Deep Sea Chondrichthyes from Madeira and Nearby Seamounts (NE Atlantic)

DOCTORAL THESIS

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DOCTORATE IN BIOLOGICAL SCIENCES

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Abstract

Chondrichthyes play a key role in the ecological balance of the ecosystems as predatory species. However, more than one-third of these species are threatened by overfishing. The lack of information on chondrichthyan species in the archipelago of Madeira led to this study, which intended to provide reliable information on their taxonomy, biology, population dynamics and fisheries. An updated checklist of cartilaginous fishes, new records, taxonomic annotations, and clarification as well filling the gaps on life history of several species were accomplished during this thesis. The checklist confirmed the presence of 67 species of sharks, rays, and chimaeras. Another 14 species previously referred for the area are now considered dubious records, and 5 species are withdrawn from the list. *Centrophorus uyato* is here recorded for the first time from Madeira. Of the species reported 24 are in the list of threatened species according to the IUCN European Red List of marine fishes. *Hydrolagus affinis* and *Chimaera opalescens* are also first recorded for the Madeira region, and their known range of distribution are extended. The clarification and resolution of uncertainties over the identification of *Deania calcea* and *Deania hystricosa* were accomplished through morphological and molecular studies, that confirm that both are the same species. The knowledge of fish diversity of several seamounts belonging to Madeira-Tore complex at different depth strata down to 2500 m was increased, bridging the information gap regarding seamount associated elasmobranchs. The checklist of cartilaginous fish species for Seine and Unicorn seamounts confirmed the presence of 17 species in Seine and 11 in Unicorn, corresponding to about 31% of the valid Chondrichthyes reported for the archipelago of Madeira. The work herein presented contributed to increase the knowledge of fish communities, diversity, and occurrence of Chondrichthyes in the archipelago of Madeira. A reliable overview of Madeira’s elasmobranch fisheries and their evolution, between

1990 and 2020, is also provided. The study on the biology and population dynamics of *Centrophorus squamosus* allowed to verify that the pressure of fishing did not cause critical changes in the life history parameters of the species over 22 years. The information obtained is essential to obtain the geographic distribution and depth of the species, as well as to evaluate the fisheries impact on the biology and population dynamics of this group, aiming to contribute to the development of suitable management strategies to preserve these species, specifically the populations under pressure by the Madeiran longline artisanal fishery.

Keywords:

Chondrichthyes; Taxonomy; *Centrophorus squamosus*; Biology; Population dynamics; Fisheries; Archipelago of Madeira; Seamounts.

Resumo

Os *Chondrichthyes* como espécies predadoras desempenham um papel fundamental no equilíbrio ecológico dos ecossistemas. Mais de um terço dessas espécies estão ameaçadas pela sobrepesca. As lacunas de informação nos *Chondrichthyes* do arquipélago da Madeira motivou a realização deste estudo, o qual pretendeu fornecer informação fiável sobre taxonomia, biologia, dinâmica populacional e pesca. Uma *checklist* atualizada de peixes cartilaginosos, novos registros, anotações taxonómicas e esclarecimentos, bem como o preenchimento de lacunas na história de vida de várias espécies, foram realizados durante esta tese. A *checklist* confirmou a presença de 67 espécies de tubarões, raias e quimeras. Outras 14 espécies anteriormente referidas para a região são agora consideradas registros duvidosos e 5 espécies são retiradas da lista. *Centrophorus uyato* foi reportado pela primeira vez para a Madeira. Das espécies relatadas na *checklist*, 24 estão incluídas na lista de espécies ameaçadas da Lista Vermelha Europeia de peixes marinhos da IUCN.

