisheries surveys led by Zajonz and Aideed from 2007 to 2014. This study collates all faunistic, taxonomic and distributional information on the coastal fish assemblages of Socotra Archipelago, which were yielded by these works. Owing to the variety of different studies and the relatively long study period covered by this paper, the data contexts i.e. the materials and methods used were diverse. In terms of data recording the present section focuses on the description of the methods employed from 1998 to 2002 because most of the faunistic and taxonomic data originate from this period. Methods, which primarily served ecological or fisheries studies and which yielded faunistic and taxonomic information as “by-products”, are only briefly mentioned hereinafter. Comprehensive descriptions of key methods were provided by Kemp (1998; 2000a), Zajonz *et al.* (2000), Zajonz & Khalaf (2002), Zajonz & Saeed (2002), and Lavergne *et al.* (2016).

Definitions and key references

The terms ‘community’ and ‘assemblage’ are used in accordance with Fauth *et al.* (1996), and also Magurran (2004), who defined that “communities consist of species found at a given place and time” and that “assemblages are communities whose species are taxonomically related”, as in the present case ‘fish assemblages’. The term ‘occurrence’ refers to the event of a species being recorded as present with at least a single individual at a given site (e.g. Gaston & He 2011). For the purpose of this paper the term ‘coastal’ encompasses marine and other aquatic habitats from the intertidal zone to 200 m depth (by convention, e.g. Randall 2007; Briggs & Bowen 2012) and marine-influenced estuaries and lagoons, including TOCEs, and the associated communities and assemblages. The term ‘inshore’ is applied to areas from the intertidal to subtidal areas reached by SCUBA. The term ‘reef-associated’ is used to describe biota and biological assemblages, which inhabit coral reefs in other parts of the Indian Ocean. In relation to fishes usually the term ‘coral-associated’ is applied if the habitat referred to is broadly coral-dominated regardless whether it is characterised by a biogenic reef framework. The term ‘Arabian/Persian Gulf’ is used because the proper name for the respective geographical entity remains internationally disputed. Institutional codes follow Leviton *et al.* (1985), except for NHCY-P, which is for the fish section of the ‘Natural History Collection of Yemen’ (currently curated at SMF, see below). Taxonomy and nomenclature of fish species names follows the ‘Catalog of Fishes’ (Eschmeyer *et al.* 2017, web resource) unless stated otherwise. The online database ‘FishBase’ (Froese & Pauly 2017, web resource) was frequently consulted to check or obtain information especially about the biology, ecology and distribution of fish species, to access fish pictures and track literature.

Data recording

During the period of 1999 to 2002, subtidal and intertidal habitats around all islands (Socotra, Darsa, Samha, Abd al-Kuri, and the rock stacks Sabuniya and Kal Farun) were assessed applying three methods:

- 1 Compilation of fish species inventories by visual underwater recording, sampling, photography, and underwater drawings.
- 2 Compilation of inventories of species caught in artisanal fisheries by visiting fish landing sites and markets.
- 3 Quantitative surveys of fish assemblages by fish transect censuses.

Qualitative subtidal recordings of fish species occurring in inshore waters were conducted by SCUBA diving (or occasionally by snorkelling), performing visual recording, sampling, photography and drawing. Sites were usually visited until no additional species were found for at least 10 minutes. Sites were considered sampled to the level of a detailed fish species inventory site (FIS), if the overall sampling effort by one or several methods approximated the sampling intensity employed at a transect survey site (see below). Although not fully standardised by statistical means, the resulting accounts are considered suitable to compare the species richness of different sites and as a basis for resemblance analyses, notably if coefficients are applied which are robust against slightly differing sampling effort. Intertidal habitats were sampled opportunistically during the main surveys in 1999 and 2000 and specifically during a dedicated faunistic survey in 2000, using mainly hand-collecting and seine netting.

Subsequently, subtidal recording was conducted primarily in 2003 and 2007 and from 2011 to 2014. Quantitative and standardised recording was conducted at nine permanent ecological monitoring sites established in 2000, and eight additional fish biomass monitoring sites established in 2011. Qualitative (faunistic) recordings were opportunistically conducted at numerous other sites during the survey work. Intertidal habitats were sampled specifically again from 2007 to 2009 (see Lavergne *et al.* 2016) and samples of subtidal species for genetic studies were explicitly collected from 2009 to 2011 (unpubl.).

Reference collections. The main part of the reference collection was compiled from 1999 to 2002 consisting of 4,440 specimens in 780 lots. Numerous samples were added to the collection later on, especially during estuarine surveys from 2007 to 2009 (approximately 3,235 specimens in 200 lots; Lavergne *et al.* 2016) and collections conducted in 2009 and 2010 explicitly in support of genetic studies (204 specimens in 129 lots; H. Pulch & Zajonz unpubl.). Additional samples were collected by T. Alpermann in 2010 and 2011 (1,296 specimens in 66 lots) and deposited at the SMF. The record of *Apogonichthyooides pseudotaeniatus* is owed to this collection and several previous visual records were confirmed by those samples. The reference collection of coastal fishes of the Socotra Archipelago compiled at the SMF consists currently of 9,175 specimens in 1,175 lots. Based on the research agreements between the SMF and the EPA Yemen and the ensuing sample export permits half of the collections will be returned to Yemen once a suitable natural history repository is operational in the country. Meanwhile the samples are temporarily stored at the SMF.

Photography and drawings. The use of underwater photography was limited during the surveys. The focus was placed on visual recording and sampling of fishes and documentation of benthic habitats. Additional photographs were obtained from many colleagues, notably from H. Kovac, A. Siklosi, R. Klaus, A. Bollen, and W. Wichmann. Approximately 1,800 photographs were analysed and yielded 324 species records which could be identified with certainty. In addition, 46 species were identified with certainty from underwater “field drawings” prepared by Zajonz.

Records at fishery landing sites. Additional records were obtained from visits to the fish landing site at Hadibo by M. Khalaf and U. Zajonz, and a number of other fish landing sites primarily during the MBS from 1998 to 2002 (see Hariri & Yusif 1999; Krupp *et al.* 2002; Mohsen 2002). Records at fish landing sites were taken again in 2011 and 2012 during length-weight recording for fish biomass studies (Zajonz & Aideed unpubl.). Freshly dead specimens were identified on-site and photographed whenever possible.

Underwater fish censuses. Fish assemblages were assessed by the first author at 34 survey sites in 1999 and 2000 by visual censuses along 50 m belt transects using SCUBA gear. The fish census transect method generally followed English *et al.* (1997). Sites were selected during rapid assessments of the general habitat surveys conducted during the MBS (Apel 2000). Each fish transect site consisted of three replicates of 50 m ropes or tape measures laid out straight and parallel to the coastline, following the benthic habitat profile. In alteration to the method of English *et al.* (1997) no second replicate set at a different depth per general site was made. The shallow topography of Socotra Archipelago’s coastal shelf, the lack of reef development and the fact that homogeneous

biotopes often cover only small areas (1–5 ha or less) required this modification. Fishes were counted by species (when possible) 2.5 m to each side of the transect line and 5 m above the line. Counts and records were collated in Microsoft Excel spreadsheets for data treatment and basic analyses (further details are provided in Zajonz *et al.* 2000; Zajonz & Khalaf 2002; Zajonz & Saeed 2002).

The fish transects of both survey years covered a total water volume of 127.5 km³ and an area of 25.5 km² of benthic biotopes. A total of 122,342 individuals were counted at 102 transect replicates, equivalent to an average sum of 40,778.3 individuals at 34 transect samples. An average total of 3,598.3 individuals per site and an average of 1,199.4 individuals across three replicates were counted per transect. Between 2003 and 2007 an additional 15 fish transects were completed at nine ecological monitoring sites. Altogether faunistic records contributed to this study, which were obtained at 49 fish transects (with three replicates of each count) covering a total water volume of 183.8 km³ and a total of 215,648 individual fish.

Fish biomass transect surveys were conducted according to the method described by English *et al.* (1997; visual length-frequency censuses based on the belt transect method) at eight ecological monitoring sites in 2007 (observer Zajonz), at 14 ecological and fish biomass monitoring sites in both the pre-monsoon and post-monsoon seasons of 2011 (observer Aideed), in both the pre-monsoon and post-monsoon seasons of 2012 (observer Aideed), in the pre-monsoon season of 2013 (observer M. Martin), and again in the pre-monsoon season of 2014 (observer Aideed). Altogether faunistic records from 64 fish biomass transects (with three replicates of each count) were taken, covering a total water volume of 240 km³ and 34,037 individual fish.

Taxonomic identification. Fish classification used here follows Eschmeyer *et al.* (2017, ‘Catalog of Fishes’, web resource) unless stated otherwise. The following literature was predominantly used to identify samples in the field or to confirm observations made in the field: Allen & Randall (1980), Randall (1983 [1992 reprint], 1995), Smith & Heemstra (1986), Allen (1991), Allen & Steene (1994), Lieske & Myers (1994, 2001), Debelius (1996, 1998, 1999), Myers (1999), Debelius & Kuiter (2001), Debelius *et al.* (2003), Kuiter & Debelius (2003), Lieske & Myers (2004), and Froese & Pauly (2017, Fishbase, web resource). Taxon-specific publications were used to identify fish samples in the laboratory, too many to be listed individually.

Study sites. During the MBS subtidal data were recorded at 82 main survey sites (targeted survey activity at a defined location and date, using defined qualitative or quantitative field methods) in 1999 and at 29 main survey sites in 2000, including 18 large sampling sites (targeted sampling activity by a team of researchers covering at least several square meters of habitat). Out of these 111 sites, 74 were designated as subtidal fish inventory sites (FIS), a category of assessment, which was used for analyses of species richness and diversity distribution as explained above. During the follow-on studies from 2003 to 2013 a total of 79 main subtidal survey sites (15 fish transects and 64 fish biomass transects) were covered at 17 different localities. The intertidal surveys comprised 33 main sites at 13 different locations. At many complementary subtidal and intertidal sites, additional fishes were recorded visually, by photography, sampled *in-situ* or obtained from fishermen.

All site locations were recorded with hand-held GPS devices (WGS 84). Detailed information on the main subtidal sites surveyed in 1999 and 2000 are given in Zajonz *et al.* (2000), Zajonz & Khalaf (2002) and Zajonz & Saeed (2002). Locality details of the main sites completed during the estuarine surveys can be found in Lavergne *et al.* (2016).

Maps of the island group show the locations of the 74 fish inventory sites (FIS), which include transect sites (/T) and ecological monitoring sites (/M) (Fig. 1a), the location of 14 ecological and fish biomass monitoring sites (Fig. 1b), and locations of the 13 main estuarine study localities (Fig. 1c).

Data analysis

The understanding and treatment of diversity and ecological data broadly followed Ludwig & Reynolds (1988), English *et al.* (1997), Clarke & Warwick (2001) and Magurran & McGill (2011), and specifically Gray (2000), Magurran (2004), Magurran *et al.* (2011), and McGill (2011). Data collation, consolidation and basic statistical calculations were computed using Microsoft Excel 2007. This paper primarily presents incidence-based results (presence and presence-absence data). Abundance-based results will be provided in a forthcoming paper on fish community ecology of the island group (Zajonz *et al.* in prep.). Abundance data are used on two occasions to support the methodological rationale and the interpretation of results. Diversity indices, resemblance (dis-similarity) matrices and other multivariate analyses were computed using the ecostatistic software PRIMER v4-v6 (Plymouth Routines in Multivariate Ecological Research) according to Carr *et al.* (1994) and Clarke & Gorley

(2006), and interpreted following Clarke & Warwick (2001) and Magurran (2004). The estimations of incidence-based richness and associated species accumulation curves were computed using the ecostatistic freeware application EstimateS 8.2 (Colwell 2005, 2013, web resource). Graphs were initially produced in Microsoft Excel 2007 or by PRIMER v4-v6; their layout was subsequently improved using the vectorial graphic editing software Inkscape™ 0.91. Data analysis methods are described in more detail below.

Species inventory. The species inventory is based on all available records (see above). These include a total of 6,966 *in-situ* recorded events (defined as the event of a species being found at a site) of which 5,405 refer to the main faunistic surveys in 1999 and 2000. The identification of a number of reference specimens is still preliminary. For certain taxa, thorough study by specialists may alter identifications at the species level or reveal the presence of additional species. The compilation of the basic species inventory for the analyses of diversity and species distribution also included a review of published records and verification of the present taxonomic status of species reported in the literature to March 2015. Records and taxonomic information published later are included in Annex 1 in order to provide a most up-to-date species account. Some of the specimens collected by E. Riebeck and G. Schweinfurth in 1881 (Taschenberg 1883) were re-discovered at the ZMH and studied by the first author (see Krupp *et al.* 2006). Specimens of 11 species, which had been described as new to science based on material collected near Socotra (Kotthaus 1967, 1968, 1970a, 1970b, 1973, 1974, 1976, 1979; Karmovskaya 1991) were checked. Estuarine and lagoonal samples were analysed in a separate study (Lavergne *et al.* 2016) in close coordination with the present research, and the results were used in both studies. Putative fish hybrids, which were recognized in the field by the present authors were included in the species inventory in order to document their presence, and because they are considered as biogeographically important constituents of the fish fauna of Socotra Archipelago (Kemp 1998, 2000a; Zajonz *et al.* unpubl.). Several of the hybrids reported by DiBattista *et al.* (2015a) are not included in the species accounts because the paper was published after the main analyses for this paper were concluded (but are added as footnotes to Annex 1).

The main aim of this paper is to characterize the coastal fish species richness of the Socotra Archipelago. The available records were classified into confirmed records, referred to as ‘species’, and preliminary records referred to as ‘Operational Diversity Units’ (ODUs). For the purpose of the study an ODU is defined as “as a biological and/or taxonomic unit recognized during diversity studies in a qualified way and distinguished with negligible error from species (or higher taxa depending on the scale of observation) and other ODUs, which allows preliminary analyses and communication of “work in progress” in terms of characterizing critical diversity features of a given study subject—without constituting a formal taxonomic or faunistic record—for the benefit e.g. of conservation and resource management”.

These ODUs comprise observations of fishes that have not yet been positively identified to species or genus level, due to a lack of sampling. Only those records qualified as ODUs, which were distinguishable from other species and other ODUs, and which likely represented distinct taxa occurring on the archipelago. Several dozen of additional observations were discarded as ill-defined for the purpose of this paper. The ‘species’ records (682) were collated into a ‘Preliminary Checklist’ (Annex 1), and the ‘ODUs’ (51) were collated into a ‘Working List’ (Annex 2). In combination, the Preliminary Checklist and the Working List are referred to as ‘Faunal List 2017’ (FL 2017) and the combined records (733) are referred to as ‘faunal records’.

The Preliminary Checklist is based on 464 species recorded visually by the authors, 280 species collected, 368 photographed and/or drawn, 208 species recorded visually by Kemp (1998; of 215 then reported), and 213 species reported elsewhere and verified. They represent a total of 6,631 *in-situ* recorded events. The means by which a species was recorded are indicated in the Annexes 1–2. The average percentages of abundance per species across 34 fish transect sites are listed in order to provide an indication of relative commonness. Species authorities are given in full (with publication year) in the FL 2017. The authority name of species which are not included in the FL 2017 is given upon first mention of a species name in the text. The Preliminary Checklist is arranged in systematic order to the subfamily level and alphabetically for genera and species.

The systematic diversity was assessed by identifying the dominant orders (according to family richness) and the dominant families (according to genus and species richness). The frequency distribution of species richness of the families was calculated according to decimal and logarhythmic richness categories (Fig. 3a, b).

Comparisons of species richness. In order to characterize the Socotra Archipelago’s coastal fish diversity the species richness of key families was compared (1) to the richness of these families in eight adjacent presumed Arabian marine ecoregions, and (2) to the richness of these families in the Red Sea. In support of Comparison (1)

the presence of species belonging to five key families (Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Pseudochromidae) in eight Arabian ecoregions (Table 2) was compiled using reviewed distributional records from published and grey literature (including FishBase 2017 web resource), unpublished distributional data from several of the authors recorded during extensive field research in the region (i.e. of Bogorodsky, Zajonz, Krupp and Kemp) and personal distributional databases maintained for the Arabian region (i.e. of Bogorodsky and Zajonz). The definition of the eight Arabian ecoregions was based on Spalding *et al.* (2007; Marine Ecoregions of the World, MEOW), but modified, covering the ecoregions 87–93 within the Red Sea—Gulf of Aden provinces (18.) and Somalia - Arabia (19.). In altering the classification of Spalding *et al.* (2007), ecoregion 87 (northern and central Red Sea) was disaggregated by collating a separate species account for the Gulf of Aqaba, and the ecoregion 89. (Gulf of Aden) was disaggregated by collating separate species accounts for the southern Gulf of Aden (primarily representing Djibouti due to the available data), the northern Gulf of Aden (primarily representing the Shabwa, Hadhramaut and Al-Mahara coasts due to the available data), and Socotra Archipelago (Annex 1). The resulting ecoregional units then are: Socotra Archipelago (Soc), Gulf of Aqaba (GoAq), northern and central Red Sea (n+c RS), southern Red Sea (s RS), southern Gulf of Aden—Djibouti (s GoA (Djib)), northern Gulf of Aden (n GoA), Oman—Arabian Sea coast (Oman (AS), Gulf of Oman (GoO), Persian/Arabian Gulf (AG).

The distributional matrix was collated in the context of a separate simultaneous study on the distributional and ecological biogeography of the Socotra Archipelago (Zajonz *et al.* submitted) and will be accessible as an electronic supplement to this paper. More details are provided there. In Comparison (2) the species richness of 12 selected families in the Socotra Archipelago is compared to the richness of these families in the entire Red Sea as reported in the most up-to-date accounts by Golani & Bogorodsky (2010), Golani & Fricke (2018), and Bogorodsky *et al.* (in press).

Significance of ‘island group’ and ‘exposure’ designations. For several of the investigations, records and samples with known sampling locality at the archipelago were aggregated according to three ‘island group’ designations: (1) Socotra & Sabuniya, (2) Darsa & Samha, and (3) Abd al-Kuri & Kal Farun. In addition, records and samples were partly interpreted according to two ‘exposure’ designations: (1) north coast, and (2) south coast. These groupings appear as natural geographical units but their validity had to be verified statistically. In a first test, the sample data at 68 FIS (incidence-based, 487 species) were used to verify these designations as *a priori* hypotheses with the ANOSIM routine of PRIMER. Six FIS (of 74) that were located in very close proximity to others were excluded in order to avoid spatial and ecological bias. The ANOSIM (‘Analysis of similarities’, Clarke & Green 1988, in Clarke & Warwick 2001) routine permits testing for *a priori* defined differences in multivariate data structures between groups (Clarke & Warwick 2001) assuming that hypotheses of normality (Shapiro & Wilk 1965) and homoscedasticity (Bartlett 1937) are not met. The island group and exposure designations were defined as options for two ‘factors’ in the PRIMER input matrix, and the 68 samples (columns) were classified accordingly. A resemblance matrix (pairwise distance matrix) was calculated based on ‘Hellinger Distance’ with

$$D_{\text{Hellinger}}(x_1, x_2) = \sqrt{\sum_{i=1}^s [\sqrt{p_{1i}} - \sqrt{p_{2i}}]^2}$$

where x_1 and x_2 are sites 1 and 2, p_{1i} and p_{2i} are the square root transformed relative abundance of the i^{th} species at sites 1 and 2. Hellinger’s distance is the Euclidean distance between the square root of the square root transformed relative abundances of the compared sites. Hellinger distance was chosen because it represents a resemblance index that is robust against not fully standardised sampling effort (Legendre & Legendre 1998, Legendre & Gallagher 2001, Legendre 2005; and for an interpretation by the authors see Lavergne *et al.* 2016). ANOSIM tests were computed using 99999 permutations. The procedure was repeated for re-confirmation using the similarity indices ‘Bray-Curtis’ (Bray & Curtis 1957, which is equivalent to the ‘Soerensen index’ for P/A data) and ‘Jaccard’ (Legendre & Legendre 1998). In a second test, the sample data of 34 fish transects (abundance-based, 342 species) and 27 fish transects (excluding south coast sites, both abundance-based and incidence-based, 313 species), were investigated following analogous procedures as for the first test using similar factors, square root and presence-absence transformed input data, and resemblance matrices based on the indices of Hellinger, Bray-Curtis and Jaccard.

‘Hierarchical agglomerative cluster analysis’ was applied to further investigate the relatedness of the samples according to the pairwise dis-/similarities applying ‘group average linkage’ (e.g. Clifford & Stephenson 1975). The resulting combinations were plotted into cluster dendograms for visual examination (Fig. 4, in part). As alternative ordination method ‘non-metric multi-dimensional scaling’ (nmMDS) was used (e.g. Kruskal & Wish 1978; Clarke & Green 1988). All multivariate analyses were conducted in PRIMER according to the procedures described by Clarke & Warwick (2001) and Clarke & Gorley (2006).

Estimates of species richness. Total (archipelagic) and partial species richness was modelled using the non-parametric ‘Species Richness Estimator’ routines of the ecostatistic freeware application EstimateS 8.2 (Colwell 2005, 2013, web resources). Incidence-based (presence-absence based) richness modelling applying the estimators ‘Chao 2’, ‘ICE’, and ‘Jackknife 2’ was preferred over sample-based rarefaction curves (expected species accumulation curves; Gotelli & Colwell 2001) because “they estimate total species richness, including species not present in any sample” (Chao 2005; Colwell *et al.* 2012; Colwell 2013 web resource; compare also Magurran 2004; Gotelli & Colwell 2011).

The classic non-parametric incidence-based richness estimator Chao 2 (Chao 1984, 1987) was computed along with log-linear 95% confidence intervals (CI). It estimates the “true number of species in an assemblage based on the frequency of rare species (‘uniques’ and ‘duplicates’) in the samples”, whereat uniques are species restricted to a single site and duplicates are species occurring at two sites only (Colwell & Coddington 1994), following: $\text{Chao 2} = S_{\text{obs}} + (Q_1^2/2Q_2)$, where ‘ S_{obs} ’ is the number of species observed in all samples pooled, Q_1 is the frequency of uniques, and Q_2 is the frequency of duplicates.

The non-parametric incidence-based coverage estimator ICE (Lee & Chao 1994; Chazdon *et al.* 1998, Chao *et al.* 2000) and the non-parametric incidence-based second-order jackknife estimator Jackknife 2 (Burnham & Overton 1978, 1979; Smith & van Belle 1984; Palmer 1991) were calculated in order to explore additional ecostatistically valid richness models. Sample-based rarefaction curves of expected richness, both as resampled S_{obs} and analytical ‘Mao Tau’ were computed in EstimateS for comparison (Colwell *et al.* 2004; Mao *et al.* 2005; Colwell 2013 web resource) (Fig. 5).

The archipelagic richness estimator computations were based on the input of 68 FIS (samples, columns, with 6 out of 74 FIS discarded to avoid spatial and ecological bias) and 487 species (S_{obs} , rows) from 66 families recorded at these sites in 1999 and 2000, using the following parameter settings for the computation: 500 randomizations and strong hash encryption. The ‘bias corrected’ Chao 2 value was initially calculated. Because Chao’s estimated co-efficient of variation (CV) for the incidence-based distribution was higher than 0.5 also the ‘classic’ Chao 2 estimator was calculated and the higher value of both used as recommended by Chao (1987) and Colwell (2013 web resource). The model computations were repeated three times with the same input data matrix and parameter settings whereat the three richness estimators were computed jointly each time. Chao 2 was chosen as the lead estimator, and the other two estimators ICE and Jackknife 2 served as additional reference values next to the 95% confidence intervals for Chao 2. The median (totalling 828 species, with 730 species as lower and 964 species as upper CI bound) of the three Chao 2 values (865, 807) was eventually selected, and the values of ICE (850) and Jackknife 2 (887) were selected from the same run (Table 3, Fig. 5). The other values of ICE (901, 870) and Jackknife 2 (907, 881) were discarded.

In addition to the total richness estimations, explorative richness estimates were computed for three critical diversity constituents: (a) individual island groups (Socotra Island & Sabuniya, Darsa & Samha and Abd al-Kuri & Kal Farun); (b) habitat types (S6 “corals”, S5 “bedrock”, S1+4+7 “other (merged)”, according to Klaus & Turner (2004), and (c) 15 selected key families, using respective subsets of the original input data (Table 3). These estimates allowed verifying the results of the total richness estimate and gaining further insights into the relationship and pattern of detected versus undetected species richness. Similar settings and procedures as for the total estimate were applied. The habitat groups S1, S4, and S7 (Klaus & Turner 2004) were only covered by four FIS altogether. The habitat groups S2 and S3 were not covered by FIS because the entire diversity of habitats and their classification was not yet known during the FIS surveys in 1999 and 2000. For the family richness estimates the values of only a single model run were used. In estimating the richness of Serranidae, Apogonidae, and Blenniidae the CV value was larger than 0.5. Thus, the higher value of either the classic or bias-corrected estimate was used, as explained before.

Distribution of diversity. Definitions of diversity follow Gray (2000) and Magurran (2004). The distribution and variation of species diversity was predominantly investigated at the scale of ‘site’ (alpha diversity, α) and

‘island group’ or ‘archipelago’ (gamma diversity, γ) and by the following data: archipelagic species records and occurrences at 74 FIS (Fig. 6). Records and occurrences were also pooled according to ‘island groups’ and compared by resemblance analyses, representing a derivate of β (beta) diversity (differentiation or turn-over diversity) (compare also Lou *et al.* 2011); the results of which are presented along with the γ diversity results. In addition, the faunal records were classified according to types of global distribution ranges and the frequencies of these types were analysed.

In order to obtain a ranking of FIS (α diversity) according to the species richness specific to the archipelago, the sites were classified into ten categories based on species richness relative to the richest site. These categories can be used in future studies to relate species richness data to the results of this study. The details of this classification are given in Table 4.

The term ‘area’ was used to characterize broad diversity patterns at “seascape scale”. Fish species richness of multiple sites which were situated within spatial units having homogeneous physical and biological attributes, was thus assessed together. Ranges and averages of richness of such areas were calculated.

‘Occurrences’ are the record events per species and site. No final inferences about the final archipelagic ‘occupancy’ of species (i.e. the archipelagic species-range size distributions) are made in this paper (e.g. Gaston & He 2011). Frequencies of occurrence categories are therefore provided as ‘occurrence-frequency distribution’ (OFD) not ‘occupancy-frequency distribution’. They were calculated for the records made at the 74 FIS according to eight frequency categories (Fig. 7) and comprise 4,900 occurrences of 497 species across all FIS, 2,933 occurrences of 444 species at Socotra Island & Sabuniyah (52 FIS), 833 occurrences of 259 species at Darsa Island & Samha Island (10 FIS), and 1,134 occurrences of 307 species at Abd al-Kuri Island & Kal Farun (12 FIS).

In order to explore the archipelagic diversity distribution (Table 5), the records of 497 species gathered from 74 FIS all over the archipelago were first aggregated (pooled) into a binary (species presence-absence) matrix representing the three major island groups: (1) Socotra (and Sabuniya in part), (2) Darsa & Samha, and (3) Abd al-Kuri & Kal Farun. Second, the count was expanded to include all other species records of the FL 2017 with known sampling locality (see Annex 1). Of the 682 confirmed species and the additional 51 ODUs in the Working List, a total of 641 faunal records (599 confirmed species and 42 ODUs) have distribution records from individual island groups (600 of which are based on records obtained at the authors’ main sampling sites from 1999 to 2013, and 41 are based on miscellaneous records from 1999 to 2014 by the authors or others). Species occurrences at archipelagic scale (74 FIS) were calculated by summing the absolute and relative occurrences by island groups, ranking them, and identifying the dominant species (Table 6). The distribution of infrequent species (uniques and duplicates) was investigated.

‘Resemblance’ of island groups according to aggregated relative occurrences was investigated in PRIMER by calculating pairwise distance matrices based on Bray-Curtis similarity and Hellinger Distance. The same data were analysed with the SIMPER (‘Similarity percentages’) routine of PRIMER. The procedure calculates, first, the average dissimilarity between all pairs of samples or groups of samples based on the Bray-Curtis index, and second, the average percentage contribution of each species to the average gross dissimilarities (Clarke & Warwick 2001). SIMPER thus helps discriminating species, which contribute most to multivariate data structures, i.e. to differences between sites. A 50% cut-off was applied (only species were included until ~50% cumulative dissimilarity per island group pair was reached) and only the first thirty species are shown (Table 7).

‘Shared species’ between island groups based on the FL 2017 were investigated. A total of 641 faunal records (599 confirmed species and 42 ODUs) have known distribution records from individual island groups. The frequencies of species records were calculated as follows: totals per island group, species shared between all three island groups, species shared between any combination of two island groups, species shared exclusively between two island groups, and species recorded only from any single island group (Fig. 8).

Global distribution ranges. The species of the Preliminary Checklist were classified according to a system of categories (and partly subcategories) of distribution ranges (see Annex 1). In their account of the fishes of the Arabian Seas Manilo & Bogorodsky (2003) adapted the method for the analysis of types of distribution developed by Golikov (1982) and Golikov *et al.* (1990; compare Porter *et al.* 2013) and the method of determining the concentration of distribution boundaries (Nesis 1982) for use in classifying the distribution of Indo-Pacific fishes. This general classification scheme was modified for this study by taking Kulbicki *et al.* (2013) into consideration in order to inform the ichthyogeographic analysis of the coastal fishes of Socotra Archipelago. This resulted in 12 main categories (types) of species distribution range patterns, broadly spanning tropical, subtropical and partially

temperate regions of all oceans. No species was assigned to any of the following categories of the global scheme: tropical Western Pacific (*WP*); tropical Eastern Pacific (*EP*); tropical Atlantic and Indian Ocean (*AI*); and tropical eastern Indian Ocean (*EI*) (mentioned for the sake of completeness).

Of 682 species the available data of 658 species were designated (Figs. 9a, b) to one of the following categories: Worldwide (cosmopolitan; circumglobal) (*WW*); circumtropical (*CT*); tropical Indo-Pacific (*IP*); tropical Indo-West Pacific (*IWP*); tropical pan-Indian Ocean (*pI*: includes East Africa and islands of the Western Indian Ocean and Chagos, often South Africa, to western Australia, the Gulf of Aden and the Red Sea, Socotra, Oman, Arabian/Persian Gulf, Maldives, India and Myanmar, to western Indonesia (western Sumatra, southern Bali) and Andaman Sea); tropical Western Indian Ocean (*WI*); tropical northern Indian Ocean (*NI*); and tropical north-western Indian Ocean (*NWI_all*).

The *NWI_all* category was further subdivided into subcategories so as to allow ichthyogeographic analyses at higher spatial resolution in future studies. The subcategories are: North-western Indian Ocean (regular) (*NWI_reg*); Red Sea and Gulf of Aden only (endemic) (*NWI_e-RSGA*); eastern and southern Arabia and Socotra only (endemic) (*NWI_e-ESA+S*); Socotra Archipelago endemic (*NWI_e-S*); Socotra Archipelago, putative endemic (described from Socotra Archipelago, but likely to occur elsewhere, or taxonomic status uncertain) (*NWI_(e-S)*; and, hybrid of a ‘Southern Arabian Hybrid Zone’ encompassing Socotra, the Shabwa, Hadramaut and Al-Mahara coast of the Yemen Gulf of Aden, and possibly southern Oman (Zajonz *et al.* in prep.); based on Kemp 1998, 2000a, 2000b; and partly DiBattista *et al.* 2015a) (*NWI_SAHZ*).

Certain combinations of main distribution types were included (e.g. *AI-WP*) of which *NI-WP* (including Somalia and Socotra, and along the northern coast of the Indian Ocean to the western Pacific Ocean) was relatively frequent (based on Zajonz *et al.* unpubl.).

It was not possible to adopt the most recent marine tropical biogeographical classification scheme of Kulbicki *et al.* (2013; also see Discussion), who presented a hierarchical quantitative delineation of biogeographic units based on a global mega-database composed of 163 checklists compiled by Parravicini *et al.* (2013). The system of Kulbicki *et al.* (2013) is global in scope, with lowest spatial units (provinces) at the level of the Western Indian Ocean and north-western Indian Ocean while this study required a partly higher spatial resolution (grain). Moreover, it seemingly used an outdated checklist for Socotra Archipelago (Kemp 1998) and did not satisfactorily resolve the ichthyogeographic position of the archipelago (see Discussion). For similar reasons too the schemes of Briggs & Bowen (2012) and Briggs & Bowen (2013) were not adopted. The scheme of Kemp (1998) was based on Arabian distribution patterns of reef fishes only. The ecoregional scheme of Spalding *et al.* (2007) was not used because with regard to the Arabian region it will be challenged in part in a forthcoming paper on the ichthyogeography of the Socotra Archipelago (Zajonz *et al.* submitted).

The present scheme accounts for all known species distribution range patterns from a regional point of view, based on expert knowledge, partly drawing on biogeographic entities established during earlier studies (Golikov 1982; Nesis 1982; Golikov *et al.* 1990; Manilo & Bogorodsky 2003; Kulbicki *et al.* 2013).

Results

First, a preliminary checklist of the coastal fishes of Socotra Archipelago is presented and certain aspects of the species diversity are highlighted. Second, an extrapolation of the islands’ total species richness is provided based on the results of incidence-based richness models, which were adjusted according to certain features of the current faunistic account. Third, site diversity, archipelagic distribution pattern and global distribution ranges of the coastal fish assemblages of Socotra Archipelago are analysed.

Species inventory

The present Faunal List of 2017 (FL 2017) includes a Preliminary Checklist of the coastal fishes of Socotra Archipelago (Annex 1) which comprises 682 confirmed species and a Working List, which includes 51 preliminary records (ODUs) (Annex 2), totalling 733 faunal records in 108 families, of which 86 families were recognised during the authors’ field work. This account includes the confirmed records of the estuarine fish assemblage study of Lavergne *et al.* (2016), the faunistic components of which formed part of this study.

In terms of systematic diversity, the list of 682 species with confirmed records comprises 36 species of

elasmobranchs in 4 orders, 14 families, and 22 genera, and 646 species of bony fishes in 17 orders, 92 families, and 266 genera, representing a total of 21 orders, 106 families and 288 genera. The 10 dominant orders in terms of family richness are Perciformes (61 families, 57.6%), Rajiformes (6 families, 5.7%), Orectolobiformes (4 families, 3.8%), Scorpaeniformes (4 families, 3.8%), and Carcharhiniformes, Elopiformes, Anguilliformes, Clupeiformes, Beloniformes, and Syngnathiformes (each with 3 families, 2.8%). The ten dominant families, in terms of genus richness, are Labridae (24 genera, 8.3%), Gobiidae (18 genera, 6.3%), Blenniidae (14 genera, 4.9%), Apogonidae (11 genera, 3.8%), Carangidae (9 genera, 3.1%), Pomacentridae (9 genera, 3.1%), and Serranidae, Scombridae and Balistidae (each with 8 genera, 2.8% each).

For 26 families, the numbers of species recorded constitute more than 1% (at least 7 species) of the total number of species (Table 1). They comprise 517 species representing 75.8% of the total species number.

TABLE 1. The 26 most species-rich families (>1% relative richness) in Socotra Archipelago arranged by number of species.

Rank	Family	Spp. no.	%	Rank	Family	Spp. no.	%
1	Labridae	65	9.5	14	Carcharhinidae	13	1.9
2	Gobiidae	42	6.2	15	Pseudochromidae	13	1.9
3	Pomacentridae	41	6.0	16	Mullidae	12	1.8
4	Serranidae	37	5.4	17	Scorpaenidae	11	1.6
5	Chaetodontidae	29	4.3	18	Lethrinidae	11	1.6
6	Acanthuridae	29	4.3	19	Balistidae	11	1.6
7	Blenniidae	25	3.7	20	Mugilidae	10	1.5
8	Apogonidae	24	3.5	21	Tetraodontidae	10	1.5
9	Lutjanidae	23	3.4	22	Pomacanthidae	9	1.3
10	Carangidae	22	3.2	23	Scombridae	9	1.3
11	Muraenidae	18	2.6	24	Syngnathidae	7	1.0
12	Haemulidae	17	2.5	25	Caesionidae	7	1.0
13	Scaridae	15	2.2	26	Sparidae	7	1.0
Total 26 families						517	75.8%
Total remaining						165	24.2%

Labridae are the most dominant family in terms of species richness, representing 9.5% of all species, followed by Gobiidae (6.2%), Pomacentridae (6.0%), Serranidae (5.4%) and Chaetodontidae (4.3%). A total of 43 families are represented by only one species each and 38 families by two to six species only. Frequency distributions of the family species richness according to decimal and logarithmic richness categories are shown in Fig. 3.

If the ODUs of the Working List (Annex 2) are considered, the relative richness dominance of the Labridae (+ 13 species) and Pomacentridae (+ 5 species) is even more pronounced.

Comparisons of species richness. When compared to the species richness recorded in adjacent presumed Arabian marine ecoregions (Table 2), the species diversity of the Acanthuridae (29 species versus 14 species in the two next highest species-rich Arabian ecoregions; being only matched by 28 species of the neighbouring Somali Current Coast), Chaetodontidae (29 species vs. 22 and 17 species), Labridae (65 species + 13 species on the Working List vs. 55 and 54 species; being only matched by 68 species of the neighbouring Somali Current Coast), and Pomacentridae (41 species + 5 species on the Working List vs. 35 and 34 species) stand out as particularly high. Also Pseudochromidae (13 species vs. 13 species at the Omani Arabian Sea Coast, and 10 species as next highest richness) appear to be especially diverse around Socotra Archipelago (compare Annex 1–2, and see also Fig. 10).

Species richness of several ecologically and biogeographically important families were found to be higher than in the entire Red Sea (Golani & Bogorodsky 2010; Golani & Fricke 2018; Bogorodsky *et al.* in press), including: Acanthuridae (29 species vs. 12 species; 2.42 times), Chaetodontidae (29 species vs. 17 species; 1.71 times), Haemulidae (17 species vs. 12 species; 1.42 times), Pomacanthidae (9 species vs. 7 species; 1.29 times), and

Pomacentridae (41 species vs. 34 species; 1.21 times). The species richness of several families is about as high as in the Red Sea, for example of the Labridae (65 species vs. 65 species) and Pseudochromidae (13 species vs. 12 species). Conversely, the yet known species richness of several other key coastal families is substantially lower than in the Red Sea, including: Callionymidae (3 species vs. 13 species), Gobiidae (42 species vs. 136 species), Tripterygiidae (5 species vs. 12 species), Apogonidae (25 species vs. 59 species), Muraenidae (18 species vs. 38 species), Carangidae (22 species vs. 39 species), and Blenniidae (25 species vs. 40 species). Possible explanations for these species richness values are discussed.

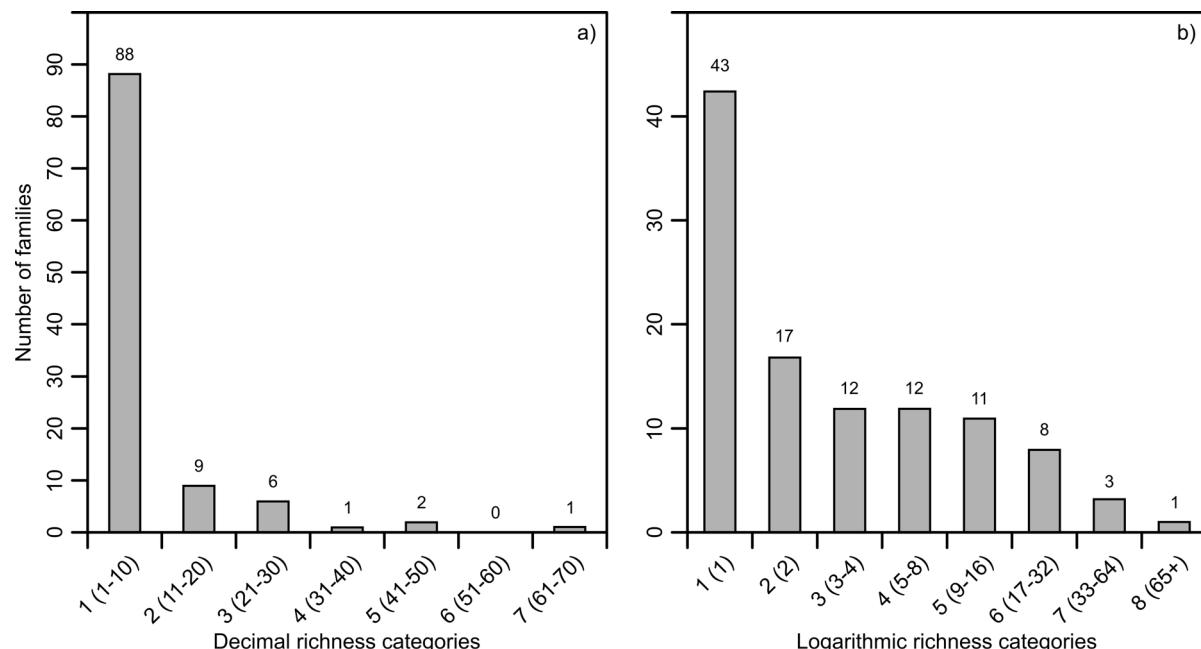


FIGURE 3. Frequency distribution of species richness of fish families in Socotra Archipelago according to (a) decimal richness categories, and (b) logarithmic richness categories.

TABLE 2. Species numbers of five fish families which are especially species-rich in Socotra Archipelago compared to species numbers in these families in eight presumed Arabian ecoregions *.

Ecoregion Family	Soc	GoAq	n+c RS	s RS	s GoA (Djib)	n GoA	Oman (AS)	GoO	AG
Acanthuridae	29	8	12	11	9	14	14	6	4
Chaetodontidae	29	13	13	14	17	22	17	8	4
Labridae	65	50	55	46	32	46	54	23	16
Pomacentridae	41	31	34	35	29	27	31	18	14
Pseudochromidae	13	10	10	10	5	8	13	7	8
Total	177	112	124	116	92	117	129	62	46

(*Abbreviations: Socotra Archipelago (Soc), Gulf of Aqaba (GoAq), northern and central Red Sea (n+c RS), southern Red Sea (s RS), southern Gulf of Aden - Djibouti (s GoA (Djib)), northern Gulf of Aden (n GoA), Oman—Arabian Sea coast (Oman (AS)), Gulf of Oman (GoO), Persian/Arabian Gulf (AG).)

Significance of ‘island group’ and ‘exposure’ designations. The statistical validity of the three ‘island group’ designations and two ‘exposure’ designations based on Hellinger Distance values of 68 FIS were tested. The ‘island group’ designations *per se* are not statistically significant (Global R: -0.138, $p = 0.938$). The ‘exposure’ designation is statistically significant at archipelagic scale (Global R: 0.265, $p = 0.004$) and even more so at the scale of Socotra Island (based on 50 FIS and 436 species; Global R: 0.651, $p = 0.0001$). A third explorative *a priori* designation combined ‘island group’ and a variation of ‘exposure’ and was statistically significant (Global R: 0.239, $p = 0.0003$). Similar results were obtained when the ANOSIMs were computed with resemblance matrices based on Bray-Curtis and Jaccard similarity indices.

Similar results (factor ‘island group’ globally insignificant, factor ‘exposure’ globally significant) were also obtained from ANOSIM tests computed with a Bray-Curtis resemblance matrix based on square root transformed abundance samples at 34 fish transect sites (342 species, Fig. 4). If, however, seven south coast sites are removed from the input data (27 samples, 313 species) the resulting ANOSIM produces a significant global test for the factor ‘island group’ (Global R: 0.247, $p = 0.002$), with the following pairwise test results: Socotra vs. Abd al-Kuri & Kal Farun (R: 0.406, $p = 0.0002$), Socotra vs. Darsa & Samha (R: 0.261, $p = 0.013$), and Darsa & Samha vs. Abd al-Kuri & Kal Farun (R: 0.194, $p = 0.034$). If the same input data set is further transformed to incidence-based data (presence-absence) and analysed using a resemblance matrix based on Jaccard’s similarity (Fig. 4), the significance of the resulting ANOSIM global test for the factor ‘island group’ rises further (Global R: 0.304, $p = 0.0005$), with the following pairwise test results: Socotra vs. Abd al-Kuri & Kal Farun (R: 0.442, $p = 0.00002$), Socotra vs. Darsa & Samha (R: 0.321, $p = 0.002$), and Darsa & Samha vs. Abd al-Kuri & Kal Farun (R: 0.196, $p = 0.025$). Similar results were obtained at slightly lower significance levels by an ANOSIM for this data set computed with a resemblance matrix based on the Hellinger Distance index. The grouping Socotra & Sabuniya couldn’t be confirmed statistically because no transect was located on Sabuniya.

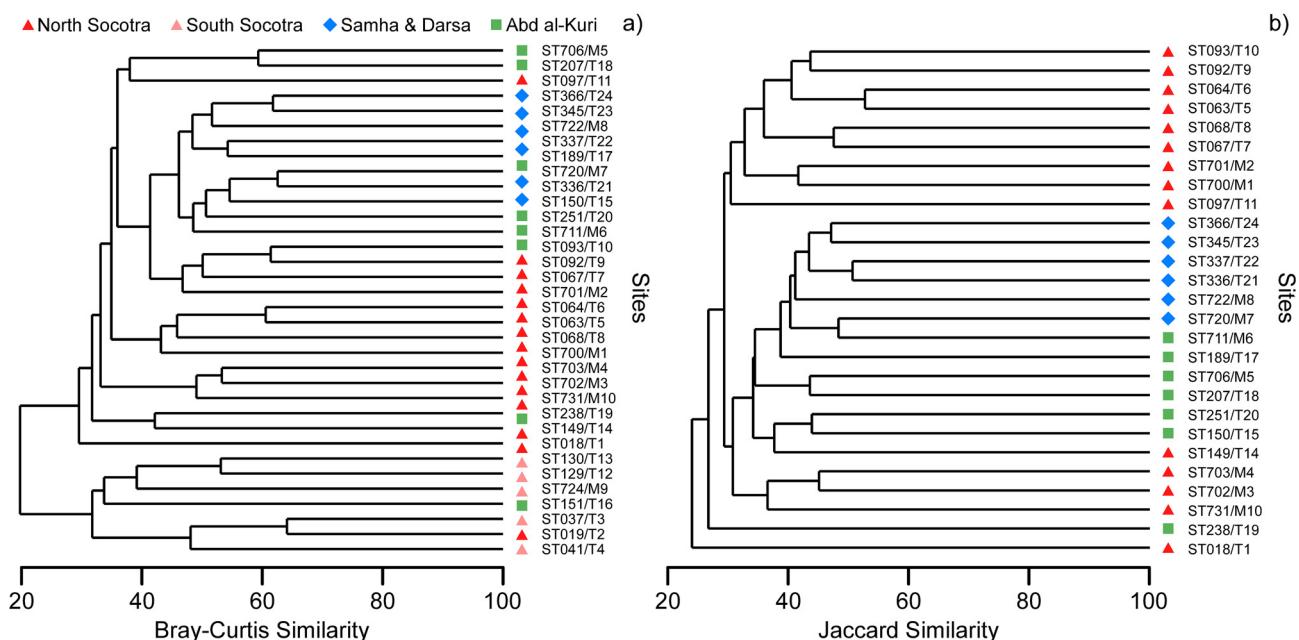


FIGURE 4. Dendrogram plots of hierarchical agglomerative cluster analyses comparing (a) abundance-based resemblance pattern of 34 fish transect sites (square root transformed, Bray-Curtis similarity), and (b) incidence-based resemblance pattern of 27 fish transect sites (presence-absence transformed, seven south coast sites removed, Jaccard similarity). See Fig. 1 for locations.

The aggregation of data into designated island groups follows an intuitive hypothetical choice based on geographical proximity, which grossly is statistically supported by evidence for a “biogeographical signal” if the strengths of confounding “ecological signals” is reduced (see Discussion).

Estimation of species richness

Between 830 and 890 species of fish are predicted to occur in the coastal waters of the Socotra Archipelago (Fig. 5) by incidence-based richness models (Chao 2 median 828 species, ICE 850 species, Jackknife 2 887 spp.).

The archipelagic Chao 2 estimate of 828 species represents a potentially undetected richness of 341 species compared to the data input (S_{obs}) of 487 species, equivalent to 41% of unrecorded species (Table 3), based on the data after the first main survey period of 1999-2000. The present FL 2017 comprises a total of 733 faunal records. The species number actually detected by 2017 therefore appears to gradually approximate the one predicted by the model based on 1999-2000 data input. The FL 2017 has crossed the lower CI bound already (730 species), with some 95 undetected species (11%) left to reach the Chao 2 value.

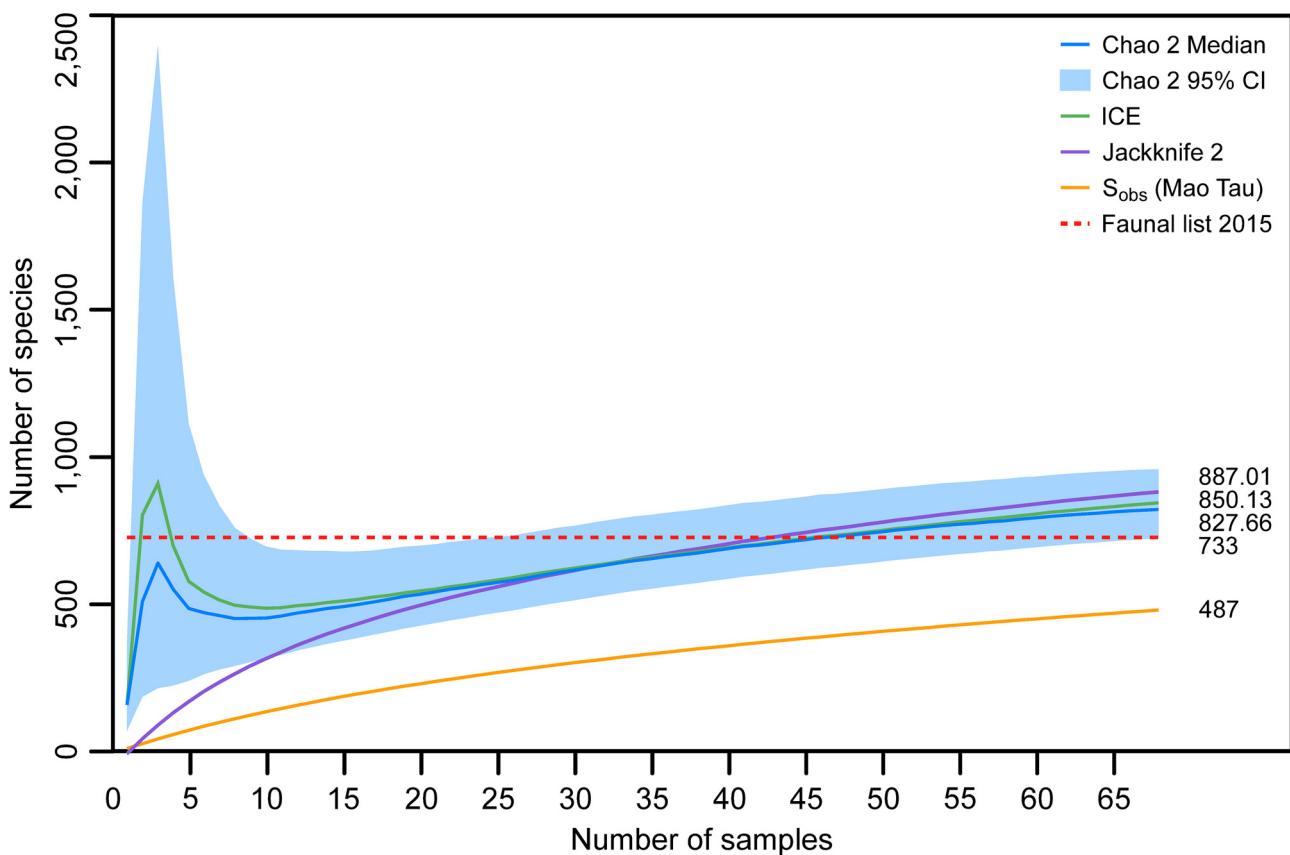


FIGURE 5. Fish species-richness modelling for Socotra Archipelago using incidence-based richness estimators (Chao 2, ICE, Jackknife 2), based on 68 fish inventory sites and 487 species; six of 74 FIS were excluded from the richness modelling in order to avoid spatial bias.

All four species accumulation curves (Fig. 5) were non-asymptotic, indicating that estimates are conservative. The higher values of the alternative estimators ICE and Jackknife 2 compared to Chao 2 suggest that the total richness might be higher, and that therefore the number of potentially undetected species would actually be higher as well (see below).

In addition to the total richness estimations explorative richness estimates were computed for critical diversity constituents at spatial, ecological, and taxonomic scale, as follows.

Island group specific richness estimates. The estimate for Socotra Island & Sabuniya represents a potentially undetected richness of 223 species compared to S_{obs} equivalent to 34%. According to the FL 2017 this has substantially decreased to 17%. The undetected richness at the other two island groups was 41% compared to S_{obs} and has been only moderately reduced to 33% (Darsa & Samha) and 28% (Abd al-Kuri & Kal Farun), respectively. This corresponds to the lower overall survey effort at the outer islands. The number of potentially undetected species at each individual island group is presently still higher than the total undetected archipelagic richness (Table 3).

Habitat group specific richness estimates. The estimate for the habitat group S6 “coral” (according to Klaus & Turner 2004) represents a potentially undetected richness of 229 species compared to S_{obs} equivalent to 35%, which appears high considering that this habitat group enjoyed more than half of the total survey effort referring to S_{obs} . The undetected richness for S5 “bedrock” was 34% compared to S_{obs} , thus also relatively high. The habitat groups S1, S4, and S7 were only covered by four FIS altogether and a joint estimate suggests an undetected richness of 84% owed to a very high estimated total richness at these habitats of 768 species, which is probably an artefact as will be discussed below. It was not possible to relate all faunal records of the FL 2017 to the habitat groups with sufficient and consistent accuracy; thence no comparison is provided (Table 3).

Family specific richness estimates. The estimate for the 15 key families represents a potentially undetected richness of 115 species compared to S_{obs} equivalent to 25%. According to the FL 2017 this has substantially

TABLE 3. Explorative comparison of fish richness values according to actual records (FL 2017), rarefied observed values (S_{obs}), and modelled richness (Chao 2).

	Faunal List (FL) 2017	S_{obs} (input)	Chao 2 median	Chao 2 CI low	Chao 2 CI high	S'obs (S)	Delta $S'_{obs} (\%)$	Delta FL (S)	Delta FL (%)
All sites (68 FIS)	733**	487	828	730	964	-341	-41%	-95	-11%
Island Groups									
Socotra Island & Sabunuya (50 FIS)	549	436	659	586	765	-223	-34%	-110	-17%
Darsa & Samha Islands (8 FIS)	273	239	408	348	501	-169	-41%	-135	-33%
Abd al-Kuri & Kal Farun Islands (10 FIS)	348	287	484	415	590	-197	-41%	-136	-28%
Habitat Groups (Klaus & Turner 2004)									
S6 “coral” (41 FIS)	433	662	586	773	-229	-35%			
S5 “bedrock” (23 FIS)	305	460	406	543	-155	-34%			
S1,4,7 “other” (4 FIS)	120	768	432	1,467	-648	-84%			
Selected Key Families									
Serranidae [classic *]	37	26	103	53	247	-77	-75%	-66	-64%
Serranidae [bias corrected *]	37	26	42	30	89	-16	-38%	-5	-12%
Pseudochromidae	13	11	14	11	36	-3	-21%	-1	-7%
Apogonidae *	27	20	48	27	124	-28	-58%	-21	-43%
Lutjanidae & Lethrinidae	37	29	36	31	61	-7	-20%	1	3%
Haemulidae	17	13	16	14	35	-3	-20%	1	4%
Mullidae	12	11	11	11	11	0	0%	1	9%
Carangidae	22	13	17	14	35	-4	-22%	5	32%
Pomacanthidae	9	6	6	6	6	0	0%	3	50%
Chaetodontidae	29	23	40	27	98	-17	-42%	-11	-27%
Pomacentridae	46	40	49	42	74	-9	-18%	-3	-6%
Labridae	78	70	80	73	103	-10	-13%	-2	-3%
Blenniidae *	30	17	24	18	53	-7	-29%	6	26%
Gobiidae	44	26	37	29	67	-11	-29%	7	19%
Acanthuridae	29	28	28	28	34	0	-2%	1	2%
Balistidae	11	8	8	8	8	0	0%	3	38%
Subtotals	441	341	456	369	833	-115	-25%	-15	-3%

* Categories with incidence-based CV values > 0.5 , for which the higher value among the classic and the bias-corrected model was to be selected, as recommended by Chao (1987). ** Refers to all records (not 68 FIS only)

decreased to 3%, equivalent to 15 potentially undetected species only within these important and often species-rich families. For a few families, such as Apogonidae and Chaetodontidae the richness models suggest numerous additional species to be recorded compared to S_{obs} and the FL 2017 both. In several families the species number recorded according to the FL 2017 is actually slightly or moderately higher than the estimated richness (Table 3). For Blenniidae and Gobiidae, however, the estimated richness of 17 and 26 species, respectively, appear implausibly low. Conversely, for the Serranidae the higher (classic) value was 103 species, compared to 42 species of the bias-corrected estimate. Both values are shown in Table 3 but the higher estimate of 103 species doesn't seem quite plausible as will be discussed.

Archipelagic richness extrapolation. Overall, the species recording trends appear to confirm the estimated richness. Starting from abundance-based records of 343 species and incidence-based records (S_{obs}) of 487 species obtained during semi-standardised surveys in 1999–2000 the faunal list had reached approximately 620 species in 104 families (including 602 own species observations) by 2000 (Zajonz *et al.* 2000), ~730 species by 2002 (Zajonz & Khalaf 2002), ~750 species by 2012 (Zajonz *et al.* unpubl.), and a more conservative number of 733 species in 108 families in the present faunal lists by 2017 (after some taxonomic corrections and removal of questionable ODUs from the lists), including records obtained from a variety of different sources. This appears to justify confidence in the incidence-based richness models as a basis for extrapolating a probable total number of coastal fish species of Socotra Archipelago. Based on the Chao 2 estimate of 828 species the following expert considerations are made: (a) all species accumulation curves were non-asymptotic and the alternative estimators ICE and Jackknife 2 produced higher expected richness values than Chao 2; (b) the upper confidence limit of Chao 2 is 934 species; (c) the estimators computationally produce conservative results at the lower bound of the probable true richness (Colwell 2013 web resource); (d) the S_{obs} input to the models is based on species from 66 families, thus species detection patterns from 54 additional families that are known to occur did not contribute to the total richness estimates; (e) certain habitat types (S1,2,3,4,7), all outer islands, and a variety of fish families are still clearly under-researched and faunistically under-sampled.

The number of 95 species estimated by Chao 2 as yet potentially undetected richness is therefore considered too low. In bringing to bear also extensive expert experience the total archipelagic richness is extrapolated at up to **875 species** of coastal fishes.

Distribution of diversity

Alpha (α) diversity is investigated primarily with regard to the 74 FIS. Gamma (γ) diversity in the present case comprises the entire Socotra Archipelago or island groups thereof, respectively. Beta (β) diversity was investigated in relation to the pooled species richness of the three pre-defined island groups constituting the archipelago.

Site (alpha) diversity. Detailed inshore fish inventories conducted between 1999 and 2000 at 74 FIS found between 14 and 132 species per site with an average of 66 species per site. Site diversity decreased across the archipelago from west to east and from north to south (Fig. 6, (see also Zajonz & Khalaf 2002). South coast values are positively biased due to the selection of survey sites. Total fish diversity was highest around Socotra Island, followed by Abd al-Kuri & Kal Farun and Darsa & Samha (see also further below).

The frequency distribution of the 10 established relative species richness categories among 74 FIS (Table 4) indicates a normal (unimodal) distribution of site diversity across the samples. Compared to the maximum richness of 132 species, the relative richness was higher than 50% at 35 FIS and lower than 50% at 39 FIS.

TABLE 4. Frequency distribution of richness categories relative to the richest site (132 species).

Class	1	2	3	4	5	6	7	8	9	10
% of max.	91–100	81–90	71–80	61–70	51–60	41–50	31–40	21–30	11–20	1–10
No. of sites	3	4	7	9	12	14	11	7	7	0

The mean species richness at 34 visual fish transect sites was 71, ranging between 117 and 33 species (south Socotra Island). Looking at Socotra Island only, a mean S' value of 65 (55–80) was recorded along the north coast and a mean of 54 (33–73) along the south coast (biased).

Diversity was also explored by ‘area’. North coast areas of Socotra, Darsa and Samha are generally more diverse in terms of species richness than those at south coasts. The richness of only a single southern area, Qatana

Bay (Socotra Island), matches the average richness of north coast areas with 136 species recorded in total and 60–73 species recorded in transect censuses. The richest areas of Abd al-Kuri are found in the easternmost (with 172 species recorded from a small reef patch in Anjara Bay) and in the western (with 223 species recorded from several biologically heterogeneous sites within the Khaysat an-Naum area) parts of the island. In close proximity to Abd al-Kuri, a small coral patch at the south side of Kal Farun is very rich in reef-associated and inshore epipelagic species. With 156 species recorded, it ranks among the richest areas of the archipelago, which besides the aforementioned three also include Samha east (157 species), two areas at the north coast of Socotra Island, the wider Roosh area (196 species) and Qadamha-Medina (134 species), and Ras Qatanin (136 species) in the south of Socotra Island.

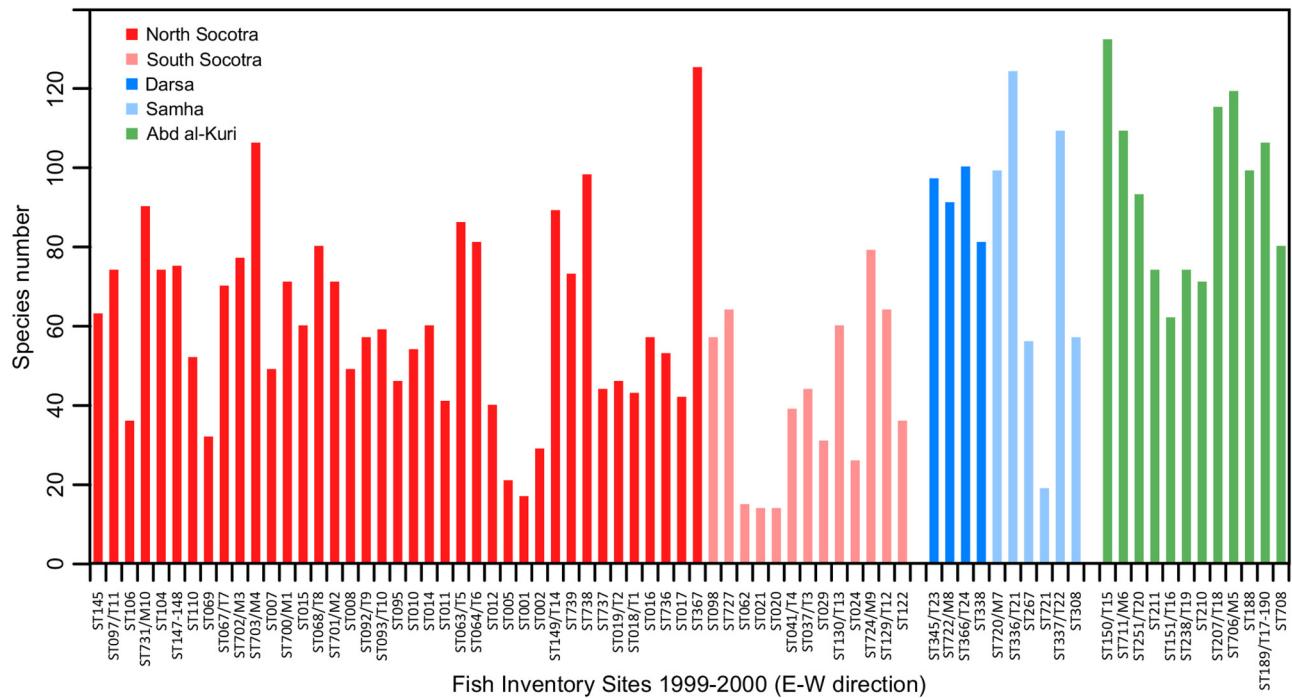


FIGURE 6. Fish species richness distribution (S) in Socotra Archipelago at 74 FIS (497 species) in 1999-2000, arranged by island group and in east-west order, with Socotra Island sites pre-ordered in north-south direction. See Fig. 1 for locations.

‘Occurrences’ at the 74 FIS comprise 4,900 record events per species and site. The total number of occurrences at the 74 FIS ranged from 1 to 64 per species with a mean of about 10 (9.86).

‘Occurrence-frequency-distributions’ (OFD) revealed that occurrences are very unevenly distributed, showing a heavily left-skewed unimodal curve (Fig. 7). The least frequent occurrence category was the highest (Category 8, species occurring at more than 61 sites), which comprised only two dominant species: the most frequently encountered fish was *Pomacentrus caeruleus* (at 64 FIS), and the second-most frequent one *Thalassoma lunare* (at 62 FIS). No species was present at all FIS. The most frequent Category 2 (species occurring at 2–11 sites) comprised 248 species, including 62 species representing ‘duplicates’ (species encountered at two sites only; 12.5% of all species). The second-most frequent Category 1 comprises 118 species representing ‘uniques’ (species encountered at a single site; 23.7% of all species).

Thus, a total of 180 species occurred only once or twice (36.2% of all 497 species encountered at 74 FIS) and are considered rare, having a very scattered archipelagic distribution and limited occupancy. In fact, 261 species of the present FL 2017 were only recorded once or twice if all available record events - including records from non-standardised samples—are counted (see Annexes 1–2).

Archipelagic (*gamma*) diversity. The distributions of (a) records at 74 FIS, and of (b) all available site records (of FL 2017) were investigated according to the island groups. While Socotra Island has the largest total number of species recorded, which corresponds to its size and coastal length the maximum, minimum and mean counts are much higher at the FIS which are located on the outer islands (Table 5).

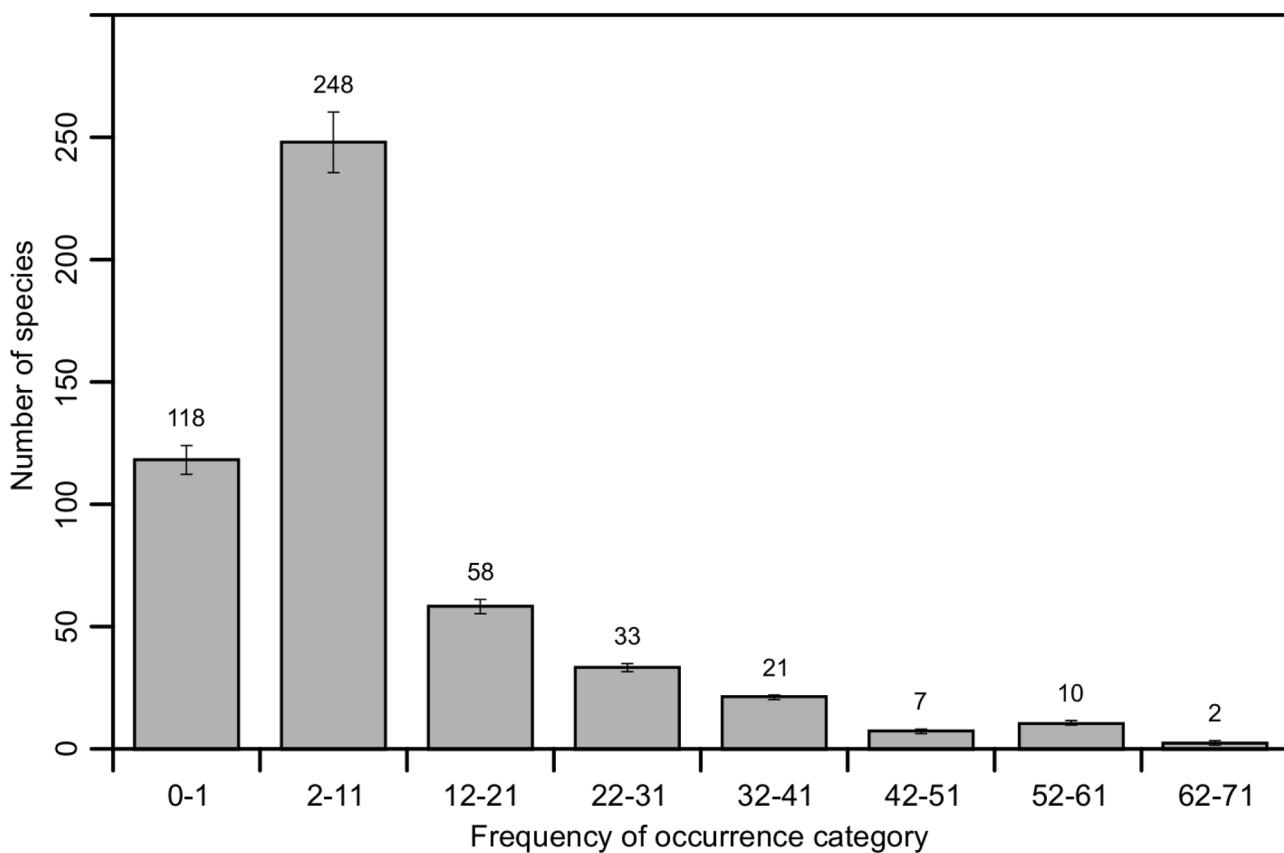


FIGURE 7. Occurrence-Frequency Distribution (OFD) of 497 fish species in Socotra Archipelago, based on 74 FIS (see Figs. 1, 6), and 4,900 occurrences (see also Zajonz & Khalaf 2002; error bars $\pm 1\text{SD}$).

TABLE 5. Species richness recorded per island group as assessed at 74 FIS during the surveys of 1999–2000.

	Entire archipelago	Socotra **	Darsa & Samha	Abd al-Kuri & Kal Farun
Number of species per FL 2017 *	599 (+42)	549 (+33)	273 (+12)	348 (+19)
Number of FIS	74	51	10	12
Number of species at FIS	497	436	259	307
Mean number of species per FIS	66	55	83	95
Standard deviation	28.2	22.2	29.4	21.3
Maximum number of species at one FIS	132	106	124	132
Minimum number of species at one FIS	14	14	19	62

* According to FL 2017 with known archipelagic distribution, number of ODUs from Working List (Annex 2) in parentheses; ** value recorded from Sabuniya (ST-367; 125 species) included in total but not in the average values for Socotra Island, because it is considered to bias the average of species richness for Socotra Island.

‘Species occurrences at archipelagic scale’ were calculated by summing the absolute and relative occurrences at 74 FIS by island groups. Thirteen species were found to be dominant with a proportion of more than 1% (1.04–1.31%) of the total number of occurrences (Table 6). Nine are coral-associated fishes (marked here below with an asterisk *) and four are demersal fishes, which often occur at coral assemblages (**) (FishBase 2017 web resource), listed as follows in decreasing order of relative occurrence: *Pomacentrus caeruleus**, *Thalassoma lunare**, *Chaetodon pictus**, *Labroides dimidiatus**, *Pomacentrus leptus**, *Sufflamen fraenatum***, *Parupeneus macronemus***, *Chromis weberi**, *Zebrasoma xanthurum***, *Zanclus cornutus***, *Lutjanus bohar**, *Melichthys indicus**, and *Pomacanthus imperator**. Together they represent ~15.5% of all occurrences but make up only

~2.6% of all species. At Socotra Island & Sabuniya 15 species had a share of more than 1% (1.02–1.47%; led by *Thalassoma lunare*, *Pomacentrus caeruleus* and *Chaetodon pictus*) representing 18.9% of all occurrences and 3.4% of the species recorded at this island group. At Darsa & Samha eight species had a share of more than 1% (1.08–1.20; see Table 6) representing 8.9% of all occurrences and 3.1% of the species. At Abd al-Kuri & Kal Farun seven species had a share of more than 1% (all seven at 1.06%; see Table 6) representing 7.4% of all occurrences and 2.3% of the species recorded as this island group. The evenness of occurrence distribution appears to increase in east-west direction. The 30 most frequently recorded species at the archipelagic level comprise 29% of the total occurrences (Table 6). The 30 most frequently recorded species at Socotra Island & Sabuniya represent 31.1% of the total occurrences, 29.7% at Darsa & Samha, and 27.3% at Abd al-Kuri & Kal Farun. Also these values indicate that evenness of occurrences increases in east-west direction.

Of the total of 118 uniques and 62 duplicates, 80 uniques (67.8%) and 54 duplicates (representing 58.1% of 93 island group specific duplicate records) were recorded at Socotra Island & Sabuniya, 15 uniques (12.7%) and 14 duplicates (15.1%) were recorded at Darsa & Samha, and 23 uniques (19.5%) and 25 duplicates (26.9%) were recorded at Abd al-Kuri & Kal Farun. At archipelagic scale on the average 1.6 uniques were encountered per FIS, with averages of 1.5 at Socotra Island & Sabuniya, 1.5 at Darsa & Samha, and 1.9 at Abd al-Kuri & Kal Farun. The higher rate of uniques per study site suggests that the latter island group is inhabited by a higher number of species which are rare at archipelagic scale.

‘Resemblance’ of island groups according to aggregated relative occurrences based on Bray-Curtis similarity, represents a basic investigation of β diversity. Darsa & Samha and Abd al-Kuri & Kal Farun share the highest similarity (73.7%), followed by Socotra Island & Sabuniya and Abd al-Kuri & Kal Farun (69.8%), and Socotra Island & Sabuniya and Darsa & Samha (65.9%). Hierarchical agglomerative clustering combined Darsa & Samha and Abd al-Kuri & Kal Farun first at 73.7% similarity, and then the resulting group with Socotra Island & Sabuniya at 67.9% similarity. The order of these similarities was corroborated by analysing the same data set using Hellinger’s distance. ‘SIMPER analyses’ of the same data set are shown in Table 7.

The three species contributing the greatest share (cumulatively 4.07 %) to the dissimilarity percentages between Socotra Island & Sabuniya and Darsa & Samha are *Apolemichthys xanthotis* (1.10% dissimilarity; 0.99% vs. 0.24% relative occurrence), *Ecsenius nalolo* (1.03%; 0.14% vs. 0.84%), and *Stethojulis albovittata* (1.01%; 0.27% vs. 0.96%). The three species contributing the greatest share (cumulatively 3.20%) to the dissimilarity percentages between Socotra Island & Sabuniya and Abd al-Kuri & Kal Farun are *Larabicus quadrilineatus* (1.13%; 0.68% vs. 0.00%), *Zanclus cornutus* (1.09%; 1.36% vs. 0.71%), and *Lethrinus borbonicus* (0.98%; 0.20% vs. 0.79%). The three species contributing the greatest share (cumulatively 4.07%) to the dissimilarity percentages between Darsa & Samha and Abd al-Kuri & Kal Farun are *Pomacentrus trichrourus* (1.49%; 0.96% vs. 0.18%), *Acanthurus tennentii* (1.43%; 0.84% vs. 0.09%), and *Sargocentron diadema* (1.14%; 0.60% vs. 0.00%).

‘Shared species’ between island groups were investigated according to all species in the FL 2017 which have archipelagic distribution records. The number of species recorded at the different islands and island groups are shown in Fig. 8. Only 36.5% of the fish species have been recorded at all three island groups. Socotra Island & Sabuniya and Darsa & Samha share 41.0% of all species with known archipelagic distributions, Socotra Island & Sabuniya and Abd al-Kuri & Kal Farun share 50.6%, and Darsa & Samha and Abd al-Kuri & Kal Farun share 37.6%. A total of 19.5% of all species have been recorded from two island groups only. Of these, 23.2.8% (4.5% of the total) are shared between Socotra Island & Sabuniya and Darsa & Samha; 71.2% (13.9% of the total) are shared between Socotra Island & Sabuniya and Abd al-Kuri & Kal Farun; and the remaining 5.6% (1.1% of the total) are shared between Darsa & Samha and Abd al-Kuri & Kal Farun. Another 44.0% of all species have been recorded from a single island group only. Of these, 81.6% (35.9% of the total) are restricted to Socotra Island & Sabuniya, 5.3% (2.3% of the total) to Darsa & Samha and 13.1% (5.8% of the total) to Abd al-Kuri & Kal Farun.

Although separated by a greater distance from the main island, Abd al-Kuri & Kal Farun have a higher number of species in common with Socotra Island & Sabuniya than these have with Darsa & Samha. The lowest number of species shared between two island groups is the one that Abd al-Kuri & Kal Farun have in common with Darsa & Samha.

Global species distribution ranges. A basic classification of 658 species out of 682 species of the Preliminary Checklist is presented. The numeric frequencies of all designated distribution categories and subcategories are shown in Fig. 9. Almost half of the species have an Indo-West Pacific distribution (*IWP*, 49.2%), followed by species, which have a north-western Indian Ocean distribution pattern (*NWI_all*, 17.5%) that is further

differentiated below. Species showing a western Indian Ocean distribution pattern (*WI*, 10.3%) and a pan-Indian Ocean distribution pattern (*pI*, 7.9%) are relatively numerous as well. A distribution pattern which spans across the Indian Ocean but excludes its southern part (*NI-WP*, 3.5%) is fairly well represented. Species with a distribution range restricted to the northern Indian Ocean are uncommon (*NI*, 0.3%). Far-reaching and global distribution ranges are represented by 11.3% in total (*WW*, 2.7%; *CT*, 2.0%; *IP*, 6.2%; *AI-WP*, 0.2%; *NI-WP+EP*, 0.2%).

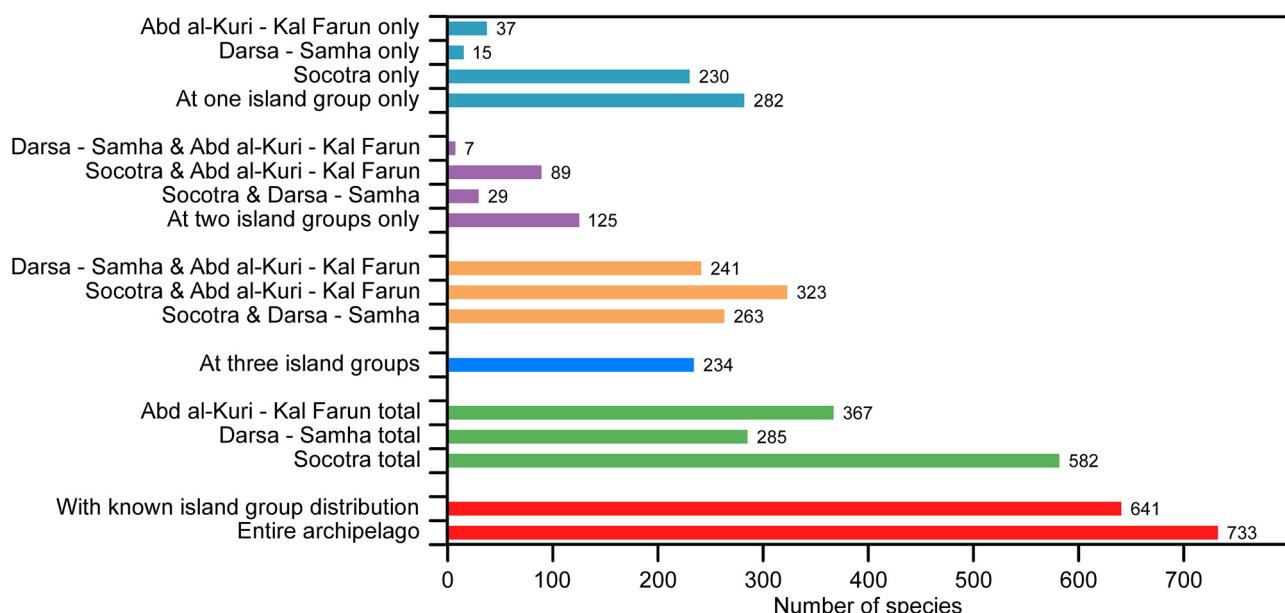


FIGURE 8. Number of fish species recorded at the islands and island groups and numbers of species shared among them (including confirmed species and ODUs). The bars are arranged in blocks as follows (from bottom to top): records from the entire archipelago and records from the entire archipelago with known island-group distribution, total number of species at each of the three island groups, species occurring at all three island groups, at two island groups combined (shared among them but not exclusively), at two combined island groups exclusively (shared only between them) and at one island group exclusively (species recorded only from a single island group) ('Socotra' stands for Socotra Island & Sabuniya).

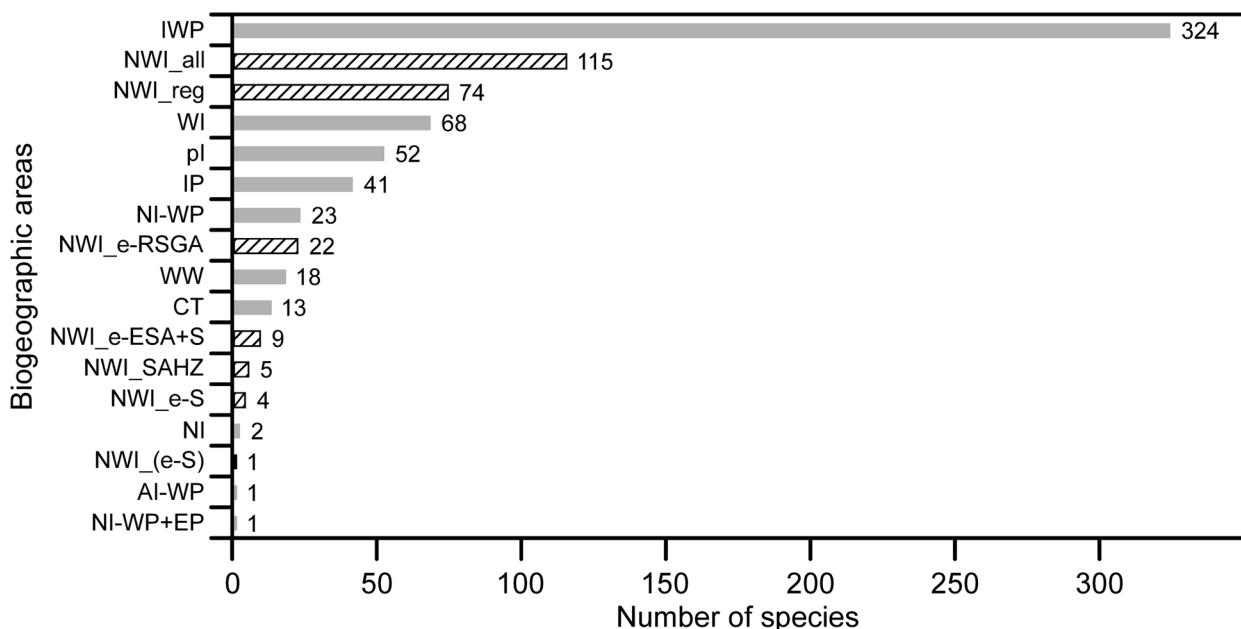


FIGURE 9. Frequencies of *a priori* defined global distribution ranges of 658 fish species from Socotra Archipelago with known ranges, showing frequencies of all distribution range categories and relative shares of the main range types (compare Materials and Methods for definitions and abbreviations of the biogeographical units, and Annex 1 for the biogeographical classification of individual species); with hatched bars indicating biogeographical categories contributing to the total given for the North-western Indian Ocean (NWI-all).

TABLE 6. List of the 30 most frequent species at 74 FIS, sorted by island group and ranked therein (R') by occurrence frequencies (O'), including relative frequencies (%).

Socotra Archipelago	Socotra Island & Sabuniya			Darsa & Samha			Abd al-Kuri & Kal Farun			
	R' Species	O'	%	R' Species	O'	%	R' Species	O'	%	
1 <i>Pomacentrus caeruleus</i>	64	1.31	1	<i>Thalassoma lunare</i>	43	1.47	1	<i>Pomacentrus caeruleus</i>	10	1.20
2 <i>Thalassoma lunare</i>	62	1.27	2	<i>Pomacentrus caeruleus</i>	42	1.43	2	<i>Pomacentrus lepus</i>	10	1.20
3 <i>Chaetodon pictus</i>	61	1.24	3	<i>Chaetodon pictus</i>	41	1.40	3	<i>Ctenochaetus striatus</i>	9	1.08
4 <i>Labroides dimidiatus</i>	59	1.20	4	<i>Labroides dimidiatus</i>	40	1.36	4	<i>Macropharyngodon bipartitus</i>	9	1.08
5 <i>Pomacentrus lepus</i>	59	1.20	5	<i>Parupeneus macronemus</i>	40	1.36	5	<i>Centropyge multisquamis</i>	9	1.08
6 <i>Sufflamen fraenatum</i>	58	1.18	6	<i>Zanclus cornutus</i>	40	1.36	6	<i>Halichoeres hortulanus</i>	9	1.08
7 <i>Parupeneus macronemus</i>	58	1.18	7	<i>Sufflamen fraenatum</i>	38	1.30	7	<i>Cephalopholis argus</i>	9	1.08
8 <i>Chromis weberi</i>	56	1.14	8	<i>Pomacentrus lepus</i>	37	1.26	8	<i>Psenicichromis secostraensis</i>	9	1.08
9 <i>Zebrasoma xanthurum</i>	55	1.12	9	<i>Chromis weberi</i>	36	1.23	9	<i>Thalassoma lunare</i>	8	0.96
10 <i>Zanclus cornutus</i>	54	1.10	10	<i>Zebrasoma xanthurum</i>	36	1.23	10	<i>Chaetodon pictus</i>	8	0.96
11 <i>Lutjanus bohar</i>	53	1.08	11	<i>Lutjanus bohar</i>	34	1.16	11	<i>Sufflamen fraenatum</i>	8	0.96
12 <i>Melichthys indicus</i>	52	1.06	12	<i>Melichthys indicus</i>	34	1.16	12	<i>Chromis weberi</i>	8	0.96
13 <i>Pomacanthus imperator</i>	51	1.04	13	<i>Pomacanthus imperator</i>	32	1.09	13	<i>Zebrasoma xanthurum</i>	8	0.96
14 <i>Chaetodon melapterus</i>	45	0.92	14	<i>Heniochus acuminatus</i>	31	1.06	14	<i>Lutjanus bohar</i>	8	0.96
15 <i>Heniochus acuminatus</i>	45	0.92	15	<i>Chaetodon melapterus</i>	30	1.02	15	<i>Pomacanthus imperator</i>	8	0.96
16 <i>Epinephelus fasciatus</i>	45	0.92	16	<i>Epinephelus fasciatus</i>	29	0.99	16	<i>Sufflamen chrysopterum</i>	8	0.96
17 <i>Sufflamen chrysopterum</i>	43	0.88	17	<i>Sufflamen chrysopterum</i>	29	0.99	17	<i>Halichoeres marginatus</i>	8	0.96
18 <i>Macropharyngodon bipartitus</i>	43	0.88	18	<i>Apolemichthys xanthotis</i>	29	0.99	18	<i>Plagiotremus rhinorhynchos</i>	8	0.96
19 <i>Halichoeres marginatus</i>	42	0.86	19	<i>Halichoeres marginatus</i>	26	0.89	19	<i>Chromis flavavilla</i>	8	0.96
20 <i>Ctenochaetus striatus</i>	40	0.82	20	<i>Ctenochaetus striatus</i>	24	0.82	20	<i>Odontos niger</i>	8	0.96
21 <i>Plagiotremus rhinorhynchos</i>	40	0.82	21	<i>Scarus ferrugineus</i>	24	0.82	21	<i>Thalassoma lutescens</i>	8	0.96
22 <i>Centropyge multisquamis</i>	40	0.82	22	<i>Ostorhinchus sp.</i>	23	0.78	22	<i>Dascyllus marginatus</i>	8	0.96
23 <i>Halichoeres hortulanus</i>	39	0.80	23	<i>Canthigaster solandri</i>	23	0.78	23	<i>Pseudochelium hexataenia</i>	8	0.96
24 <i>Scarus ferrugineus</i>	39	0.80	24	<i>Macropharyngodon bipartitus</i>	22	0.75	24	<i>Pomacentrus trichrourus</i>	8	0.96
25 <i>Ostorhinchus sp.</i>	38	0.78	25	<i>Centropyge multisquamis</i>	22	0.75	25	<i>Coris caudimacula</i>	8	0.96
26 <i>Pseudochelium hexataenia</i>	37	0.76	26	<i>Chaetodon trifascialis</i>	22	0.75	26	<i>Hologymnosus doliatus</i>	8	0.96
27 <i>Coris frerei</i>	36	0.73	27	<i>Abudefduf vaigiensis</i>	22	0.75	27	<i>Stethojulis albovittata</i>	8	0.96
28 <i>Apolemichthys xanthotis</i>	36	0.73	28	<i>Plagiotremus rhinorhynchos</i>	21	0.72	28	<i>Labroides dimidiatus</i>	7	0.84
29 <i>Chromis flavavilla</i>	36	0.73	29	<i>Halichoeres hortulanus</i>	21	0.72	29	<i>Parupeneus macronemus</i>	7	0.84
30 <i>Odontos niger</i>	35	0.71	30	<i>Chromis flavavilla</i>	30	0.71	30	<i>Melichthys indicus</i>	7	0.84
Totals of 30 dominant species	1421	29.0			912	31.1			247	29.7
Totals of remaining species	3479	71.0			2021	68.9			586	70.3
Totals of all species	4900	100.0			2933	100.0			833	100.0

TABLE 7. Results of the SIMPER analyses of relative occurrence frequencies, showing the 30 species contributing the greatest share to the average dissimilarities between island groups.

R ^a	Species	Socotra Isl. & Sabuniya versus Darsa & Samha			Socotra Isl. & Sabuniya versus Abd al-Kuri & Kal Farun			Darsa & Samha versus Abd al-Kuri & Kal Farun			
		Av. Dissim.	Contrib. %	Cum. %	Species	Av. Dissim.	Contrib. %	Cum. %	Species	Av. Dissim.	Contrib. %
1	<i>Apolemichthys xanthotis</i>	0.37	1.10	1.10	<i>Larabicus quadrilineatus</i>	0.34	1.13	1.13	<i>Pomacentrus trichrourus</i>	0.39	1.49
2	<i>Ecsenius natalo</i>	0.35	1.03	2.13	<i>Zanclus cornutus</i>	0.33	1.09	2.22	<i>Acanthurus tennentii</i>	0.38	1.43
3	<i>Sethojulis albovittata</i>	0.34	1.01	3.14	<i>Lethrinus borbonicus</i>	0.29	0.98	3.20	<i>Sargocentron diadema</i>	0.30	1.14
4	<i>Larabicus quadrilineatus</i>	0.34	1.00	4.14	<i>Naso unicornis</i>	0.28	0.93	4.12	<i>Abudefduf vaigiensis</i>	0.29	1.11
5	<i>Hologymnosus deliciatus</i>	0.33	0.96	5.09	<i>Apolemichthys xanthotis</i>	0.27	0.91	5.03	<i>Taeniamia fucata</i>	0.29	1.11
6	<i>Zanclus cornutus</i>	0.32	0.94	6.04	<i>Taeniamia fucata</i>	0.27	0.89	5.92	<i>Cephalopholis argus</i>	0.28	1.05
7	<i>Abudefduf vaigiensis</i>	0.32	0.92	6.96	<i>Sethojulis albovittata</i>	0.26	0.86	6.78	<i>Amblyeleotris wheeleri</i>	0.27	1.04
8	<i>Amblyeleotris wheeleri</i>	0.31	0.91	7.87	<i>Lethrinus mahsena</i>	0.25	0.83	7.61	<i>Thalassoma amblycephalum</i>	0.26	1.01
9	<i>Pseudochromis socotrensis</i>	0.30	0.88	8.75	<i>Thalassoma lunare</i>	0.25	0.82	8.43	<i>Caranx melampygus</i>	0.26	0.97
10	<i>Heniochus acuminatus</i>	0.29	0.85	9.59	<i>Acanthurus tennentii</i>	0.25	0.81	9.25	<i>Plectrohinchus gaterinus</i>	0.24	0.93
11	<i>Diodon holocanthus</i>	0.27	0.80	10.39	<i>Pseudochromis linda</i>	0.24	0.80	10.04	<i>Lethrinus mahsena</i>	0.23	0.89
12	<i>Chromis fieldi</i>	0.27	0.78	11.18	<i>Pseudochromis nigrovittatus</i>	0.24	0.78	10.82	<i>Ctenochaetus striatus</i>	0.23	0.88
13	<i>Pseudochromis nigrovittatus</i>	0.26	0.77	11.95	<i>Cirrhitichthys oxycephalus</i>	0.23	0.77	11.60	<i>Sufflamen chrysopterum</i>	0.22	0.82
14	<i>Labroides dimidiatus</i>	0.26	0.77	12.72	<i>Siganus argenteus</i>	0.23	0.76	12.36	<i>Dascyllus marginatus</i>	0.22	0.82
15	<i>Parupeneus macronemus</i>	0.26	0.77	13.48	<i>Acanthurus leucosternon</i>	0.23	0.76	13.12	<i>Coris caeruleus</i>	0.21	0.81
16	<i>Thalassoma lunare</i>	0.25	0.74	14.22	<i>Sufflamen chrysopterum</i>	0.23	0.76	13.88	<i>Cantherhines pardalis</i>	0.21	0.81
17	<i>Hologymnosus annulatus</i>	0.25	0.73	14.95	<i>Halichoeres iris</i>	0.22	0.74	14.62	<i>Hologymnosus annulatus</i>	0.21	0.81
18	<i>Coris caudimacula</i>	0.24	0.71	15.66	<i>Pomacentrus trichrourus</i>	0.22	0.72	15.35	<i>Sargocentron seychellense</i>	0.20	0.78
19	<i>Acanthurus ghahm</i>	0.24	0.70	16.36	<i>Parapeneus forsskali</i>	0.22	0.72	16.07	<i>Acanthurus leucosternon</i>	0.20	0.78
20	<i>Epinephelus flavofasciatus</i>	0.23	0.67	17.03	<i>Lethrinus microdon</i>	0.21	0.71	16.78	<i>Heniochus acuminatus</i>	0.20	0.76
21	<i>Variola louti</i>	0.22	0.66	17.69	<i>Bodianus axillaris</i>	0.21	0.68	17.46	<i>Gomphosus caeruleus</i>	0.20	0.76
22	<i>Acanthurus leucocheilus</i>	0.22	0.66	18.35	<i>Dermatolepis striolatus</i>	0.20	0.67	18.14	<i>Chlorururus strongylocephalus</i>	0.20	0.75
23	<i>Chlorururus strongylocephalus</i>	0.22	0.65	19.00	<i>Pseudochromis sotocraensis</i>	0.20	0.67	18.81	<i>Bodianus axillaris</i>	0.19	0.72
24	<i>Chaetodon pictus</i>	0.22	0.64	19.64	<i>Hologymnosus doliatus</i>	0.20	0.66	19.47	<i>Apogon aeneus</i>	0.18	0.70
25	<i>Anampses caeruleopunctatus</i>	0.21	0.63	20.27	<i>Chromis fieldi</i>	0.20	0.66	20.13	<i>Cheilodipterus macrodon</i>	0.18	0.70
26	<i>Hemigymnus fasciatus</i>	0.21	0.61	20.88	<i>Parapeneus macronemus</i>	0.20	0.65	20.78	<i>Hemigymnus fasciatus</i>	0.18	0.70
27	<i>Plectroglyphidodon johnstonianus</i>	0.21	0.60	21.48	<i>Ecsenius natalo</i>	0.20	0.65	21.43	<i>Parapercis punctulata</i>	0.18	0.69
28	<i>Naso unicornis</i>	0.20	0.60	22.08	<i>Acanthopagrus bifasciatus</i>	0.19	0.62	22.05	<i>Lutjanus ehrenbergii</i>	0.18	0.67
29	<i>Cephalopholis argus</i>	0.20	0.58	22.66	<i>Pomacanthus maculosus</i>	0.19	0.62	22.67	<i>Cephalopholis sonneratii</i>	0.18	0.67
30	<i>Cheilodipterus macrodon</i>	0.19	0.56	23.22	<i>Pomacentrus caeruleus</i>	0.19	0.62	23.29	<i>Cephalopholis hemistictos</i>	0.18	0.67
At 50% cut-off threshold (91 spp.)		0.35	50.20	At 50% cut-off threshold (87 spp.)		0.11	0.36	50.02	At 50% cut-off threshold (75 spp.)		0.12
All 471 contributing species		34.12	100.0	All 478 contributing species		30.18	100.0	All 353 contributing species		26.27	100.0

The subcategories constituting the category *NWI_all* have the following shares of all distribution frequencies (the first number in parentheses), and of distribution frequencies classified as *NWI_all* (second number in parentheses): North-western Indian Ocean regular (*NWI_reg*; 11.2%, 64.3%), Red Sea and Gulf of Aden endemics (*NWI_e-RSGA*; 3.3%, 19.1%), eastern and southern Arabia and Socotra endemics (*NWI_e-ESA+S*; 1.4%, 7.8%); Socotra Archipelago endemics, including putative endemics (*NWI_e-S+(e-S)*; 0.8%, 4.4%), and hybrids of the ‘Southern Arabian Hybrid Zone’ (*NWI_SAHZ*; 0.8%, 4.3%).

Discussion

The Socotra Archipelago in the eastern Gulf of Aden has a unique marine environment which combines tropical and ‘pseudo-temperate’ characters (Klaus & Turner 2004). Little has been published yet about its coastal fish assemblages. The existing knowledge is largely documented in the grey literature and existing published information does not reflect the current state of knowledge.

Descriptions of species richness, occurrences and abundances, and of species distribution patterns on local and regional scales are all basic ecological measures, yet this information is still lacking for the coastal fish assemblages of the Socotra Archipelago. Somewhat surprisingly, studies on the fish biogeography of the areas surrounding the archipelago, e.g. DiBattista *et al.* (2015a, 2015b), Saenz-Agudelo *et al.* (2015), DiBattista *et al.* (2016a, 2016b), Di Battista *et al.* (2017), partially framed in regional or global megastudies, e.g. Spalding *et al.* (2007), Briggs & Bowen (2012, 2013), Kulbicki *et al.* (2013), Mouillot *et al.* (2013), Parravicini *et al.* (2013), Bender *et al.* (2017), Cowman *et al.* (2017), or Gaboriau *et al.* (2017), have substantially outpaced critical baseline research on the archipelago’s fish diversity, community ecology and taxon-specific phylogenetics. Without an appreciation of the basic ecology and diversity measures the basis is lacking to understand the evolutionary and ecological patterns and processes that underlie biogeographic and biodiversity patterns on larger scales.

To begin to address these issues, this paper presents a preliminary species inventory of the coastal fishes of Socotra Archipelago and a basic investigation of its taxonomic composition, an extrapolation of the archipelago’s total species richness, and basic investigations of patterns of site richness, archipelagic distribution and global distribution ranges.

Given the repeated impediments to travel and field work posed by the political and security situation in the country, it has not been possible to accomplish an exhaustive checklist as yet. With current work in progress, the authors will update the faunal list in the future. Detailed analyses of diversity patterns (i.e. taxonomic, trophic and functional assemblage compositions), community ecology (i.e. relationships between environmental parameters and assemblage structures) and biogeography (i.e. in distributional and ecological terms) will be provided by the first author and several of the present co-authors in forthcoming publications. The present account provides the basis for future studies and documents the status of the coastal fish diversity of the Socotra Archipelago at a time when the coastal and marine habitats of the island group are still in near-pristine conditions. The impacts of coastal development and pollution of local land-based sources (i.e. sewage) are currently largely limited to two coastal urban areas, few larger villages and a harbour. Conceivably, the effects of climate change are yet to unfold their full strength (Van Damme & Banfield 2011; Zajonz *et al.* unpubl.). The main contemporary impact on fish diversity and assemblage structures at archipelagic scale is exerted by the artisanal fisheries (Zajonz *et al.* 2016; Zajonz *et al.* in prep.), as discussed further below.

Species inventory. The species included in the Preliminary Checklist increase the archipelagic richness by 467 species (3.2 times) compared to Kemp (1998). This substantial increase is explained by the great difference in cumulative survey effort between both studies. Kemp’s initial surveys were conducted by a single surveyor as part of a rapid assessment study and with limited logistic support. Kemp was able to demonstrate the particular position of the archipelago at zoogeographic crossroads of major adjoining biogeographic regions and to thus advance the knowledge of the marine biogeography of the Indian Ocean substantially. Based on his limited data he inevitably failed to recognize the archipelago as a diversity hotspot for fishes. This study recognizes the Socotra Archipelago as such a major hotspot of coastal fish diversity in the wider Arabian region and the Indian Ocean as a whole.

In terms of combined generic and species richness, the Labridae stand out as being especially diverse in Socotra Archipelago, followed by Gobiidae, Blenniidae, Pomacentridae and Apogonidae. In terms of species richness alone again Labridae appear as especially diverse, followed by Pomacentridae, Serranidae,

Chaetodontidae and Acanthuridae. Certain small, cryptic, and nocturnal groups are still under-researched both in terms of survey effort and taxonomic work in the laboratory. More thorough studies by specialists are therefore expected to reveal the presence of additional species, particularly within the Blenniidae, Gobiidae, Tripterygiidae, Platyccephalidae, Mugilidae, Ophichthidae, Scorpaenidae, Syngnathidae and various families within the Pleuronectiformes. Numerous additional species records, including species new to science, are expected to be recognized in the future especially in the families Blenniidae, Gobiidae and Tripterygiidae. In both the Labridae and Pomacentridae numerous ODUs included in the Working List and additional observations (Zajonz pers. obs.) not reported herein suggest that their total species richness is ultimately higher than reported in the Preliminary Checklist. A substantial number of preliminary observations of fishes in both families could not be related to valid species despite substantial efforts to do so. These field observations likely relate to either undescribed species or yet unrecognized hybrids requiring additional dedicated sampling and taxonomic effort, including molecular genetics.

Hybrids represent a characteristic element of the fish fauna of the Socotra Archipelago and are therefore included in the species inventory. Kemp (2000b) was the first to recognize the eastern Gulf of Aden as an important region for the hybridization of reef fishes based on the occurrence of *Pomacanthus semicirculatus* x *P. maculosus* at the Hadhramout and Shabwa coast in the eastern Gulf of Aden. The occurrence of *P. semicirculatus* x *P. maculosus* in Socotra Archipelago was first reported by Zajonz & Khalaf (2002) followed by additional yet unpublished observations, which suggest that Kemp's proposed eastern Arabian hybrid zone actually encompasses the eastern Arabian mainland coast and the Socotra Archipelago combined (Zajonz *et al.* in prep.). Those observations included putative hybrids in the genera *Chaetodon* (*C. collare* x *C. lunulatus*), *Pomacanthus* (*P. maculosus* x *P. asfur*), *Amphiprion* (*A. bicinctus* x *Amphiprion* sp.) and *Dascyllus* (*D. carneus* x *D. marginatus*) during surveys in 2007, 2009 and 2013. The hybrids included in the present Faunal List 2017 refer to observations by the present authors. Before, Kemp (1998) had already noted a high frequency of sympatric co-occurrences of "Indian Ocean and Arabian sister species" on Socotra but obviously had too little survey time available to also record the respective hybrid specimens, e.g. of *Dascyllus carneus* and *D. marginatus*, and of *Acanthurus sohal* and *A. lineatus*. In a recent study DiBattista *et al.* (2015a) identified seven fish hybrids from Socotra Island during a survey in 2013 involving combinations of 14 species, including *Acanthurus sohal* x *A. lineatus*. These authors recognized the archipelago as a main hotspot for fish hybridization globally and provided genetic support for the observed hybrids, including evidence that some of them were reproductively fertile. Four of their hybrid records were not included in the FL 2017 because the paper appeared after the work on the present species inventory was concluded. They have been added as footnotes to Annex 1. The ODU *Amphiprion* sp. of the Working List is probably identical with the *A. bicinctus* x *A. omanensis* reported by DiBattista *et al.* (2015a; but note the complex genetic pattern reported for this putative hybrid). The inclusion of hybrids in the species inventory is supported by the following facts: (a) certain hybridizations appear to occur frequently, e.g. *Chaetodon collare* x *C. lunula*, *Pomacanthus maculosus* x *P. semicirculatus*, *Dascyllus carneus* x *D. marginatus*, thus establishing "stable" diversity components; (b) some hybrids are evidently fertile (DiBattista *et al.* 2015a); and (c) several hybrids appear to be more frequent than "regular" species, given the high number of uniques and duplicates among the FIS-based OFD data. In a forthcoming paper Zajonz *et al.* (in prep.) report additional putative hybrids from the eastern Gulf of Aden mainland coast and Socotra Archipelago, summarize the current state of knowledge, and propose to recognize a combined hybridization zone of global importance.

The intuitive aggregation of data into three designated 'island groups' (1) Socotra & Sabuniya, (2) Darsa & Samha, and (3) Abd al-Kuri & Kal Farun is grossly supported by statistic evidence for a "biogeographical signal" (i.e. 'distance') embedded in the occurrence data. The 'island group' designations *per se* were not statistically significant when using all FIS or all visual fish transects as input data for resemblance analyses. The biogeographical signal in the archipelagic fish distribution pattern becomes evident, if the strengths of confounding "ecological signals" are reduced. This includes i.e. removing south coast sites, where species assemblages are strongly determined by the influence of the summer monsoon and the cold upwelling; by emphasizing sites located in coral-dominated biotopes (thus further reducing ecological variability), and by using incidence-based data instead of abundance-based data. The level of statistical significance of the pairwise ANOSIM differences between the island groups seems to grossly correspond to the mean geographic distance between them (measured from the assumed mid point of each group). It is interesting to note though that the difference between Darsa & Samha vs. Abd al-Kuri & Kal Farun has the least statistical support, in spite of a deep water trench (e.g. Fischer *et al.* 1996;

Schott *et al.* 1997) and a temporarily strong current system (Zajonz pers. obs.) separating them. The assumption that south coast sites grossly differ in species composition from north coast sites across the archipelago was supported by statistical evidence, underpinning their strong ecological segregation.

Comparisons of similarity with neighbouring areas (i.e. mainland Yemen and Somalia) are still pending, but the low significance of the island group designations supports the assumption that the islands actually form a larger consistent ecological and biogeographic unit within the Indian Ocean.

More research is needed to investigate the roles of area size (total, habitat, and occupancy), geographic and ecological distance, and ecological filters, thus of site-based and seascape-based controls in shaping the fish assemblages at the individual islands, the island groups, and the archipelago as a whole. The interplay among diversity at the (α) alpha, (γ) gamma and (ε) epsilon level, patterns of (β) beta and (λ) delta diversity and processes of diversity partitioning and nestedness (Magurran 2004; Magurran *et al.* 2011; McGill 2011) require additional study in order to fully appreciate the particular diversity composition and assembly of the Socotra Archipelago's coastal fishes.

Estimates of species richness. Incidence-based and abundance-based richness estimators, e.g. Chao 1-2, ICE and ACE, Jackknife 1-2, Michaelis-Menten, Bootstrap or Cole (Colwell 2005, 2013 web resource; Magurran 2004; Gotelli & Colwell 2011) have seemingly enjoyed relatively limited use in freshwater and marine biology, compared to terrestrial studies. 'Species accumulation curves' (SAC) and 'rarefaction' algorhythms are apparently more commonly used, i.e. to test whether sampling effort effectiveness was adequate (e.g. Gandanho *et al.* 2003; Sánchez Márquez *et al.* 2008). A search in Google Scholar (web resource, sourced November 2015) revealed 6,369 papers citing the use of EstimateS with reference to Colwell (1997-2013 web resource). Of the first 1,000 documents listed by Google Scholar only 4.6% represented marine studies. The vast majority of the documents reported studies investigating terrestrial ecosystems and few dealt with freshwater or coastal zones.

Most of the marine studies investigated deep-sea diversity, microbial diversity (e.g. fungi, bacteria), or molecular diversity. Only 12 marine studies related to tropical inshore or reef diversity. Of the 46 marine studies 32 used rarefied (Colwell *et al.* 2004) or extrapolated species accumulation algorhythms (Colwell *et al.* 2012), similarity measures or other routines provided by EstimateS (Colwell 2013 web resource). Only 14 papers used incidence-based or abundance-based richness estimators. Examples include Ellingsen (2001) who investigated benthic soft sediment diversity of the Norwegian continental shelf, Alonso *et al.* (2007) who investigated flavobacteria in the North Sea revealing 50% undetected richness, Prieto-Davó *et al.* (2008) who studied actinomycete diversity in marine sediments, Sánchez Márquez *et al.* (2008) who assessed endophytic fungi on coastal grass, and Bodil *et al.* (2011) who investigated the diversity of arctic deep-sea benthos.

Of the studies related to tropical inshore or reef diversity a majority used SAC to determine sampling effort effectiveness (e.g. Zuschin & Graham 2003; Colton & Sweare 2010), including fish studies of temperate, rocky or deep reefs (Angel & Ojeda 2001; Gladstone 2007; Brokovich *et al.* 2008).

Six studies successfully used richness estimators to extrapolate total richness of selected taxa of tropical or sub-tropical reef ecosystems. These include studies of invertebrates by Bouchet *et al.* (2002), who assessed the diversity of reef-associated mollusc assemblages in New Caledonia; by Castro *et al.* (2005), who investigated coral communities on the Abrolhos Archipelago (Brazil); by Plaisance *et al.* (2009), who assessed crustacean crypto-diversity in central Pacific reefs; and by Bridge *et al.* (2012), who studied the diversity of mesophotic scleractinians and octocorals in the Great Barrier Reef (Australia).

Two studies only dealt with reef fishes. Cryptic reef fish diversity at the U.S. Virgin Islands, Caribbean, was investigated by Smith-Vaniz *et al.* (2006) using both SAC and incidence-based estimators for *inter alia* comparing the sampling effectiveness of visual recording and rotenone collecting. Total and habitat-specific fish diversity of the temperate-subtropical reefs of the Abrolhos Archipelago was extrapolated by Moura & Francini-Filho (2005) using the incidence-based coverage estimator ICE.

The results of the Google Scholar search were obviously not statistically representative. Alternative software packages offer similar routines and especially marine studies tend to resort to computing richness estimations with PRIMER (e.g. Obura 2012, investigating the diversity of Western Indian Ocean reef-building corals), or the *R* open source applications. Nonetheless, an appreciation of non-parametric richness estimator algorhythms in marine and especially reef studies, somewhat surprisingly, seems lagging substantially behind the appreciation granted to the application of these methods in terrestrial disciplines. Sufficient sampling coverage in marine diversity studies is often difficult to achieve because dense sampling grains and comprehensive biodiversity collections are costly.

Moreover, marine sampling aims cannot always be fully achieved as planned because of logistic, access or weather constraints. Despite such obstacles, non-parametric richness estimators *sensu* Chao (2005) and Colwell *et al.* (2012) appear especially suitable methods in tropical and reef studies with constrained sampling coverage. In the absence of complete taxonomic inventories non-parametric richness estimators can provide useful data for conservation management and follow-on study planning.

Richness estimators have thus far rarely - if at all - been used to extrapolate the total fish species richness for a marine region or island group in the tropical Indian Ocean. Not a single similar study from the Arabian region appears to have been carried out at any time. This paper therefore pioneers the use of these methods in investigating marine fish diversity of undersampled coastal areas of the Arabian region and the Indian Ocean.

Between 828 and 887 fish species are predicted to occur in the coastal waters of the Socotra Archipelago depending on the incidence-based richness models. The archipelagic Chao 2 estimate of 828 species represents a conservative value. The higher values of the alternative estimators ICE (850 species) and Jackknife 2 (887 species) suggest that the total richness may be higher. The inherent logic of non-parametric richness estimator algorhythms needs to be considered in interpreting these results. For example, Foggo *et al.* (2003) indicated that Chao 2 and ICE/ACE may overestimate species richness, while Ugland & Gray (2004), in reply, suggested that these algorhythms may actually tend to underestimate richness, not least in analysing marine datasets. The study by Melo (2004) highlighted that the performance of non-parametric estimators such as Jackknife 1-2 and Chao 1-2 may strongly depend on the specific behaviour of the accumulation curve of the rare species in a data set. Therefore, on the one hand, the high number of uniques and duplicates in the input dataset (68 FIS) may have led to high estimates of Chao 2 and Jackknife 2. On the other hand, Chao 2 produced the most conservative estimate and ICE, which algorhythm is less sensitive to rare species, produced a medium value, suggesting that Chao 2 did not overestimate. Moreover, since all four species accumulation curves (Fig. 5) were non-asymptotic the estimates likely range at the lower bound of the true richness (Gotelli & Colwell 2001). Ultimately, many additional species records have been obtained over time since the model input data of 1999-2000. They have contributed to a total faunal record (FL 2017) that slowly approaches the range of archipelagic species richness predicted by various models. The attributes, capabilities and potential pitfalls of non-parametric richness estimators were reviewed by Magurran (2004) and Gotelli & Colwell (2011), and dealt with by other works, for example: Moreno & Halffter (2001), Willott (2001), Brose *et al.* (2003), Brose & Martinez (2004), Chao (2005), Ulrich & Ollik (2005), Hortal *et al.* (2006), Sobéron *et al.* (2007), and Beck & Schwanghart (2010).

In their global study of patterns and predictors of tropical reef fish species richness Parravicini *et al.* (2013) compiled a mega-dataset composed of 163 individual fish inventories, including that of Kemp (1998) for the Socotra Archipelago. The study classified (according to 10 richness classes ranging from < 168 to > 1,350 species) the observed reef-associated fish species richness of the archipelago at 307–410 species and predicted the actual richness two classes higher (510–600 species, with an uncertainty of 2–2.75%, indicating that this might be an overestimate) by applying ‘boosted regression trees’ (BRT; Friedmann 2001, in Parravicini *et al.* 2013) as the estimation method, based on a variety of biotic, environmental and geographical variables. Their model has a generally high goodness of fit (> 80%), yet it seems largely to fail to predict the total reef fish species richness of the archipelago. Both estimates can, however, not simply be compared because (a) Parravicini *et al.* (2013) investigated tropical reef fishes only while this study deals broadly with coastal fishes, and (b) the designation of species as “reef fish” varies among authors. The underestimation of fish species diversity in this study has potential repercussions on the accuracy of subsequent studies which capitalize on the same basic dataset (see further below).

Explorative richness estimates were also computed in this study for critical diversity constituents at spatial, ecological and taxonomic scale. The particular value of these partial estimates is their capacity to inform future or follow-up sampling strategies. Island group specific richness estimates suggested that future sampling at the outer islands will be more efficient in recording undetected archipelagic richness than at the main island Socotra. Habitat-group specific richness estimates suffered somehow from the non-representative habitat-coverage of the FIS. It is interesting to note though that the best covered habitat S6 “coral” (Klaus & Turner 2004) still harbours more than 30% of undetected fish species richness. The quality of the estimates for the habitat groups S1, S4, and S7 was probably very low as these were only covered by four FIS. On the one hand, the models suggested an undetected richness of 84% that is likely an overestimate resulting from the algorhythms’ inherent logic, which emphasize rare species (e.g. Melo 2004). On the other hand, there is thus undoubtedly a substantial potential of yet unrecorded species from these habitats that need further study.

The family specific richness estimates need to be interpreted with caution but are nevertheless useful. The fact that the undetected richness within 15 key families decreased from 25% predicted by the models for the 1999–2000 data to a residual 3% only according to the FL 2017, indicates that the models have by-and-large not overestimated the diversity in these groups, thus providing confidence in their results. Surprisingly, the models predicted relatively low and implausible species numbers for Gobiidae and Blenniidae, where actual records (FL 2017) surpassed the estimated richness by 19% and 26%, respectively. This suggests biases in the data input for these families, which are likely owed to low taxonomic accuracy and/or omission of rare and secretive species, especially during the visual underwater observations contributing to S_{obs} . These biases likely reduced the incidences of ‘uniques’ and ‘duplicates’ in the dataset and led the models to underestimate the species richness. Conversely, the classic Chao 2 richness estimate for Serranidae of 103 species is very high and outside the range of possible species numbers for this family in the wider region given the archipelago’s size, and was thus not used. This high estimate is perhaps due to a bias caused by fishery effects (see also Haemulidae), which might introduce an “artificial rarity” to members of this commercially important family within the dataset (thus increasing the incidences of ‘uniques’ and ‘duplicates’), which could potentially confuse the incidence-based Chao 2 model. Reduced abundances do theoretically impact probabilities of occurrence detection; especially of vagile species (compare Brose & Martinez 2004). If so, such resource-use effects likely exert an even stronger bearing on abundance-based models such as Chao 1, ACE or Jackknife 1; a hypothesis that will be tested based on quantitative transect data in forthcoming studies (Zajonz *et al.* in prep.). The extrapolation of a total richness of the archipelago of up to 875 species of coastal fishes represents an informed synoptic estimate that is based on relative confidence in the richness estimates, additional considerations, and to a certain extent expert knowledge. Several of the present authors continue to work on the archipelago’s fish fauna. An ‘Annotated Checklist of the Coastal Fishes of the Socotra Archipelago’ and a full pictorial guide to the fishes of the island group are currently in preparation (Zajonz *et al.* in prep.).

The islands appear to be endowed with the highest diversity of marine fishes of any reasonably comparable biogeographic unit in the wider Arabian region. This finding is in contrast to other studies which summarize the observed and estimated species richness of the region (e.g. Parravicini *et al.* 2013; as discussed above). In comparing the species richness of eight key families (Acanthuridae, Balistidae, Chaetodontidae, Labridae, Pomacentridae, Pomacanthidae, Pseudochromidae and Serranidae, 411 species in total) used to analyse the relatedness of 10 Arabian eco-regions (modified from Spalding *et al.* 2007) in terms of distributional biogeography (Zajonz *et al.*, submitted), the richness in Socotra Archipelago was the highest (Fig. 10).

Certain coral-associated and ecologically important families are as diverse at the Socotra Archipelago, or more diverse, than those taxa in the entire Red Sea, even though the archipelago’s coastline is eight times less in length and supports considerably smaller expanses of biogenic reefs (Klaus & Turner 2004 compared to Edwards & Head 1987). The total area within a 5 km zone around the archipelago’s coastline is estimated at 2,691 km², with sublittoral biotopes occupying about 671 km², of which only 184.1 km² represent reefs (1.98 km²) and non-reef coral-dominated biotopes (Klaus & Turner 2004). The Red Sea, by comparison, is nearly 2,000 km long and has about 5,143 km of shoreline, encompassing approximately 450,000 km² of water surface (Morcos 1970; Head 1987; Rasul & Stewart 2015). Over much of its length, especially in its northern and central section, the Red Sea coastal shelf supports well-developed biogenic reefs (e.g. Roberts *et al.* 2016), amounting to ~17,000 km² of coral-dominated habitat for the entire basin (ReefBase 2017, web resource; UNEP-WCMC *et al.* 2010, web resource; both based on Spalding *et al.* 2001 for Red Sea reefs¹). Recently, Rowland & Purkis (2015) reported ~20,500 km² for the inshore (“shore-attached”) and offshore (“shore-detached”) reef area of the Saudi Arabian Red Sea coast, based on state-of-the art remote sensing methods. A comparison with ~6,500 km² mapped by Spalding *et al.* (2001) for Saudi Arabian reefs indicates a threefold difference. This suggests that the Red Sea reef area *s.lat.* (coral-dominated habitats) has been grossly underestimated and may ultimately be in the order of 51,000 km² (tentative extrapolation by the present authors based on the value of ~17,000 km² of Spalding *et al.* (2001) and an assumed threefold underestimation). By comparison, the coral-dominated habitat area of the Red Sea exceeds that of the Socotra Archipelago 277 times, or 92 times respectively, if the older estimate of Spalding *et al.* (2001) is used.

1. The Red Sea maps of the *Millenium Coral Reef Mapping Project* (UNEP-WCMC *et al.* 2010 web resource) were not available for the UNEP-WCMC v1.3 dataset.

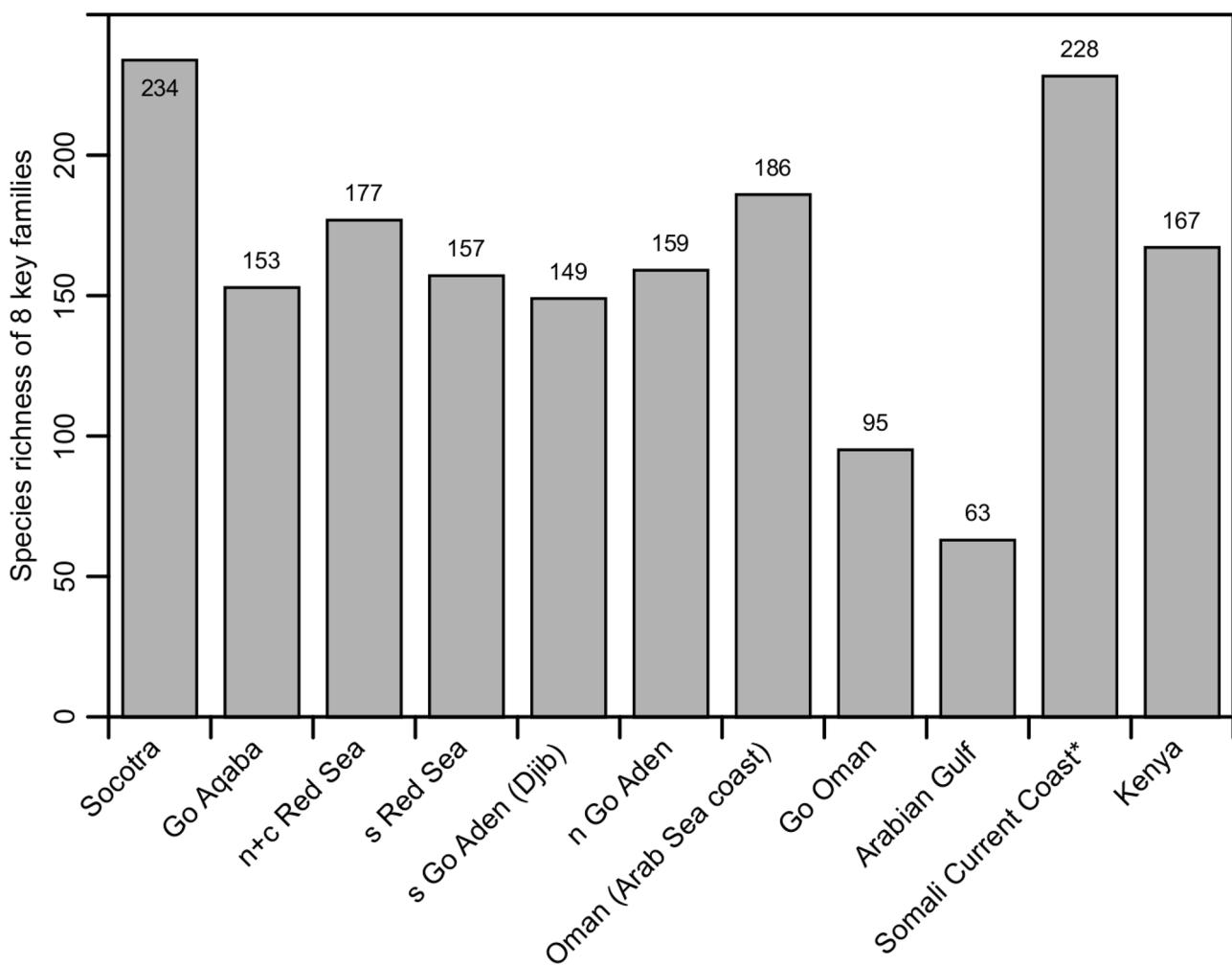


FIGURE 10. Comparison of species richness of eight key fish families (Acanthuridae, Balistidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Pseudochromidae, Serranidae) in 10 presumed ecoregions (modified from Spalding *et al.* 2007, see Materials and Methods; Zajonz *et al.* submitted) composing the wider Arabian region and Kenya as an external reference (refer to Zajonz *et al.* (submitted) for a regional species distribution list for these families) (* combines approximately the eco-regions 'Central Somali Coast' and 'Northern Monsoon Coast' of Spalding *et al.* 2007).

The comparative richness of Chaetodontidae (i.e. in relation to reef area) and Acanthuridae (i.e. in relation to sea area) is particularly striking. With no endemic species recognized as yet for these taxa, the Socotra Archipelago appears to act as a 'sink' for their diversity from surrounding source regions. The underlying parameters and processes require further study. Also, the species richness of the Labridae and Pomacentridae exceeds those found in the Red Sea. While the archipelago conceivably accumulates species from neighbouring regions, additional cryptic species, new hybrids and ongoing speciation processes can be anticipated in these taxa. New, possibly including endemic species are likely, especially in the families Gobiidae, Blenniidae, Apogonidae and Tripterygiidae. This expectation comes from a thorough taxonomic study on the Pseudochromidae, led to the description of three new endemic species and the discovery of a fourth, potentially new, species (Gill & Zajonz 2003, 2011).

Considering the still limited survey efforts and the relatively small area covered by the island group, the fish species richness of the archipelago is also relatively high, when compared exploratively to adjacent continental and island regions in the western and northern Indian Ocean (Fig. 11).

The actual richness reported by the FL 2017 is about as high as those for Kenya or the Chagos Archipelago. The extrapolated richness of Socotra Archipelago substantially exceeds the reported diversity of Kenya (FishBase 2017, sourced 2012) and Chagos Archipelago (FishBase 2017, sourced 2012, based primarily on Winterbottom & Anderson 1997). Comparing the extrapolated richness values of Socotra Archipelago (not just that documented)

with reported richness appears justified because Kenya and the Chagos Archipelago have been much more extensively studied than the Socotra Archipelago, and assuming that their documented richness approximates their actual total richness.

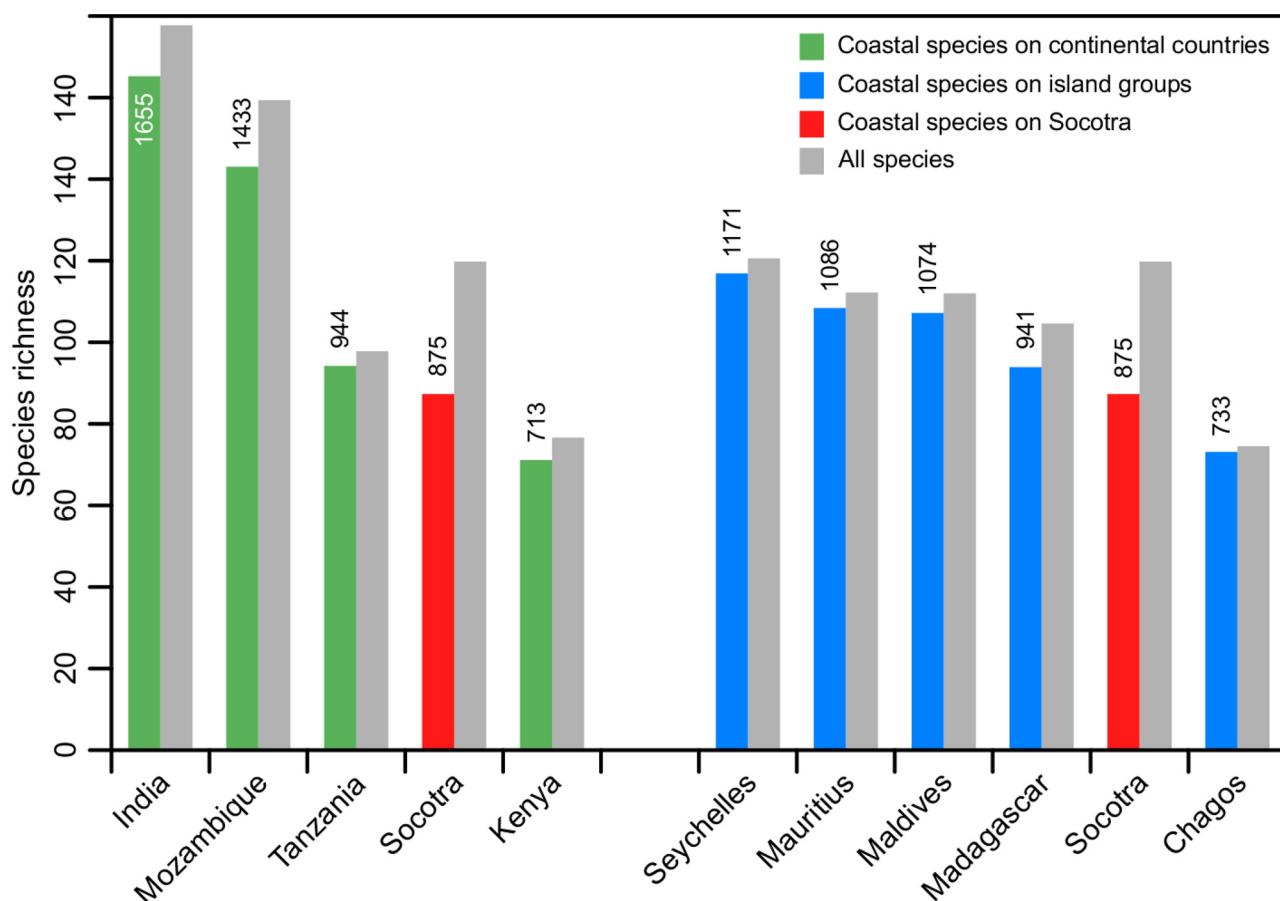


FIGURE 11. Comparison of coastal and marine (All) fish species richness between Socotra Archipelago and continental countries or island groups. Coastal species number follows the total archipelagic richness extrapolated from the species richness models; All species include an estimate of expected deep-dwelling species based on unpublished regional data of Zajonz & Bogorodsky and neighbouring geographical units (comparative data from Froese & Pauly 2017, FishBase, sourced 2012; verified and adjusted).

The area hypothesis (e.g. Rosenzweig *et al.* 2011) predicts that larger areas can maintain more species. The diversity of fishes around the Socotra Archipelago is thus especially striking when comparing species-area relationships exploratively (SAR, e.g. Gray 2001; Parravicini *et al.* 2013; using coastal length and coral habitat as simple “area proxies”, Table 12), with the same adjacent continental and island regions in the western and northern Indian Ocean (Fig. 12).

In relation to the length of the coastline, the coastal fish diversity of the Socotra Archipelago exceeds those of India, Mozambique, Tanzania, Madagascar¹, or the Chagos Archipelago. In relation to coral habitat area its coastal fish diversity is higher than in any other comparable region and ranks highest in the western and northern Indian Ocean perhaps with the exception of Réunion Island. This island combines a very high coastal fish species richness (902 species, FishBase 2017, sourced 2012; web resource, verified and adjusted) with a short coastline (207 km; Reefbase 2017, sourced 2012; web resource) and very limited expanses of reef area (< 50 km², Spalding *et al.* 2001). Both Socotra Archipelago and Réunion Island would therefore be interesting study sites for a comparative investigation of processes which lead to the accumulation of tropical and especially “coral-associated” diversity in “reef-poor” environments.

1. By the time Fricke *et al.* (2018) was published, analyses and main write-up of the present paper had already been concluded.

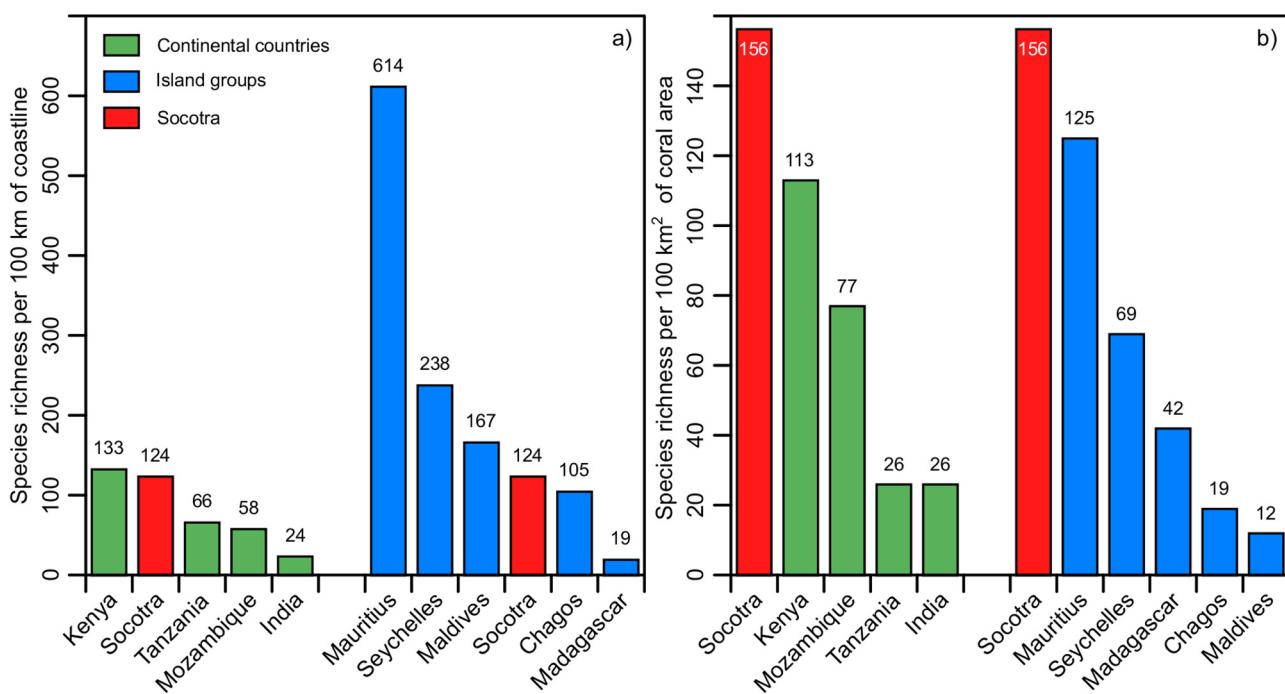


FIGURE 12. Comparison of fish species-area relationships (SAR) between Socotra Archipelago and neighbouring geographical units, using (a) the number of species per 100 km of coastal length, and (b) the number of species per 100 km² of coral area (comparative data from Froese and Pauly 2017, FishBase, sourced 2012, and ReefBase 2017, sourced 2015; web resources, verified and adjusted), based on Fig. 11.

TABLE 8. Spatial data used as “area proxies” for the calculation of explorative SARs (Fig. 12).

Area “proxy * Region”	Coastline length (km)	Coral habitat (km ²)
Socotra	705	**560
Kenya	536	630
Tanzania	1,424	3,580
Mozambique	2,470	1,860
India	7,000	6,470
Seychelles	491	1,690
Maldives	644	8,920
Mauritius	177	870
Madagascar	4,828	2,230
Chagos	698	3,770

(* comparative spatial data from ReefBase 2017, sourced 2015, web resource)

(** referring to the habitat area with substantial coral coverage, not only coral-dominated biotopes (Klaus & Turner 2004), thus providing conservative SAR estimates)

Distribution of diversity. The basic analyses of broadscale patterns of fish richness and diversity distribution reveals interesting insights requiring further investigation.

The species richness at individual sites varied within a very wide range corresponding to the variety of different habitats surveyed. Of 74 FIS, only 41 represented coral-dominated habitats, including a few sites with biogenic reef accretion (S6, Klaus & Turner 2004). The maximum (132 species) and mean values (66 species) are relatively high compared to other studies in the Arabian region. For example, Khalaf & Kochzius (2002) recorded average species numbers ranging between ~18 and ~59 species (with maxima close to 70 species) during visual transect censuses on coral reefs near the city of Aqaba (Jordan). Like reefs in the Gulf of Aqaba, coral assemblages of Bahrain belong to the northernmost coral areas of the Arabian region and globally. Al-Baharna (1986) recorded

and described 238 coastal fish species from Bahrain. Krupp & Müller (1994) and Krupp & Al-Marri (1996) recorded 280 coastal fish species from the Jubail Marine Wildlife Sanctuary in eastern Saudi Arabia, with a coastline length of 400 km and a sea area of 1300 km². They counted between 19 and 50 fish species per 100 m² (200 m³) reef transect (individuals smaller than 20 mm were not included in the counts). Overall fish species richness of reefs in the southern Arabian/Persian Gulf (Dubai, UAE) was reported by Riegl (2002) as 95 species in 1996 and 64 species in 1998, based on visual point counts (the decrease was related to positive sea-surface temperature anomalies). The adjoining north-eastern Arabian Peninsula was covered by a visual transect census study by Burt *et al.* (2011) at 24 sites, spanning the southern Arabian/Persian Gulf, the western Gulf of Oman and the north-western Arabian Sea (Oman), with southernmost sites at Halaniyat Island and Mirbat. Overall fish species richness ranged between 14 and 59 species, with a mean of 36.5 species per site. If adjusted by a correction factor of 1.3 in order to account for the small transect area covered (150 m²) and the fact that individuals smaller than 5 cm were neglected the overall richness extrapolatively ranged between 18 and 77 species, with a mean of 47.5 species per site. The two richest sites were located at the Mirbat coast of Oman, thus in relative proximity to the Socotra Archipelago. Further to the west, the overall species richness at Belhaf headland (Shabwa) at the Yemeni Gulf of Aden coast ranged between 101 (72) and 126 (90) species at five visual inventory sites (Zajonz *et al.* unpublished data of 2005), with a mean of 109.6 (90) species (numbers in parentheses indicate values of five associated visual transect censuses only). Visual inventories at 11 sites spanning almost the entire Yemeni Red Sea coast from Hanish Island to the northern Kamaran Archipelago (Zajonz *et al.* unpublished data of 2004) recorded between 57 (60) and 97 (81) species in terms of overall richness, with a mean of 76 (71.5) species (numbers in parentheses indicate values of four associated visual transect censuses only). A recent study by Roberts *et al.* (2016) reported a maximum of 101 species (one site) and a minimum of 68 species, with a mean of 84 species, from visual transect censuses on 40 inshore and offshore coral reefs spanning 1,100 km of Red Sea coastline of Saudi Arabia. Whilst the mean richness value recorded by this study is higher than that at 74 FIS in Socotra Archipelago, the maximum values at these archetypal Red Sea reef sites, spanning “8 degrees of latitude” (Roberts *et al.* 2016), appear to be lower (the richness at the ten richest FIS ranged between 100 and 132 species). Krupp *et al.* (1994) counted between 36 and 56 fish species per 100 m² (200 m³) reef transect at Sanganeb Atoll, Sudan, central Red Sea (individuals smaller than 20 mm were not included in the counts). Due to the inconsistent survey methods used the results of these studies are not fully comparable, thus providing only a rough indication of fish species richness around the Arabian Peninsula. It nonetheless appears to be justified to recognize a ‘South-eastern Arabian Centre of Fish Diversity’ at the eastern limits of the Gulf of Aden that encompasses two main hotspots, the Socotra Archipelago and the Belhaf Headland and the adjoining coast to the east, known as ‘Bir Ali—Belhaf Area’ (Zajonz, Aideed, Kemp, Lavergne, Krupp pers. obs.; Kemp 2000a).

The richness at the scale of individual island groups at the archipelago seems to accord to classic species-area relationships (e.g. Rosenzweig *et al.* 2011; see below) and does not follow a clear geographic direction. By contrast, the variation of site and area richness (the latter representing aggregated neighbouring sites from consistent ecological environments) follows a generalised pattern across the archipelago, in that richness increases from west to east and from south to north, the latter primarily in regard to the exposure of the coast at the individual islands. Mean species richness values of 54 (33–73) recorded along the south coasts were positively biased due to the selection of survey sites. The actual diversity is clearly lower due to the pseudo-temperate environment created by the hydrodynamic conditions and the occurrence of upwelling along the southern coasts. Abd al-Kuri and Kal Farun are somewhat particular in that very rich areas are also found at the south coasts. Contrary to the conditions found at the other islands, the differences between north and south coast habitats at Abd al-Kuri are not distinct. On the one hand, field observations based on the FIS and numerous additional so-called ‘rapid ecological assessment sites’ suggest that sites on the northern coast of Abd al-Kuri are generally richer in their number of fish species than are sites on the southern coast. Several areas in the south, on the other hand, were found to be more diverse than the richest areas in the north, and are therefore considered as distinctive “biodiversity pockets”.

The analyses of species occurrences revealed very uneven OFDs as was to be expected (assuming that occurrences are ecostatistically related to abundances, see further below) from tropical and coral-associated fish assemblages (Sale 1991; Polunin & Roberts 1996). Uneven OFDs are generally characteristic for most ecological communities (Magurran 2004; Magurran & Henderson 2011; McGill 2011). Few species dominate the occurrence frequencies, thus are spatially most common and distributionally dominant around the archipelago, while the majority of species are spatially infrequent and many of them can be considered as ‘rare’. Inferences about actual

archipelagic ‘occupancy’ of species are not made because occupancy is highly dependent on the sampling grain and the size of the sampled sites (Gaston & He 2011). More sampling effort is needed i.e. in order to improve the species inventories of the fish assemblages at the outer islands, at all south coasts and at marginal habitats.

The numbers of uniques and duplicates appear to be high (180 species according to 74 FIS; or 261 species of the present FL 2017, respectively; see Annexes 1–2). The unique and duplicate species may include strays and waifs which are, however, hard to tell apart from rare species that have established reproductive populations in the archipelago. The high total number of uniques and duplicates strongly suggests that rare species represent a diversity attribute—many species with limited archipelagic occupancy and small population sizes—in its own right that is peculiar to the coastal fish assemblages of the archipelago. This assumption is also supported by repeated observations of rare species (i.e. species initially believed to be strays, Zajonz & Khalaf 2002) over long time spans, e.g. of *Chaetodon lineolatus*, *C. guttatissimus*, *C. zanzibarensis*, *Hemitaurichthys zoster*, *Amphiprion omanensis*, *Abudefduf septemfasciatus*, *Plectroglyphidodon dickii*, *Cheilinus undulatus*, *Cirrhitabrus cyanopleura*, *Naso vlamingii*, *Balistoides conspicillum*, or *Cantherhines dumerili*, to name some of them. Whether these species represent “core species” or “occasional species” *sensu* Magurran *et al.* (2011) or an exceptional case to the rule requires further investigation. The attribute of ‘persistence’, that is “repeated presence when resampled through time” is used by Magurran *et al.* (2011) to define ‘core community’ members of a wider community in a given area. Their definition is based on the assumption that species that are persistent in the record are also more abundant, thus more frequent both in the sense of abundance and occurrence (as occupancy is obviously a function of the distribution of the individuals present, e.g. Gaston & He 2011). Accordingly, infrequent species are considered occasional species. The general concept likely also applies to the coastal fish assemblages of the Socotra Archipelago, yet there seem to be assemblage members which are persistent but infrequent, or rather persistent on a low level.

Other rare species yet remain seldom records and perhaps truly occasional species *sensu* Magurran *et al.* (2011) although their first observation was reliable, including *Epinephelus erythrurus*, *Chaetodon bennetti*, *C. mesoleucus*, *Amphiprion chagosensis*, *Chrysiptera brownriggi* (as *C. leucopoma* in Zajonz *et al.* 2000), *Zebrasoma scopas*, and *Arothron nigropunctatus*. Other species are perhaps seldom recorded because of sampling biases such as, for example, *Pseudanthias cooperi*, *P. evansi* or *Chromis xouthos*. Such species with a predilection for deeper coastal habitats, have been sampled only rarely to date, and may actually occur more frequently. The archipelago’s diversity attribute of “rich in rare species” hypothetically results from a particular combination of its geographic location at adjoining biogeographical regions and a suite of specific local conditions, as discussed further below. Understanding the prevalence of these rare species is important for both archipelagic and regional conservation planning.

‘Socotra Island & Sabuniya’ form the richest part of the archipelago in terms of total species richness, consistent with their relative share of the archipelago’s total size, whereas the highest maximum and mean site richness and three of the five richest ‘areas’ are found at ‘Abd al-Kuri & Kal Farun’. The island group ‘Darsa & Samha’ assumes an intermediate position with regard to site richness, while its total richness is lowest because of the small size of the islands. The evenness of occurrence distribution appears to increase from east to west, indicating more homogeneous assemblages at the outer islands and notably ‘Abd al-Kuri & Kal Farun’. At the same time, ‘Abd al-Kuri & Kal Farun’ are also comparatively rich in species which are rare at archipelagic scale. The relatively high numbers of uniques and duplicates recorded at Socotra Island suggest that survey effort was not unevenly high there compared to the other islands (as otherwise the number of uniques would assumably be lower) and therefore the observed frequency distribution of uniques and duplicates is likely representative for the island groups. These gross richness distribution patterns would suggest a special conservation importance for ‘Abd al-Kuri & Kal Farun’. Socotra Island, however, is home to the largest human population and thus the least pristine island, while still harbouring the majority of the species. Consequently, targeted conservation measures should aim at protecting the pristine environment and associated fish assemblages of the outer islands, and seek to preserve key habitats and assemblages and reduce the overall pressure at the main island.

All thirteen species dominating the relative archipelagic occurrences were either coral-associated (“reef”) species, or demersal species that frequently occur on coral reefs. Species dominating the occurrences at the individual island groups were also primarily coral-associated. This finding is striking on account of the fact that the Socotra Archipelago has only few biogenic reefs and limited expanses of coral-dominated habitats (DeVantier *et al.* 2004; Klaus & Turner 2004). Further investigations into fish-habitat relationships are needed and underway

(Zajonz *et al.* in prep.). It is also noteworthy, that hardly any commercially important species formed part of the suite of dominant species, which might hypothetically indicate impacts of the local fisheries (see below) on the assemblage structure. Only at ‘Darsa & Samha’ a single species, *Cephalopholis argus*, was recorded relatively frequently.

The investigation of the fish assemblage resemblance between individual island groups using hierarchical agglomerative cluster analysis and SIMPER analysis based on pooled relative occurrences revealed an intra-archipelagic structure. This structure is characterised by a presumably closer association of ‘Darsa & Samha’ to ‘Abd al-Kuri & Kal Farun’ than to ‘Socotra Island & Sabuniya’. Interestingly, the sets of species contributing most to the dissimilarities are quite different for each of the island group pair comparisons. Further evidence for this structure is provided by the ANOSIM tests of the island group designations, which yielded the lowest support for a distinction between ‘Darsa & Samha’ and ‘Abd al-Kuri & Kal Farun’, and also by the cluster analysis of quantitative transect data (Fig. 4). This result is somewhat unexpected, because ‘Darsa & Samha’ is located at about similar distance to the other two island groups, shares a shallow geological platform with ‘Socotra Island & Sabuniya’, and is separated by a deep water trench from ‘Abd al-Kuri & Kal Farun’. Ecological and distributional processes (i.e. dispersal by transport of eggs and larvae by ocean currents) over geological time spans may presumably have supported the homogenization of the faunal assemblages of the outer islands in spite of “adverse” geological and oceanographic settings.

The analysis of the species shared between island groups (according to all species of the FL 2017 with distribution records) reveals that only about one third of the species are presently recorded from the entire archipelago, which indicates a faunal structure. The ratios of species shared between any two island groups, especially those shared exclusively, partly contrast those of the island-group resemblance analyses of relative occurrences at the 74 FIS, as discussed before. This discrepancy is probably explained by island group size and the resulting total species numbers, which permits more matches between the larger species pools of the larger island groups.

The ecological and potentially biogeographical controls of the observed archipelagic richness distribution patterns require further investigation. The variables driving the north-south variation are most probably mainly related to the Indian Monsoon, notably the strong wind and wave dynamics and cold upwelling that temporarily create unfavourable conditions for reef-associated taxa especially along the south coasts. The variables, which are responsible for the east-west variation as well as those controlling the between-island group and between-site variation, and their interactions, are obviously complex.

Biogeography. This paper does not undertake to investigate the biogeographic affinities of the fish assemblages of the Socotra Archipelago in detail. Some general observations facilitating future works are offered as follows.

Biogeographically, the Socotra Archipelago has long since been considered as located at the intersection of several distinct biogeographic entities, based on early works e.g. of Rosen (1971), Klausewitz (1972), Briggs (1974), and Hayden *et al.* (1984). In terms of the zoogeography of corals and fishes the archipelago was thought to be at the junction of the Arabian and the western Indian Ocean subprovinces within an Indian Ocean marine province, or just north to their boundary, respectively (e.g. Klausewitz 1978; Ormond & Edwards 1987; Klausewitz 1989; Sheppard & Salm 1988; Sheppard & Sheppard 1991; Sheppard *et al.* 1992; Kelleher *et al.* 1995; Watts *et al.* 1999). The archipelago is located in proximity to the boundaries between the Eritrean and South Arabian section and between the South Arabian and “Persian” section of the Arabian subprovince according to the zoogeographical concept of Klausewitz (1989), and to a centre of speciation and endemism identified at the Arabian Sea coast of Oman (Randall & Hoover 1995; Randall 1995). These studies, however, were based altogether on very limited data with regard to the Socotra Archipelago.

The marine biogeographic affinities of the archipelago were summarised by Kemp (1998), DeVantier *et al.* (2004), Klaus & Turner (2004), Schils & Coppejans (2003b) and Schils (2006). DeVantier *et al.* (2004) coined the term “zoogeographic crossroads” to characterise the particular biogeographic attributes of the archipelago. The locations of hypothetical biogeographical boundaries and the evidence for putative barriers that cause faunal and floral breaks in the seas around the archipelago, have been and are still a matter of vivid scientific debate (e.g. Sheppard & Salm 1988; DiBattista *et al.* 2015a, Priest *et al.* 2015; Coleman *et al.* 2016; DiBattista *et al.* 2016a, 2016b; Hodge & Bellwood 2016; Di Battista *et al.* 2017).

Kemp (1998) was the first to study the zoogeography of “coral reef fishes” of the Socotra Archipelago. This

and three subsequent papers (Kemp 2000a, 2000b; Kemp & Benzoni 2000) advanced the knowledge of the marine biogeography of the north-western Indian Ocean substantially. Kemp identified a distinct “South Arabian region”, combining parts of southern Oman and eastern Yemen, and recognised strong affinities of this region to the Socotra Archipelago, next to a parallel “East African influence”. Kemp’s and Kemp and Benzoni’s studies suggest that the Gulf of Aden, including the Socotra Archipelago, is probably not a homogenous and consistent biogeographic entity; an important result that was largely overlooked by most subsequent authors referring to these papers. The papers dealt primarily with the regional distribution of five families of reef-associated fishes, with a focus on Chaetodontidae. Tentatively corroborating Kemp’s main findings, additional information was provided by Zajonz & Khalaf (2002).

The global megastudies of Spalding (2007, MEOW), Briggs & Bowen (2012), and Kulbicki *et al.* (2013) included inferences about the possible marine ecoregional and biogeographic position and relative biodiversity of the archipelago which, in terms of fish distribution data, were predominantly based on the limited faunal account of Kemp (1998); who, for example reported a total of 53 species in Chaetodontidae, Pomacentridae and Labridae. By comparison this study records 135 species (see Table 2) and estimates 169 species (see Table 3) from these families, thus roughly three times the diversity and potential biogeographic information.

Spalding *et al.* (2007) presented a global hierarchical bioregional classification system (MEOW) whereby the Socotra Archipelago was assigned to a ‘Gulf of Aden’ ecoregion (89.) as part of a ‘Red Sea–Gulf of Aden’ province (18.) within a ‘Western Indo-Pacific’ realm. The MEOW scheme has been widely adopted since (compare e.g. Obura 2012; DiBattista *et al.* 2016b and Cowman *et al.* 2017).

Updating earlier most influential marine biogeographic concepts with special respect to fish distributions (i.e. Ekman 1953 and Briggs 1974, updated by Briggs 1995) Briggs & Bowen (2012) proposed that Socotra Archipelago belongs to a ‘Western Indian Ocean’ province - within a ‘Tropical Indo-West-Pacific Region’ - that extends all along the east African coast and also includes the Arabian/Persian Gulf, and excluded Socotra Archipelago from a ‘Red Sea’ province.

Kulbicki *et al.* (2013) provided a global biogeography of tropical reef fishes which couldn’t satisfactorily resolve the position of the archipelago, placing it along with “Somalia” in either a ‘Western Indian Ocean’ province or a ‘North-western Indian Ocean’ province (within a Western Indian Ocean region). Relying primarily on the then outdated checklist of Kemp (1998) the species richness values for Socotra Archipelago were likely underestimated. Neither the comparative position of Socotra Archipelago nor the proposed higher level biogeographic units conform among these studies (see also Methods; and for details compare Zajonz *et al.* submitted).

Also, the studies by Bender *et al.* (2017) on the role of isolation for taxonomic and functional nestedness and by Gaboriau *et al.* (2017) on the geography of speciation and its role in shaping coral reef fish diversity patterns, both covering the Indo-Pacific, capitalized on the datasets compiled by Kulbicki *et al.* (2013) and Parravicini *et al.* (2013), hence likely assumed too low richness values for Socotra Archipelago as well. These comments are not intended at undermining the value of the aforementioned important studies but highlight the value of faunistic baselines and the potential merits of employing diversity estimators; especially in cases where several interdependent studies rely on the same basic dataset. By contrast, the study of Mouillot *et al.* (2013) on the function of nestedness for the delineation of biogeographic regions lists Kemp (1998) as main reference for their Socotra account but effectively complemented it by other available records (likely data reported primarily by the present authors earlier) to a total of 111 species in the Chaetodontidae, Pomacentridae and Labridae which comes relatively close to the numbers reported herein.

Recently, a string of primarily phylogeographic and phylogenetic studies contributed information which is relevant to the ichthyogeography of the Socotra Archipelago and the Gulf of Aden, as reviewed by Zajonz *et al.* (submitted). This includes DiBattista *et al.* (2013), DiBattista *et al.* (2015a, 2015b), DiBattista *et al.* (2016a, 2016b), Fernandez-Silva *et al.* (2015), Priest *et al.* (2015), Saenz-Agudelo *et al.* (2015), Ahti *et al.* (2016), Waldrop *et al.* (2016), Coleman *et al.* (2016), DiBattista *et al.* (2017), and Cowman *et al.* (2017).

The study by DiBattista *et al.* (2015a) is especially noteworthy because it recognizes the archipelago as a main hotspot for marine fish hybridisation globally. The studies by DiBattista *et al.* (2016a) and DiBattista *et al.* (2016b) used outdated faunistic data from Socotra Archipelago of Kemp (1998) and the present authors (Zajonz *et al.* 2000), none of which were aimed at reviewing the ichthyogeography or marine biogeography of the Socotra Archipelago.

The review of the contemporary literature suggests that substantial advances have been made with regard to

the phylogeography of the “Arabian region”. Yet, not much progress has been made concerning the distributional and ecological biogeography of the wider Gulf of Aden–Socotra–Somalia region since the early studies by e.g. Klausewitz (1978, 1989), Ormond & Edwards (1987) or Sheppard *et al.* (1992). Both the results of contemporary global studies as well as of taxa-specific regional studies do not yet correspond to one another in a satisfactory way, and are based on outdated species lists for the Socotra Archipelago and southern Arabia. The seminal ichthyogeographic study by Kemp (1998) requires updating since the number of recorded species has more than tripled since, according to this paper. In conclusion, a revision of the distributional and ecological ichthyogeography of the Socotra Archipelago based on up-to-date faunistic data is still pending.

According to the distributional classification scheme, as modified from Manilo & Bogorodsky (2003), the fish assemblages of the Socotra Archipelago are dominated by species from the Indo-West Pacific and the north-western Indian Ocean, as was to be expected. Interestingly, the share of species with both far-reaching distribution ranges and ranges restricted to the western Indian Ocean is relatively high. Most of the thirteen species dominating the relative archipelagic occurrences have Indo-Pacific or Indo-West Pacific distribution patterns (*Lutjanus bohar*, *Thalassoma lunare*, *Labroides dimidiatus*, *Chromis weberi*, *Pomacanthus imperator*, *Zanclus cornutus*, *Sufflamen fraenatum*) and north-western Indian Ocean distribution patterns (*Pomacentrus leptus*, *Chaetodon pictus*, *Zebrasoma xanthurum*), supplemented by pan Indian Ocean (*Parupeneus macronemus*, *Melichthys indicus*) and western Indian Ocean elements (*Pomacentrus caeruleus*). Considering that the species listed above are either coral-associated (“reef”) species, or demersal species that frequently occur at coral reefs, the coastal fish assemblages of the Socotra Archipelago can be broadly characterised as Arabian reef assemblages which are substantially enriched in a unique way (by regional and possibly global standards; see also DiBattista *et al.* 2015a), through various short-, medium- and long-ranging dispersal trajectories (Zajonz *et al.* submitted, Zajonz *et al.* in prep.).

In accordance with the findings of Kemp (1998, 2000a), this study revealed the extension of distribution ranges of Red Sea (Eritrean section *sensu* Klausewitz 1989) species westward, of western Indian Ocean (East African) species northward and of ‘Arabian’ species southward. The biogeographic influence of the Arabian region appears to be dominant on all islands. However, the faunal assemblages of the outer islands, particularly those at Abd al-Kuri, receive a strong influx of transgressing “East African” species. The term East African is used here to refer to species whose northern boundaries of distribution within the western Indian Ocean were so far believed to be the Horn of Africa or island groups in the east of Africa, such as the Seychelles, the Comores, the Mascarenes or Madagascar. Examples of such species are *Sargocentron seychellense*, *Pseudanthias cooperi*, *P. evansi*, *Chlidichthys bibulus*, *Chaetodon bennetti*, *C. interruptus*, *C. zanzibarensis*, *Hemitaurichthys zoster*, *Abudefduf notatus*, *Plectroglyphidodon dickii*, *P. johnstonianus*, *Halichoeres cosmetus*, *H. iridis*, *Oxycheilinus bimaculatus*, *Thalassoma hardwicke*, *T. lutescens*, *T. hebraicum*, *Acanthurus leucocheilus*, *A. leucosternon*, *A. lineatus*, *A. nigricans*, *A. thompsoni*, *A. triostegus*, *Ctenochaetus truncatus*, *Naso vlamingii*, *Zebrasoma scopas*, and *Balistoides conspicillum*.

Randall (1995) and Randall & Hoover (1995) expected certain species with known distributions restricted to the northern or southern Arabian Sea coasts to be found in the study area as well. A number of these species were actually recorded, including *Pseudanthias marcia*, *Cirrhitichthys calliurus*, *Thalassoma loxum*, *Diplodus cf. kotschy*, *Halichoeres cf. lapillus*, *Alloblennius cf. parvus*, and *Amphiprion omanensis*.

Rosen (1971), Sheppard *et al.* (1992), Kemp (1998), Coleman *et al.* (2016), DiBattista *et al.* (2016a, b), and DiBattista *et al.* (2017), among others, theorised that the seasonal cool upwelling in the Gulf of Aden and related temperature thresholds possibly pose barriers to the dispersal of inshore fishes between the Red Sea and Gulf of Aden and the wider Indian Ocean. While there is evidence that such upwelling-related barrier effects exist, at least for certain taxa e.g. macroalgae (Schils & Wilson 2006) and certain fish species (Coleman *et al.* 2016; DiBattista *et al.* 2017), the Socotra Archipelago obviously also counters this effect by providing a “stepping stone” for the dispersal of marine organisms in the wider region (Kemp 2000a, Schils & Coppejans 2003b, DeVantier *et al.* 2004, DiBattista *et al.* 2015a, Zajonz *et al.* present paper, Zajonz *et al.* submitted). Also the oceanographic current patterns in the Gulf of Aden and Arabian Sea rather suggest temporally and spatially complex but powerful dispersal trajectories in the region (compare Fig. 2). The hypothetical upwelling and temperature barriers thus appear to be quite permeable (Klaus *et al.* 2002) and should be considered partial, temporally and spatially dynamic barriers that do not affect all organisms equally. They contribute to the assembly of transition zones where areas of related but distinct faunal and floral assemblages overlap, contributing to a biogeographically complex picture especially in the seas around the Socotra Archipelago.

At the same time, these biogeographic settings seem to limit the evolution of endemic species at the archipelago, explaining in part the yet comparatively low number of endemics (< 1.0%). There are presently four species which are considered as “endemic” to Socotra Archipelago, or are known thus far from there only, respectively: *Halidesmus socotraensis*, *Pseudochromis chrysospilos*, *Pseudochromis socotraensis*, and *Pempheris zjonzi*. A fifth species, *Cheilopogon socotranus* described by Steindachner (1902), and previously considered “endemic” probably represents a junior synonym of a species that is not known from Socotra Archipelago exclusively (I. Shakhovskoy, pers. comm.). Another species described by Steindachner (1902) from Socotra Island, *Gerres socotranus*, is regarded as a junior synonym of the widespread common silver-biddy *G. oyena* (Iwatsuki *et al.* 1999; Kottelat 2013). A new species of the blenniid genus *Ecsenius* is currently being described by Springer *et al.* based on morphological and molecular characters of specimens from Socotra Archipelago and southern Oman. It is probably restricted to this combined region.

The anthiine *Plectranthias intermedius*, the moray *Gymnothorax sokotrensis*, and the conger *Pseudophichthys macroporis* were collected from deep waters off Socotra Archipelago and may potentially occur at depths shallower than 200 m, hence were included in the FL 2017. The conger *Ariosoma sokotranum* was described based on two specimens collected by the R.V. Vityaz in 1989 from 395–420 m off Socotra Archipelago. Four additional specimens stored at the USNM were collected from deep waters off northern Somalia by the R.V. Beinta in 1987 (Anonymous 2001, FishBase 2017 web resource; unpublished, identifier unknown). Three of these specimens were recorded from a depth range of 315–397 m. One specimen (USNM 305918) was collected at R.V. Beinta station 18-3 with a non-closing prawn trawl at 0–335 m depth (given by GBIF 2017 as 167.5 m ± 167.5 m; sourced 2015, web resource). Because the collecting depth cannot be recorded precisely with this sampling gear, the species was not included in the FL 2017. The deep-sea shark *Planonasus parini* is only known from depths of 360–1,120 m from the deep slope of the northern ‘Socotra Platform’ (the geological platform uniting Socotra Island and the so-called ‘Brothers’ Darsa Island and Samha Island; Birse *et al.* 1997; Cheung & DeVantier 2006), the deep-sea shark *Apristurus breviventralis* is only known from depths of 1,000–1,120 m and the deep-sea skate *Okamejei ornata* is only known from depths of 375–380 m at the same locality. All deep-dwelling species are likely to have a wider distribution at least in the Gulf of Aden and therefore shouldn’t be considered as endemic to the archipelago.

In comparison, the Red Sea is considered the area with the highest degree of endemism in the Indian Ocean, with 46% of the chaetodontid species (Klausewitz 1978) and 29% of the pomacentrid species (Allen & Randall 1980) regarded as endemic. An endemism level among fish species of 17% was calculated by Ormond & Edwards (1987; based on 508 species analysed), a figure which was later amended to 13.7% by Goren & Dor (1994; based on 1,248 species), to 12.9% (and 14.1% endemic in the Red Sea and Gulf of Aden) by DiBattista *et al.* (2016b; based on 1,071 species), and to 14% by the most up-to-date inventory of Bogorodsky *et al.* (in press; based on 1,122 species). By comparison, Rodrigues Island also has a comparatively high richness of coastal fishes (~600 species) but endemism as low as ~ 1% (Heemstra *et al.* 2004), which is due to the fact that it shares most species with the other Mascarene islands for which an endemism of 3.7% is reported (Fricke 1999, in Heemstra *et al.* 2004). For Réunion Island an endemism level of 0.7% and a presence of 2.6% of Mascarene endemics, pertinent to an exceptionally high diversity of 984 species of fish, is reported by Fricke *et al.* (2009). The combination of high species diversity and low endemism levels represents a diversity attribute that the Socotra Archipelago obviously has in common with other island groups in the Western Indian Ocean (WIO *sensu* Briggs & Bowen 2012).

Notwithstanding the low endemism level preliminarily reported herein, the yet undetected crypto-genetic diversity among the coastal fishes of the Socotra Archipelago is expected to be substantial. For example DiBattista *et al.* (2017) recently detected evidence for a mitochondrial lineage (CO1 gene) of the Common bluestripe snapper *L. kasmira* from Socotra Island and Oman that diverges from the widespread CO1 lineage that Gaither *et al.* (2010) reported as inhabiting most of the Indo-West Pacific, including the Red Sea and the western Gulf of Aden (i.e. Djibouti). More thorough taxonomic studies combining genetic and morphological characters will likely reveal numerous additional species as new to science, of which some may represent neo-endemics or paleo-endemics (Cowman *et al.* 2017) at archipelagic or regional scale.

Fish diversity and fisheries. Fishing activities are well known as having direct and indirect effects on coastal and notably reef fish populations and their habitats (e.g. Buxton & Smale 1989; Roberts & Polunin 1991; Russ 1991; Jennings & Polunin 1997; Pauly *et al.* 1998; Hawkins & Roberts 2004). For example the removing of apex predators, carnivores and herbivores can change species diversity, composition, abundances and community structure (e.g. Russ & Alcala 1989; Jennings *et al.* 1995), life history (e.g. Buxton 1993), population structure,

biomass, trophic and functional relationships (e.g. Jennings *et al.* 1995; Jennings & Lock 1996), morphological traits (e.g. Hammerschlag *et al.* 2018) and also the composition of the benthic communities and the entire ecosystem (e.g. Roberts 1995). The removal especially large individuals in higher trophic groups from the fished populations, the predation pressure on lower trophic groups and small-sized taxa possibly decreases and thus alter the species composition and population structure of assemblages (e.g. Russ 1991; Hammerschlag *et al.* 2018). Alternatively, the removal of certain predators may cause other predators to opportunistically switch their prey (Jennings *et al.* 1995), allowing the entry of smaller phylogenetically or functionally related species (e.g. Jennings *et al.* 1999; Hoggarth *et al.* 2006).

Fishing has been a primary livelihood occupation of the people inhabiting the Socotra Archipelago for hundreds and most likely thousands of years (Cheung & DeVantier 2006). The local fishery has gone through a period of substantial expansion over the past two decades and shows severe signs of overexploitation (Zajonz *et al.* 2016; Zajonz *et al.* in prep.). It is therefore very probable that fishing activities have contributed to shape the coastal fish diversity in the archipelago as it is encountered today. Conceivably, fisheries may have reduced the diversity of certain groups of fish on the island group (Roberts 1995; Jennings *et al.* 1999). The lower average site diversity at Socotra Island may possibly result from more intense fishing pressure at this most densely-populated island, compared to the other islands of the archipelago. Fisheries may also have affected fish diversity positively at the archipelagic scale, hypothetically for example by synergistic effects combining the (a) archipelago's favourable biogeographic position at crossing dispersal trajectories and overlapping distribution range limits (as discussed above), the (b) high habitat [and niche] diversity (as also discussed above, compare Klaus & Turner 2004), and an assumed (c) reduced predation pressure due to intense fishing (Zajonz *et al.* in prep.) on species with small body size, limited occupancy, and low abundances. This could, theoretically, explain at least in part the remarkable species richness of e.g. the Labridae and Pomacentridae. The interaction between the artisanal fisheries and the fish diversity and assemblage structure on the Socotra Archipelago is yet to be investigated.

Conclusions

The Socotra Archipelago in the eastern Gulf of Aden has a unique marine environment which combines tropical and 'pseudo-temperate' characters. Studies on fish biogeography of the archipelago have substantially outpaced critical baseline research on the archipelago's fish diversity and ecology. This study was designed to in part fill these gaps. It recognizes the Socotra Archipelago, which is rich in rare species and hybrids, as a major hot spot of coastal fish diversity in the wider Arabian region and the Indian Ocean as a whole.

The islands support unique coastal fish assemblages which are predominantly composed of coral-associated ("reef") species in spite of limited biogenic reef frameworks in the archipelago. A Preliminary Checklist comprises 682 confirmed species and a Working List of another 51 preliminary records (ODUs), totalling 733 species records in 108 families. Labridae are the most speciose family, followed by Gobiidae, Pomacentridae, Serranidae and Chaetodontidae. The richness of the archipelago is higher than in any of the adjacent Arabian ecoregions. The species richness of the Acanthuridae, Chaetodontidae, Labridae, Pomacentridae and Pseudochromidae stand out as particularly high, and the richness of several fish families is higher than in the entire Red Sea.

Between 830 and 890 fish species are predicted to occur by incidence-based richness models; the total archipelagic richness is extrapolated at up to 875 species. Inshore fish inventories, covering 497 species, found between 14 and 132 species per site (66 species on average). Site diversity decreased across the archipelago from west to east and from north to south. Total fish diversity was highest around Socotra Island, followed by Abd al-Kuri & Kal Farun, and Darsa & Samha. Occurrence frequencies were very unevenly distributed and dominated by *Pomacentrus caeruleus* and *Thalassoma lunare*, whilst many species were rare. Hierarchical agglomerative clustering of pooled relative occurrences combined Darsa & Samha and Abd al-Kuri & Kal Farun at 73.7% similarity, and the resulting group with Socotra Island & Sabuniya at 67.9% similarity. The fish assemblages are dominated by species from the Indo-West Pacific and the north-western Indian Ocean. They include a low number of endemics (4–5), and high shares of species with western Indian Ocean ranges and beyond.

The ongoing crises in Yemen adversely affects environmental and conservation management in the country, including the Socotra Archipelago, and its coastal ecosystems (EPA Socotra pers. comm.; Zajonz *et al.* 2016; Zajonz pers. obs.). An ongoing conservation project by UNE and GEF is designed to help addressing the most

pressing issues related to conservation and resource management. Moreover, the archipelago has been declared as ‘Ecologically or Biologically Significant Marine Area’ (EBSA) at the Conference of Parties of the Convention of Biological Diversity (CBD) in 2016 (CBD web resource). This summary of the current knowledge of the archipelagic fish assemblages provides critical evidence in support of conservation and resource management at large.

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ANNEX 1. Preliminary Checklist of the coastal fishes of the Socotra Archipelago, Yemen.

Preliminary species account, listing positively identified species and their archipelagic distribution records (if known), data on recording methods, total record frequencies of this study and record frequencies during the semi-standardised surveys in 1999-2000 (at 74 fish inventory sites), and mean abundances per 1.25 km³ of 34 transect sites. The species account is arranged in systematic order to the subfamily level and alphabetically at lower levels. Subfamilies are only given, if required to understand the systematic arrangement.

Total no. of species: 682	Cumulative data:	Socotra & Sabuniyah	Darsa & Samha	Abd al-Kuri & Kal Farun	In-situ recs (Archipelago (own in-situ rec))	Sample records	Photo records	Kemp's (1998)	Other records	Record events total (in-situ)	Record events 1999-2000	Abundances (%)	Biogeographic classification	Remarks	
<i>Orectolobiformes</i>															
Rhincodontidae: 1 sp.		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	WW	Various observations, e.g. a stranded young of 6 m in length by EPA team.	
Hemiscylliidae: 1 sp.		0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	NWI_r eg		
<i>Chiloscyllium arabicum</i> Guinanov, 1980		+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +	IWP	As <i>S. varium</i> in Kemp (1998).	
Stegostomatidae: 1 sp.		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	IWP	Observed by EPA team.	
Siegestoma fasciatum (Hermann, 1783)		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	WW	In Saeed (2000).	
Ginglymostomatidae: 1 sp.		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	IWP		
<i>Nebrius ferrugineus</i> (Lesson, 1831)		+	+	+	+	+	+	+	+	+	+	+			
<i>Lamniformes</i>															
Lamnidae: 1 sp.		1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	WW	In Saeed (2000).	
<i>Isurus oxyrinchus</i> Rafinesque, 1810		+	+	+	+	+	+	+	+	+	+	+			
<i>Carcharhiniformes</i>															
Triakidae: 1 sp.		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	WI	Observed by EPA team.	
Mustelidae: 1 sp.		11 1 2 2 2 1 4 3 12 7 5 5 5 5 5	11 1 2 2 2 1 4 3 12 7 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	1 2 2 2 1 4 3 12 7 5 5 5 5 5 5 5	IP		
Carcharhinidae: 13 spp.		+	+	+	+	+	+	+	+	+	+	+			
<i>Carcharhinus albimarginatus</i> (Ruppell, 1837)															

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

Species Summary										Remarks		
Geographic Distribution												
Taxonomic Distribution												
Dasyatinae	Taeniurus meyeni (Müller & Henle, 1841)	+ +	+ +	+ +	+ +	11	10	0.002	IP	In Cheung & DeVantier (2006) as <i>T. melanostictos</i> Bleeker, 1853, a synonym.		
Neotrygoninae	Taeniura lympna (Forsskål, 1775)	+ +	+ +	+ +	+ +			0.000	IWP	Visual observation from Klaus <i>et al.</i> (2002); confirmed by own sightings in 2011-2014, indeed rarely seen.		
Urotrygoninae	Himantura uarnak (Forsskål, 1775)	+ +	+ +	+ +	+ +	1	1	0.000	IWP	As <i>Himantura gerrardi</i> (Gray) in Lavergne <i>et al.</i> (2016); described as a distinct species by Last <i>et al.</i> (2016a).		
Maculabatis ambigua Last, Bogorodsky & Alpermann, 2016	Pateobatis jenkinsii (Annandale, 1909)	+ +	+ +	+ +	+ +	5	5	0.004	IWP	In Kemp (1998), and own visual observation and identification from photograph.		
Hypopholidae	Pastinachus sephen (Forsskål, 1775)	+ +	+ +	+ +	+ +	+	3	2	0.000	IWP		
Gymnuridae: 2 spp.	Gymnura cf. poecilura (Shaw, 1804)	1 0 0 0 0 0 0 0 0 0 0 0				1 1 1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1 1 1	0.000	0.000	Observed by EPA team.		
Gymnura sp. [aff. tentaculata (Müller & Henle, 1841)]	Rhinoptera jayakari Boulenger, 1895	+	+	+	+	+	1	1	0.000	IWP	A second species of the genus observed which best fit would be <i>G. tentaculata</i> .	
Rhinopteridae: 1 sp.	Aetobatus ocellatus (Kuhl, 1823)	+	+	+	+	+	2	2	0.000	IWP	Observed by EPA team.	
Actobatidae: 1 sp.	Myliobatidae: 1 sp.	1 0 0 0 1 1 0 1 1 2 2 2				0.000	0.000	NI-WP	NI-WP	White & Naylor (2016) placed <i>Aetobatus</i> in own family.		
Actobatidae: 1 sp.	Atomyiaetus nichofii (Bloch & Schneider, 1801)	+	+	+	+	+	+	0.000	NI-WP	As <i>A. narinari</i> (Euphrasen) in Zajonz <i>et al.</i> (2000); distribution range is IWP based on the eastern Pacific nominal species is valid.		
										Observed by EPA team.		

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ANNEX 1. (Continued)

Taxonomy of the family following Last <i>et al.</i> (2016c).									
Remarks									
Mobulidae: 3 spp.									
<i>Mobula birostris</i> (Walbaum, 1792)									
<i>Mobula thurstoni</i> (Lloyd, 1908)									
<i>Mobula</i> sp.									
<i>Elopiformes</i>									
Elopidae: 1 sp.									
<i>Elops macchnata</i> (Forsskål, 1775)									
<i>Megalopidae: 1 sp.</i>									
<i>Megalops cyprinoides</i> (Broussonet, 1782)									
<i>Albuliformes</i>									
Albulidae: 1 sp.									
<i>Albulia oligolepis</i> Hidaka, Iwatsuki & Randall, 2008									
<i>Anguilliformes</i>									
Anguillidae: 2 spp.									
<i>Anguilla bicolor</i> McClelland, 1844									
<i>Anguilla marmorata</i> Quoy & Gaimard, 1824									
<i>Muraenidae: 12 spp.</i>									
<i>Echidna nebulosa</i> (Ahl, 1789)									
<i>Enchelycore pardalis</i> (Temminck & Schlegel, 1846)									
<i>Enchelycore schismatophrynchus</i> (Bleeker, 1853)									
<i>Gymnomuraena zebra</i> (Shaw, 1797)									
Abundances (%)	Biogeographic classification								
Record events total (<i>in-situ</i>)	Record events 1999-2000								
Other records	Kemp's (1998)								
Sample records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
<i>Elopiformes</i>	<i>Elopidae: 1 sp.</i>								
<i>Albuliformes</i>	<i>Albulidae: 1 sp.</i>								
<i>Anguilliformes</i>	<i>Anguillidae: 2 spp.</i>								
<i>Muraenidae</i>	<i>Muraenidae: 12 spp.</i>								
Taxonomy of the family following Last <i>et al.</i> (2016c).	Taxonomy of the family following Last <i>et al.</i> (2016c).								
Remarks	Remarks								
Record events total (<i>in-situ</i>)	Record events total (<i>in-situ</i>)								
Other records	Other records								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Socotra & Sabuniyah	Socotra & Sabuniyah								
Darsa & Sabra	Darsa & Sabra								
Abd al-Kuri & Kal Farnun	Abd al-Kuri & Kal Farnun								
Kemp's (1998)	Kemp's (1998)								
Photo records	Photo records								
Visual records	Visual records								
Archipelago (own <i>in-situ</i> rec)	Archipelago (own <i>in-situ</i> rec)								

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ANNEX 1. (Continued)

		Remarks									
		Biogeographic classification									
		Abundances (%)									
Socotra & Sabultiya	<i>Gymnothorax cf. chilospilus</i> Bleeker, 1864	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	Voucher specimen under study, possibly representing an undescribed species.					
	<i>Gymnothorax favagineus</i> Bloch & Schneider, 1801	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	<i>G. tessellata</i> (Richardson) listed in Zajonz <i>et al.</i> (2000) is a synonym.	Tentative visual observation in Zajonz <i>et al.</i> (2000) confirmed by photo of 2011 (courtesy W. Wichmann).				
	<i>Gymnothorax flavimarginatus</i> (Rüppell, 1830)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax flavoculus</i> (Böhlke & Randall, 1996)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax griseus</i> (Lacepède, 1803)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax javanicus</i> (Bleeker, 1859)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax meleagris</i> (Shaw, 1795)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax midwomer</i> (Günther, 1867)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax pictus</i> (Ahl, 1789)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Gymnothorax pseudoherreri</i> Böhlke, 2000	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
Archipelago (own in-situ rec.)	<i>Gymnothorax cf. pseudothyrsoideus</i> (Bleeker, 1853)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	Identification of a specimen from Detwah lagoon confirmed by D.G. Smith (USNM). As <i>G. cf. herrei</i> Beebe & Tee-Van in Zajonz & Khalaif (2002).					
	<i>Gymnothorax richardsonii</i> (Bleeker, 1852)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	The voucher specimen is a juvenile of 24.1 cm; also in Lavergne <i>et al.</i> (2016).					
	<i>Gymnothorax undulatus</i> (Lacepède, 1803)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	In Steindachner (1902), Lavergne <i>et al.</i> (2016).					
	<i>Gymnothorax zonipectis</i> Seale, 1906	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E	Identification based on a photo taken by H. Kovacs/A. Siklosi at Darsa 2005.					
	Oploichthidae: 1 sp.	0 1 1 1 0 0 0 2 2	2 10 2	0.000	IWP						
	<i>Myrichthys maculosus</i> (Cuvier, 1816)	+ + + + + + + + + +	1 25 2 7	0.000 0.007 0.002 0.000	IWP IWP IP NWI_E						
	<i>Clupeiformes</i>	4 0 0 4 0 0 0 2 2	2 10 2	0.000	IWP						
	Clupeidae: 5 spp.	+ + + + + + + + + +	2 10 2	0.000	NWI_E						
	<i>Clupeinae</i>	+ + + + + + + + + +	2 10 2	0.000	NWI_E						
	<i>Herkloisichthys lossei</i> Wongratana, 1983	+ + + + + + + + + +	2 10 2	0.000	NWI_E	As <i>H. cf. lossei</i> in Zajonz <i>et al.</i> (2000), confirmed by Lavergne <i>et al.</i> (2016).					

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ANNEX 1. (Continued)

		Remarks	
		Abundances (%)	Biogeographic classification
<i>Herklotischthys quadrimaculatus</i> (Rüppell, 1837)	+ +	0.000 0.000	IWP NWI reg
<i>Sardinella longiceps</i> Valenciennes, 1847	+ +	1 5	0.000 0.000
Dorosomatinae			
<i>Anodontostoma cf. chacunda</i> (Hamilton, 1822)		1 1	0.000
<i>Nematalosa arabica</i> Regan, 1917		0 0	IWP
Engraulidae: 1 sp.		0 0	
<i>Thryssa baelama</i> (Forsskål, 1775)	+ +	0 0	
Abd al-Kuri & Kal Farun		1 1	
Darsa & Samha		0 0	
Socotra & Sabuniya	+ +	1 1	
Kal Farun		0 0	
Abd al-Kuri &		0 0	
Darsa & Samha		0 0	
Socotra & Sabuniya	+ +	1 1	
Chirocentridae: 1 sp.		0 0	
<i>Chirocentrus dorab</i> (Forsskål, 1775)	+ +	0 0	
Channidae: 1 sp.		0 0	
<i>Chanos chanos</i> (Forsskål, 1775)	+ +	0 0	
Siluriformes			
Clariidae: 1 sp.		0 0	
<i>Netuma</i> sp.		0 0	
Plotosidae: 1 sp.		0 0	
<i>Plotosus lineatus</i> (Thunberg, 1787)	+ +	0 0	
Autopiformes			
Synodontidae: 5 spp.	5 2 2 5 4 3 2 0 1	26 17	0.007
Harpadontinae			

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

	Beryciformes										Remarks									
	Holocentridae: 6 spp.										Biogeographic classification									
Socotra & Sabuniyā	6	5	5	5	5	5	5	5	5	5	116	97	1.310							
Darsa & Samha	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	12	7	0.020	IWP						
Abd al-Kuri & Kal Farum	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	25	20	0.307	IWP						
Myripristinae											16	14	0.236	IWP						
<i>Myripristes murdjani</i> (Forsskål, 1775)											19	18	0.047	WI						
Syngnathiformes	0	1	0	1	0	0	0	0	0	0	1	1	0.001	IP						
<i>Aulostomidae: 1 sp.</i>											1	1	0.001	IP						
<i>Aulostomus chinensis</i> (Linnaeus, 1766)	7	3	4	7	0	7	2	0	1	24	19	0.000								
Syngnathidae: 7 spp.																				
Syngnathinae																				
<i>Choeroichthys brachysoma</i> (Bleeker, 1855)	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	7	6	0.000	IWP						
<i>Coryeoichthys benedetto</i> Allen & Erdmann, 2008	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	1	0.000	0.000	NI-WP						
<i>Coryeoichthys</i> sp.	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	3	3	0.000							

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

³ DiBattista *et al.* (2015a) reported the following additional hybrid from Socotra after the present account and related statistics had been completed: *Cirripectes callinus* × *oxycephalus*.

ANNEX 1. (Continued)

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ANNEX 1. (Continued)

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							Remarks
<i>Cheilodipterus macrodon</i> (Lacepède, 1802)							
<i>Cheilodipterus novemstriatus</i> (Rüppell, 1838)							
<i>Cheilodipterus persicus</i> Gon, 1993							
<i>Cheilodipterus quinquefasciatus</i> Cuvier, 1828							
<i>Fowleria vanidae</i> (Jordan & Seale 1906)							
<i>Jaydia quecketti</i> (Gilchrist, 1903)							
<i>Lepidamia multitaeniatus</i> (Cuvier, 1828)							
<i>Ostorhinchus aureus</i> (Lacepède, 1802)							
<i>Ostorhinchus cookii</i> (Macleay, 1881)							
<i>Ostorhinchus cyanosoma</i> (Bleeker, 1853)							
<i>Ostorhinchus fleuri</i> Lacepède, 1802							
<i>Ostorhinchus holotaenia</i> (Regan, 1905)							
<i>Pristiopogon fraenatus</i> (Valenciennes, 1832)							
<i>Pristiopogon kallopterus</i> (Bleeker, 1856)							
<i>Siphonia tubifer</i> Weber, 1909							
<i>Taeniaria fucata</i> (Cantor, 1849)							
<i>Venularia cypselurus</i> (Weber, 1909)							
Sillaginidae: 1 sp.	1	0	1	1	0	0	10
<i>Sillago</i> cf. <i>sithama</i> (Forsskål, 1775)	+		+	+	+	+	10
Malacanthidae: 1 sp.	1	0	0	1	0	0	5
<i>Malacanthus latovittatus</i> (Lacepède, 1801)	+		+	+	+	+	5
Pomatomidae: 1 sp.	1	0	0	1	1	0	1
Abundances (%)	24	21	0.087	IWP	NWI_r eg	NWI_r eg	
Record events total (in-situ)					0.000	0.000	
Recorded events 1999-2000					1	1	
Biogeographic classification							

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

		Remarks	
	Biogeographic classification	Abundances (%)	
Record events total (in-situ) 1999-2000		2 2 2 0.000 CT	In Mohsen (2002), sampling desired. Observed by EPA team, sampling desired.
Record events total 1999-2000		0.000 CT 0.000 pl 0.000 IWP	In Mohsen (2002), sampling desired. Observed by EPA team, sampling desired.
Kemp's (1998)	Photo records	2 2 2 0.000 IWP	In Lavergne <i>et al.</i> (2016).
Other records	Sample records	1 2 2 0.000 IWP	In Lavergne <i>et al.</i> (2016).
Archipelago (own in-situ rec)	Visual records	0 6 4 0.000 IWP	In Mohsen (2002); species not reported from NWI according to FishBase 2017, but listed so by Debelius (1998).
Darsa & Samha Abd el-Kuri & Kai Farm	Abd el-Kuri & Kai Farm	2 1 2 0.000 IWP	Species not reported from NWI according to FishBase 2017.
Socotra & Sabuniyah	2 0 0 0.000 IP	0 6 2 0.000 IWP	Also observed by EPA team; species not reported from NWI according to FishBase 2017, but listed so by Debelius (1998).
Leiognathidae: 2 spp.	<i>Aurigequula fasciata</i> (Lacepède, 1803)	+	0 0 0 0.000 IWP
	<i>Leiognathus equulus</i> (Forsskål, 1775)	+	0 0 0 0.000 IWP
Lutjanidae: 23 spp.	<i>Etelinae</i>	+	0 0 0 0.000 IWP
	<i>Aphareus furca</i> (Lacepède, 1801)	+	0 0 0 0.000 IWP
	<i>Aphareus rutilans</i> Cuvier, 1830	+	0 0 0 0.000 IWP
	<i>Apriion virescens</i> Valenciennes, 1830	+	0 0 0 0.000 IWP
	<i>Pristipomoides cf. filamentosus</i> (Valenciennes 1830)	+	0 0 0 0.000 IWP
	<i>Lutjaninae</i>	+	0 0 0 0.000 IWP
	<i>Lutjanus argentimaculatus</i> (Forsskål, 1775)	+	0 0 0 0.000 IWP
	<i>Lutjanus bohar</i> (Forsskål, 1775)	+	0 0 0 0.000 IWP
	<i>Lutjanus coeruleolineatus</i> (Rüppell, 1838)	+	0 0 0 0.000 IWP
	<i>Lutjanus ehrenbergii</i> (Peters, 1869)	+	0 0 0 0.000 IWP
	<i>Lutjanus fuliflamma</i> (Forsskål, 1775)	+	0 0 0 0.000 IWP

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

							Remarks
<i>Diagramma punctatum</i> Cuvier, 1830							
<i>Plectorhinchus cf. chubbi</i> (Regan, 1919)							
<i>Plectorhinchus flavomaculatus</i> (Cuvier, 1830)							
<i>Plectorhinchus gaterinus</i> (Forsskål, 1775)							
<i>Plectorhinchus gibbosus</i> (Lacepède, 1802)							
<i>Plectorhinchus pictus</i> (Tortonese, 1936)							
<i>Plectorhinchus pictus</i> (Cuvier, 1830)							
<i>Plectorhinchus playfairi</i> (Pellegrin, 1914)							
<i>Plectorhinchus scholae</i> (Forsskål, 1775)							
<i>Plectorhinchus sordidus</i> (Klunzinger, 1870)							
Sparidae: 7 spp.							
<i>Acanthopagrus benda</i> (Forsskål, 1775)							
<i>Acanthopagrus bifasciatus</i> (Forsskål, 1775)							
<i>Acanthopagrus catenula</i> (Lacepède, 1801)							
<i>Argyrops cf. spinifer</i> (Forsskål, 1775)							
<i>Crenidens crenidens</i> (Forsskål, 1775)							
<i>Diagramma labiosum</i> Macleay, 1883 is a synonym of <i>D. pictum</i> in Zajonz et al. (2000), more likely it is the Red Sea subspecies representing an eastward out-of-endemic-range extension.							
<i>Record events total (in-situ)</i>		3	3	0.000	NWI_e-RSGA		
<i>Record events total (1999-2000)</i>	1	1	0.000	pI			
Abundance (%)							
Biogeographic classification							

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										Remarks	
										Biogeographic classification	
										Abundances (%)	
<i>Diplodus cf. kotschyii</i> (Steindachner, 1876)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Pageodus affinis</i> Boulenger, 1888	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
Lethrinidae: 11 spp.											
<i>Lethrininae</i>											
<i>Lethrinus borbonicus</i> Valenciennes, 1830	+ 11	7	7	11	11	5	7	5	6	1	0.606 NWI _r eg NWI _r eg
<i>Lethrinus harak</i> (Forsskål, 1775)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus lentjan</i> (Lacepède, 1802)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus mahsena</i> (Forsskål, 1775)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus microdon</i> Valenciennes, 1830	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus nebulosus</i> (Forsskål, 1775)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus obsoletus</i> (Forsskål, 1775)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus cf. olivaceus</i> Valenciennes, 1830	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Lethrinus variegatus</i> Valenciennes, 1830	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Monotaxinae</i>											
<i>Gymnocephalus grandoculis</i> (Valenciennes, 1830)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
<i>Monotaxis grandoculis</i> (Forsskål, 1775)	+ 11	7	7	11	11	5	7	5	6	1	0.000 NWI _r eg NWI _r eg
Nemipteridae: 5 spp.											
<i>Nemipterus japonicus</i> (Bloch, 1791)	+ 5	1	1	4	4	1	2	0	3	44	0.119 IWP
<i>Scolopsis bimaculatus</i> Rüppell, 1828	+ 5	1	1	4	4	1	2	0	3	37	0.000 pl
<i>Scolopsis ghanam</i> (Forsskål, 1775)	+ 5	1	1	4	4	1	2	0	3	37	0.115 pl
<i>Scolopsis taeniatus</i> Cuvier, 1830	+ 5	1	1	4	4	1	2	0	3	3	0.003 NWI _r eg IWP
<i>Scolopsis vosmeri</i> (Bloch, 1792)	+ 5	1	1	4	4	1	2	0	3	2	0.000 NWI _r eg IWP
										Also observed by EPA team.	
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ANNEX 1.(Continued)

Biology and Distribution												Remarks	
Taxonomy and Systematics													
Mullidae: 12 spp.	11	10	9	11	11	3	11	8	4	283	235	2,124	0.000 pI
<i>Mulloidichthys cyathifer</i> Uiblein, 2011	+												
<i>Mulloidichthys flavolineatus</i> (Lacepède, 1801) [<i>M. flavolineatus flavicandus</i> Fernandez-Silva & Randall, 2016]	+ +	+ +								6	6	0.192 IWP	P. <i>vanicola</i> nsis by Zajonz & Khalaf (2002), and Zajonz et al. (2000).
<i>Mulloidichthys vanicolensis</i> (Valenciennes, 1831)	+ +	+ +								19	15	1,240 IWP	The yellow-tailed subspecies was recently identified by Fernandez-Silva et al. (2016) based on a photo from Socorro; whether all <i>M. flavolineatus</i> from the archipelago belong to this subspecies requires confirmation.
<i>Parupeneus barberinus</i> (Lacepède, 1801)	+ +	+ +								33	30	0.033 IWP	In the Red Sea <i>P. barberinus</i> is replaced by <i>P. forsskali</i> ; Kemp (1998) already reported both species, and so do we.
<i>Parupeneus cyclostomus</i> (Lacepède, 1801)	+ +	+ +								34	24	0.050 IWP	See remark on <i>P. barberinus</i> .
<i>Parupeneus forsskali</i> (Fourmanoir & Guèze, 1976)	+ +	+ +								29	23	0.089 NWI_e-RSGA	
<i>Parupeneus indicus</i> (Shaw, 1803)	+ +	+ +								9	9	0.009 IWP	
<i>Parupeneus macronemus</i> (Lacepède, 1801)	+ +	+ +								75	61	0.289 pI	
<i>Parupeneus pleurostigma</i> (Bennett, 1831)	+ +	+ +								7	7	0.006 IWP	
<i>Parupeneus rubescens</i> (Lacepède, 1801)	+ +	+ +								21	20	0.081 WI	
<i>Parupeneus trifasciatus</i> (Lacepède, 1801)	+ +	+ +								46	36	0.128 pI	As <i>P. bifasciatus</i> (Lacepède) in Zajonz et al. (2000); a synonym (Randall & Myers 2002).
<i>Upeneus heemstra</i> Uiblein & Gouws, 2014	+ +	+ +								4	4	0.008 pI	As <i>U. trigula</i> Richardson in Zajonz et al. (2000).
Pempheridae: 4 spp.	3	2	3	3	3	2	2	2	0	27	25	1,324	NWI_r eg
<i>Parapriacanthus guentheri</i> (Klunzinger, 1871)	+ +	+ +								13	12	1,177	As <i>P. ransonnetii</i> Steindachner in Zajonz et al. (2000); synonymy adopted from Randall & Bogorodsky (2016).
<i>Pempheris flavicyclia marisnubri</i> Randall, Bogorodsky & Alpermann, 2013	+ +	+ +								4	3	0.013 pI	As <i>P. vanicolensis</i> Cuvier in Zajonz et al. (2000), re-identified following Randall et al. (2013a).

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ANNEX 1. (Continued)

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² DiBattista *et al.* (2015a) reported the following two additional hybrids from Socotra after the present account and related statistics had been completed: *Chaetodon gordoni* x *teucolepis*, and *Chaetodon melapterus* x *trifasciatus*.

ANNEX 1. (Continued)

Remarks									
Biogeographic classification									
Abundances (%)									
Record events total (in-situ) 1999-2000	0.000	NWI_e -RSGA	Depicted in Cheung & DeVantier (2006), yet photograph of the species perhaps taken in the Red Sea.						
Record events total (in-situ) 1999-2000	0.000	NWI_r eg WI	As <i>C. unimaculatus</i> Bloch in Zajonz <i>et al.</i> (2000).						
Other records	12	10	0.019	NI					
Kemp's (1998)	7	5	0.007	pI					
Photo records	2	2	0.000	pI					
Sample records	21	18	0.014	IWP					
Visual records	14	12	0.018						
In-situ recs)	2	1	0.000	IWP					
Archipelago (own in-situ rec)	31	26	0.047	IWP					
Darsa & Sabunya	5	4	0.005	IWP					
Socotra & Sabunya	61	49	0.618	NWI_r eg NWI_e -RSGA					
Abd al-Kuri & Khal Furun	1	1	0.004						
Chaetodon fasciatus Forsskål, 1775	+ + + + +	+ + + + +	+ + + + +						
Chaetodon gardineri Norman, 1939	+ + + + +	+ + + + +	+ + + + +						
Chaetodon guttatusimus Bennett, 1833	+ + + + +	+ + + + +	+ + + + +						
Chaetodon interruptus Ahl, 1923	+ + + + +	+ + + + +	+ + + + +						
Chaetodon kleinii Bloch, 1790	+ + + + +	+ + + + +	+ + + + +						
Chaetodon larvatus Cuvier, 1831	+ + + + +	+ + + + +	+ + + + +						
Chaetodon leucopleura Playfair, 1867	+ + + + +	+ + + + +	+ + + + +						
Chaetodon lineolatus Cuvier, 1831	+ + + + +	+ + + + +	+ + + + +						
Chaetodon lunula (Lacepède, 1802)	+ + + + +	+ + + + +	+ + + + +						
Chaetodon melanotus Bloch & Schneider, 1801	+ + + + +	+ + + + +	+ + + + +						
Chaetodon melapterus Guichenot, 1863	+ + + + +	+ + + + +	+ + + + +						
Chaetodon cf. mesoleucus Forskål, 1775	+ + + + +	+ + + + +	+ + + + +						
Chaetodon meyeri Bloch & Schneider, 1801	+ + + + +	+ + + + +	+ + + + +						
Chaetodon pictus Forskål, 1775	+ + + + +	+ + + + +	+ + + + +						
Chaetodon semilarvatus Cuvier, 1831	+ + + + +	+ + + + +	+ + + + +						
Chaetodon trifascialis Quoy & Gaimard, 1825	+ + + + +	+ + + + +	+ + + + +						
Chaetodon trifasciatus Park, 1797	+ + + + +	+ + + + +	+ + + + +						
Chaetodon zanzibarensis Playfair, 1867	+ + + + +	+ + + + +	+ + + + +						
Chaetodon collaris x lunula [hybrid]	+ + + + +	+ + + + +	+ + + + +						
Forcipiger flavissimus Jordan & McGregor, 1898	+ + + + +	+ + + + +	+ + + + +						

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ANNEX 1. (Continued)

		Remarks	
		Biogeographic classification	
		Abundances (%)	
<i>Forcipiger longirostris</i> (Broussonet, 1782)		5	3
<i>Hemitaurichthys zoster</i> (Bennett, 1831)		4	3
<i>Heniochus acuminatus</i> (Linnaeus, 1758)		51	44
<i>Heniochus diphreutes</i> Jordan, 1903		2	2
<i>Roa jayakari</i> (Norman, 1939)			0.000 NWI_F eg
Pomacanthidae: 9 spp.			
<i>Apolemichthys xanthotis</i> (Fraser-Brunner, 1950)	+ + + + +	+ + + + +	47 37 0.089 NWI_F eg
<i>Centropyge acanthops</i> (Norman, 1922)	+ + + + +	+ + + + +	3 3 0.001 WI
<i>Centropyge multispinis</i> (Playfair, 1867)	+ + + + +	+ + + + +	56 42 0.247 pl
<i>Pomacanthus asfur</i> (Forsskål 1775)			0.000 WI
<i>Pomacanthus imperator</i> (Bloch, 1787)	+ + + + +	+ + + + +	64 51 0.067 IWP
<i>Pomacanthus maculosus</i> (Forsskål, 1775)	+ + + + +	+ + + + +	11 11 0.001 WI
<i>Pomacanthus semicirculatus</i> (Cuvier, 1831)	+ + + + +	+ + + + +	26 21 0.021 IWP
<i>Pomacanthus asfur</i> x <i>maculosus</i> [hybrid]			0.000 NWI_S AHZ
<i>Pomacanthus semicirculatus</i> x <i>maculosus</i> [hybrid]	+ +	+ +	1 1 0.002 NWI_S AHZ
			Identification based on photos taken by M. Martin at Socota in 2013 (Zajonz et al. in prep.); inclusion of hybrids justified in the paper's text. From adjacent Yemen mainland by Kemp (2000 b); and in Zajonz et al. (in prep.).

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ANNEX 1. (Continued)

		Recorded events total (<i>in-situ</i>)						Record events total (<i>in-situ</i>)						Abundances (%)						Biogeographic classification						Remarks					
Pomacentridae: 41 spp.³		33	19	28	38	38	22	24	16	2	696	553	53,560																		
<i>Amphiprioninae</i>																															
<i>Amphiprion akallopisos</i> Bleeker, 1853																															
<i>Amphiprion bicinctus</i> Rüppell, 1830																															
<i>Amphiprion cf. chagosensis</i> Allen, 1972																															
<i>Amphiprion omanensis</i> Allen & Mee, 1991																															
<i>Chrominae</i>																															
<i>Chromis cf. acares</i> Randall & Sewardloff, 1973																															
<i>Chromis fieldi</i> Randall & DiBattista, 2013																															
<i>Chromis flavavilla</i> Randall, 1994																															
<i>Chromis cf. nigrura</i> Smith, 1960																															
Socotra & Sabunuya	Darsa & Samha	+																													
	Abd al-Kuri & Kal Farun																														
Kemps' (1998)	Photo records																														
Other records	Sample records																														
	Visual records																														
	Archipelago (own <i>in-situ</i> rec.)																														
	Records total 1999-2000	33	19	28	38	38	22	24	16	2	696	553	53,560																		
	Biogeographic classification																														
	Abundances (%)																														
	Remarks																														

³ DiBattista *et al.* (2015a) reported the following additional hybrid from Socotra after the present account and related statistics had been completed: *Amphiprion bicinctus* × *omanensis*.

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

		Remarks
	Abundances (%)	Biogeographic classification
<i>Cheilinae</i>		
<i>Cheilio inermis</i> (Forskål, 1775)		IWP
<i>Cheilininae</i>		
<i>Cheilinus cf. fasciatus</i> (Bloch, 1791)	7 6 0.014	IWP
		<i>C. quinquecinctus</i> Rüppell, 1835 was redescribed by Bogodotsky <i>et al.</i> (2016), the record should subsequently be compared to this species.
<i>Cheilinus lunulatus</i> (Forsskål, 1775)	7 6 0.009	IWP
<i>Cheilinus oxycephalus</i> Bleeker, 1853		
<i>Cheilinus trilobatus</i> Lacepède, 1801		
<i>Cheilinus undulatus</i> Rüppell, 1835		
<i>Cirrhitabrus cf. cyanopleura</i> (Bleeker, 1851)		
<i>Cirrhitabrus exquisitus</i> Smith, 1957	11 10 0.026	IWP
<i>Cirrhitabrus rubriventralis</i> Springer & Randall, 1974	6 4 0.002	NWL_r eg
<i>Epibulus insidiator</i> (Pallas, 1770)		
<i>Oxycheilinus bimaculatus</i> (Valenciennes, 1840)		
<i>Oxycheilinus digramma</i> (Lacepède, 1801)		
<i>Oxycheilinus cf. mentalis</i> (Rüppell, 1828)		
<i>Paracheilinus octotaenia</i> Fourmanoir, 1955	2 2 0.001	IWP
<i>Pseudocheilinus evanidus</i> Jordan & Evermann, 1903	3 3 0.000	NWL_e -RSGA NWL_e -RSGA IWP
		Visual identification, confirmation by sampling desired; a Red sea endemic.

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Biogeographic classification										Remarks		
Abundances (%)												
Scotra & Sabunuya	Darsa & Samha	Abd al-Kuri & Kal Farun	Archipelago (own in-situ rec)	Sample records	Photo records	Kemp's (1998)	Record events total (in-situ)	Record events 1999-2000	Biogeographic classification			
Scarus niger Forsskål, 1775	+ +	+ +	+ + +	+ + +	+ + +	+ + +	13	8	0.007 pl			
Scarus cf. persicus Randall & Bruce, 1983	+ +	+ +	+ + +	+ + +	+ + +	+ + +	36	27	0.083 IWP			
Scarus psittacus Forsskål, 1775	+ +	+ +	+ + +	+ + +	+ + +	+ + +	1	0.000 NWI_r eg	Observed by Aideed; sampling desired.			
Scarus rubroviolaceus Bleeker, 1847	+ +	+ +	+ + +	+ + +	+ + +	+ + +	4	3	0.176 IWP			
Scarus cf. scaber Valenciennes, 1840	+ +	+ +	+ + +	+ + +	+ + +	+ + +	22	17	0.042 IP			
Scarus cf. tricolor Bleeker, 1847	+ +	+ +	+ + +	+ + +	+ + +	+ + +	1	1	0.001 pl	Observation by M. Martin (pers. comm.); sampling desired.		
Sparisomatinae										Only observed once at Abd al-Kuri, as with several other "East African" species which northernmost ranges extend to it, but not further to the other islands.		
Calotomus carolinus (Valenciennes, 1840)	+ 3	+ 2	+ 3	+ 3	+ 1	+ 3	0	0	36 28	0.024 IWP		
Pinguiipedidae: 3 spp.	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	26 7	0.021 IWP		
Parapercis hexophtalma (Cuvier, 1829)	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	7 3	0.002 WI		
Parapercis punctata (Cuvier, 1829)	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	3	0.000 WI		
Parapercis robinsoni Fowler, 1929	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +			Reliable photo record closing the distribution gap between Arabian Sea and Somalia (Randall & Stroud 1985).	
Tripterygiidae: 5 spp.	3 0	4 0	5 1	5 0	0 0	0 0	11	9	0.000	Family needs further study		
Eneapterygius abelii (Klausewitz, 1960)	+ +	+ +	+ +	+ +	+ +	+ +	2	2	0.000 WI	Identified by M. Meguro (unpubl.).		
Eneapterygius pusillus Rüppell, 1835	+ +	+ +	+ +	+ +	+ +	+ +	1	1	0.000 WI	Identified by M. Meguro (unpubl.).		
Eneapterygius sp.	+ +	+ +	+ +	+ +	+ +	+ +	1	1	0.000 NWI_r eg	Voucher specimen under study.		
Helcogramma cf. obusirostris (Klunzinger, 1871)	+ +	+ +	+ +	+ +	+ +	+ +	3	2	0.000 NWI_r eg			
Helcogramma steinitzi Clark, 1980	+ +	+ +	+ +	+ +	+ +	+ +	4	3	0.000 NWI_r eg			

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ANNEX 1. (Continued)

CULTURE AND CIVILISATION

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5 Di Battista *et al.* (2015) reported the following additional hybrid from Socotra after the present account and related statistics had been completed: *Acanthurus lineatus* × *sodalineatus*.

ANNEX 1. (Continued)

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ANNEX 1. (Continued)

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ANNEX 1. (Continued)

	Socotra & Sabuniyah										Biogeographic classification										Remarks	
	Record events total (in-situ)										Abundances (%)											
Monacanthidae: 5 spp.	3	4	4	4	4	1	4	1	2	28	19	0.022	CT	0.002	IP							
<i>Aluterus scriptus</i> (Osbeck, 1765)	+	+	+	+	+	+	+	+	+	4	3	0.001	IP									
<i>Cantherhines dumerilii</i> (Hollard, 1854)	+	+	+	+	+	+	+	+	+	7	1	0.019	IWP									
<i>Cantherhines pardalis</i> (Rüppell, 1837)	+	+	+	+	+	+	+	+	+	16	15	0.000	IWP									
<i>Pardularius priornurus</i> (Bleeker, 1851)	+	+	+	+	+	+	+	+	+	1	0.000	NI-WP										
<i>Thamnaconus striatus</i> (Koottanus, 1979)	+	+	+	+	+	+	+	+	+	0.000												
Ostraciidae: 2 spp.	2	1	2	2	2	0	2	2	0	29	20	0.007	IWP									
<i>Ostracion cubicus</i> Linnaeus, 1758	+	+	+	+	+	+	+	+	+	27	19	0.007	IWP									
<i>Ostracion cyanurus</i> Rüppell, 1828	+	+	+	+	+	+	+	+	+	2	1	0.000	NWI_r									
Tetraodontidae: 10 spp.	10	3	4	8	6	4	5	6	2	116	87	0.187	eg									
<i>Arothron hispidus</i> (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+	1	1	0.000	IP									
<i>Arothron meleagris</i> (Anonymous, 1798)	+	+	+	+	+	+	+	+	+	18	13	0.025	IP									
<i>Arothron nigropunctatus</i> (Bloch & Schneider, 1801)	+	+	+	+	+	+	+	+	+	1	1	0.000	IWP									
<i>Arothron stellatus</i> (Anonymous, 1798)	+	+	+	+	+	+	+	+	+	2	2	0.000	IWP									
<i>Lagocephalus lunaris</i> (Bloch & Schneider, 1801)	+	+	+	+	+	+	+	+	+	+	+	0.000	IWP									
<i>Lagocephalus sceleratus</i> (Gmelin, 1789)	+	+	+	+	+	+	+	+	+	1	1	0.000	IWP									
<i>Torquigenes</i> sp.	+	+	+	+	+	+	+	+	+	3	3	0.016	pI									
<i>Canthigaster cyanospilota</i>	+	+	+	+	+	+	+	+	+													
Randall, Williams & Rocha, 2008																						
Zajonz et al. (2000).																						
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Data Summary: Observations and Record Events										Remarks							
Species		Geographic Range		Record Events		Abundance (%)		Biogeographic Classification									
<i>Canthigaster petersii</i> (Bianconi, 1854)																	
<i>Canthigaster valentini</i> (Bleeker, 1833)																	
Diodontidae: 5 spp.																	
<i>Cyclichthys orbicularis</i> (Bloch, 1785)																	
<i>Cyclichthys spilostylus</i> (Leis & Randall, 1982)																	
<i>Diodon holocanthus</i> Linnaeus, 1758																	
<i>Diodon hystrix</i> Linnaeus, 1758																	
<i>Diodon liturosus</i> Shaw, 1804																	
Moridae: 1 sp.																	
<i>Mola alexandrinii</i> (Ranzani, 1839)																	
Cumulative statistical data⁷										Observed by EPA team; formerly known as <i>Mola mola</i> (Linnaeus) until redescribed by Sawai <i>et al.</i> (2017).							
Preliminary Species Account:	682	549	273	348	561	464	280	368	208	213	6631	5136	95.706	654	*		
Working List:	51	33	12	19	39	31	17	10	4	6	154	129	1.27	See Annex 2.			
ODUs	733	582	285	367	600	495	297	378	212	219	6785	5265	96.976	See Materials and Methods.			
Subtotal:																	
Discarded:	66	46	11	34	64	29	47	5	3	9	181	140	3.03				
obs..	Total:	628	296	401	664	524	344	383	215	219	6966	5405	100.0				
“obs.”																	
Mean abundances: 1,228.3/1.25 km³																	

⁷ Five additional putative fish hybrids are not included because by the time they were reported by DiBattista *et al.* (2015a) work on the account and statistical analyses had been completed; see preceding footnotes)

ANNEX 2. Working List of additional Operational Diversity Units

Preliminary list of ODUs (compare Materials and Methods) pertinent to Annex 1, listing their archipelagic distribution records (if known), data on recording methods, total record frequencies of this study and record frequencies during the semi-standardised surveys in 1999–2000 (at 74 fish inventory sites), and mean abundances per 1.25 km² of 34 transect sites. Species are arranged in the same systematic order as Annex 1 and alphabetically within the genera.

	Total no. of species: 51	Cumulative data:	33	12	19	39	31	17	10	4	6	154	129	1.27	Remarks
<i>Sphyraena</i> sp.														0.000	A second congener expected, also reported by Kemp (1998). Expected to occur but yet to be confirmed.
<i>Mobula alfredi</i> (Krefft, 1868)														0.000	A large colony observed by drop camera tows during ground-truthing surveys at Socotra Island; sampling required.
Heterocongrinae gen. sp.														0.000	Species similar to <i>G. punctatus</i> Bloch & Schneider and <i>G. moluccensis</i> (Bleeker), further study required.
<i>Gymnothorax sokotrensis</i> Kottthaus, 1968														0.000	Two putative species with voucher specimens, under study.
Ophichthidae gen. sp. 1–2														0.000	Listed in Zajonz <i>et al.</i> (2002) as <i>T. setirostris</i> (Broussonet) based on ZMH 10670 (5 spcmcs.) of Taschenberg (1883, based on Schweinfurth and Riebeck material of 1881); identity as distinct species needs to be confirmed.
<i>Thryssa</i> cf. <i>setirostris</i> (Broussonet, 1782)														0.000	Keys out close to <i>O. cummiesius</i> ; re-sampling required; not identical with preceding <i>O. cf. cummiesius</i> .
<i>Osteomugil</i> sp. 1 [aff. <i>cummiesius</i> (Val.)]														0.000	Additional scorpaenids which do not belong to any of the recorded species require further research.
Scorpaenidae gen. spp.														0.000	Family needs further study; dedicated sampling and study required.
Platycephalidae gen. spp.														0.000	A deep dwelling species, to be confirmed in coastal waters.
<i>Plectranthias intermedius</i> (Kottthaus, 1973)														0.000	

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ANNEX 2. (Continued)

							Remarks
<i>Pseudanthias</i> sp.							Field drawing available, orange-red with two horizontal golden stripes on body sides, occurred concurrently with <i>P. cooperi</i> ; sampling required.
<i>Apogon</i> sp. [aff. <i>doederleinii</i>]							Listed as <i>Apogon</i> sp. 2 by Zajonz & Khalaf (2002), tentative, to be compared against <i>O. holotaenia</i> .
<i>Ostorhinchus</i> sp. [aff. <i>properius</i> -complex]							Listed as <i>Apogon</i> sp. 10 by Zajonz <i>et al.</i> (2000), tentative, to be compared against <i>O. cyanosoma</i> .
Apogonidae spp.							Several additional species do occur, family needs further study; dedicated sampling and study required.
<i>Lutjanus</i> cf. <i>vitta</i> (Quoy & Gaimard, 1824)							Observed by EPA team, tentative, potentially confused with <i>L. lutjanus</i> .
<i>Lethrinus</i> sp.							Unidentified species; sampling required.
Nemipteridae gen. sp.							Unidentified species, possibly <i>Parasclopsis eriomma</i> Jordan & Richardson.
<i>Amphiprion</i> sp. x sp.							Not identical with any of the other <i>Amphiprion</i> , putatively a hybrid of <i>A. bicinctus</i> with either <i>A. chagosensis</i> or <i>omanensis</i> (Zajonz <i>et al.</i> in prep.); compare DiBattista <i>et al.</i> (2015a).
<i>Chrysiptera</i> cf. <i>springeri</i> (Allen & Lubbock, 1976)?							Repeated sightings of an entirely bluish damself are tentatively referred to this species, sampling required.
<i>Plectroglyphidodon</i> sp. 1 [aff. <i>lacrymatus</i>]							A species related morphologically to <i>P. lacrymatus</i> , sampling required.
<i>Pomacentrus</i> cf. <i>philippinus</i> Evermann & Seale, 1907							Tentative, a species resembling <i>P. caeruleus</i> ; sampling required.
<i>Pomacentrus</i> sp. 1 [aff. <i>coelestis</i> Jordan & Starks, 1901]							Another species resembling <i>P. caeruleus</i> observed several times in different years, field drawing available, sampling required.

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ANNEX 2. (Continued)

Remarks									
<i>Cheilinus cf. chlorourus</i> (Bloch, 1791)									
<i>Cirrhilabrus</i> sp. 1									
<i>Cirrhilabrus</i> sp. 2									
<i>Oxycheilinus</i> sp.									
<i>Anampses</i> cf. <i>melanurus</i> Bleeker, 1857									
<i>Gomphosus</i> cf. <i>varius</i> Lacepède, 1801									
<i>Halichoeres</i> sp. 1 [aff. <i>lapillus</i> Smith, 1947]									
Labridae gen. sp. 1									
Labridae gen. sp. 2									
Labridae gen. sp. 3									
Labridae gen. sp. 4 [aff. <i>Pseudojuloides atavai</i> Randall & Randall, 1981]									
Labridae gen. sp. 5 [aff. <i>Sethojulis</i>]									
Biogeographic classification	0.000								
Abundances (%)									
Record events total (in-situ)		2	2	0.000					
Record events total 1999-2000		1	1	0.002					
Other records		5	5	0.002					
Kemp's (1998)									
Photo records									
Sample records									
Visual records									
Archipelago (own in-situ rec)									
Abd al-Kuri & Kaf Farun									
Darsa & Samha									
Socotra & Sabuniya									
Kal Kuri & Khal Farn									
Archipelago (own in-situ rec)									
Other records									
Record as species close to <i>H. nebulosus</i> , however not been reported from the WIO and Arabian region; potentially a hybrid of <i>A. lineatus</i> × <i>A. meleagrides</i> ; sampling required.									
Recorded as species close to <i>H. nebulosus</i> , sampling required.									
Unidentified wrasse close to <i>Cheilinus</i> or <i>Oxycheilinus</i> ; sampling required.									
Unidentified wrasse close to <i>Cirrhilabrus</i> , two yellow stripes; sampling required.									
Unidentified species with <i>Halichoeres</i> habitus, anterior half of body dark-orange, posterior part bluish; sampling required.									
Visually the species resembles <i>Pseudojuloides</i> <i>atavai</i> ; sampling required.									
Unidentified wrasse tentatively referred to <i>Sethojulis</i> ; sampling required.									

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ANNEX 2. (Continued)

										Remarks
										Biogeographic classification
										Abundances (%)
Labridae gen. sp. 6 [aff. <i>Suezichthys</i>]										Unidentified wrasse tentatively referred to <i>Suezichthys</i> ; perhaps identical with record of <i>S. cf. caudavittatus</i> (see before). Tentative, sampling required.
<i>Scarus cf. falcipinnis</i> (Playfair, 1867)										Identified by M. Meguro (unpubl); re-examination required as thus far considered endemic to the Red Sea.
<i>Enneapterygius pallidus</i> Clark, 1980										Several additional species in this genus present, more study needed.
<i>Enneapterygius</i> spp.										Several additional species in this genus present, more study needed.
<i>Helcogramma</i> spp.										Sampling desired.
<i>Meiacanthus</i> sp.										Tentatively included, potentially occurs and misidentified occasionally as <i>C. castaneus</i> ; sampling required.
<i>Cirripectes</i> cf. <i>filamentosus</i> (Alleyne & Macleay, 1877)										Numerous visual records referred to a species related to <i>E. pulcher</i> ; possibly referable to one of the new species within the <i>pulcher</i> -complex, study needed.
<i>Ecsenius</i> sp.										In Steindachner (1902), voucher to be studied; species not yet considered to occur outside the Red Sea in literature.
<i>Istiblennius</i> cf. <i>unicolor</i> (Rüppell, 1838)										Several yet unidentified species occur, family needs further study.
<i>Blenniidae</i> gen. spp.										Voucher specimen under study.
<i>Bathygobius</i> sp.										Additional species in <i>Fusigobius</i> [Indo-Pacific <i>Coryphopterus</i> sensu H. Larson] observed, e.g., putatively <i>F. neophytus</i> (Günther); sampling and study required.
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ANNEX 2. (Continued)