Hydrolagus affinis e *Chimaera opalescens* também foram reportadas pela primeira vez e a sua área de distribuição conhecida foi ampliada. Para o esclarecimento e resolução de dúvidas sobre a identificação de *Deania calcea* e *Deania hystricosa* foram realizados através de estudos morfológicos e moleculares, que confirmam que ambas são a mesma espécie. Aumento do conhecimento da diversidade de peixes de vários montes submarinos pertencentes ao complexo Madeira-Tore em diferentes estratos de profundidade até 2500 m, colmatando a lacuna de informação sobre os elasmobrânquios associados aos montes submarinos. A *checklist* de peixes cartilaginosos dos montes submarinos confirmou 17 espécies no Seine e 11 no Unicórnio, correspondendo a cerca de 31% dos *Chondrichthyes* válidos reportados para o arquipélago da Madeira. O trabalho aqui apresentado contribuiu para aumentar o conhecimento das comunidades piscícolas, diversidade e ocorrência no arquipélago da Madeira. Foi fornecida uma visão geral fiável da pesca de elasmobrânquios e da sua evolução na Madeira, entre 1990 e 2020. O estudo da biologia e dinâmica populacional de *Centrophorus squamosus* permitiu verificar que a pressão da pesca não provocou alterações críticas nos parâmetros da história de vida da espécie no período de 22 anos. A informação obtida é fundamental para definir a distribuição geográfica e de profundidade da espécie e para avaliar o impacto da pesca na biologia e dinâmica populacional deste grupo, com o objetivo de contribuir para o desenvolvimento de estratégias de gestão adequadas, visando a preservação destas espécies, especificamente as populações sob pressão da pesca artesanal pelo palangre derivante.

Palavras-Chave:

Chondrichthyes; Taxonomia; *Centrophorus squamosus*; Biologia; Dinâmica populacional; Pescas; Arquipélago da Madeira; Montes Submarinos.

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PART I

GENERAL INTRODUCTION

Chapter 1

General introduction

Introduction

1. Chondrichthyes

Sharks, batoids (rays and skates), and chimaeras are cartilaginous fishes (Chondrichthyes), a fish group with a cartilaginous internal skeleton as a distinguishing characteristic. The Class Chondrichthyes is divided into two major groups, each with a long and separate, pre-Devonian history, the chimaeroids, Holocephali (with a single living order Chimaeriformes), and the sharks and batoids proper (Elasmobranchii), with the surviving group Neoselachii divided into two cohorts, the Selachii (sharks) and the Batoidea (rays and skates) and includes all the modern living species (Ebert and Dando, 2021). The Class Chondrichthyes includes 1257 of Elasmobranchii species (540 shark species belonging to 34 families, and 665 batoid species belonging to 20 families), and 52 species of Holocephali belonging to 3 families (Last *et al*., 2016; Nelson, 2006; Scharpf and Lazara, 2019; Roskov *et al*., 2020; Ebert *et al*., 2021).

This class includes the oldest and most ecologically diverse vertebrate lineages and represents only approximately 3.5 % of the modern fish fauna (Nelson, 2006; Ebert *et al*., 2013). They arose at least 420 million years ago and rapidly radiated out to occupy the upper tiers of aquatic food webs (Kriwet *et al*., 2008; Ebert *et al*., 2013).

The majority of chondrichthyans are widely distributed in marine ecosystems, whereas only 5 % are restricted to freshwater environments (Fowler *et al*., 2005; Helfman *et al*., 2009; Ebert *et al*., 2013; Weigmann, 2016). In general, chondrichthyans occur rarely deeper than 3000 m and are exceptionally uncommon, or possibly absent, in the abyssal region (>4000 m) (Priede *et al.*, 2006). The available known data reveal that chondrichthyan species diversity drops with depth more sharply than teleosts (Priede *et. al*., 2006; Priede and Froese, 2013). The factors that limit the depth distribution of Chondrichthyes are still unclear (Kyne and Simpfendorfer, 2010). However, possible explanations for exclusion of this group from the abyss region, could be the high-energy demand, including an oil-rich liver for buoyancy, which cannot be sustained in extreme oligotrophic conditions and which might also limit growth and reproductive output (Priede *et al*., 2006; Treberg and Speers-Roesch, 2016). Further, the urea-based osmoregulatory strategy might conflict with the interactive effects of low temperature and high pressure on protein and membrane function at great depth. Also, their osmoregulatory strategy may make them unusually nitrogen limited (Treberg and Speers-Roesch, 2016).

Chondrichthyes are highly adaptable organisms to their environment and extremely diverse in terms of their taxonomy and ecology (Pethybridge, 2010). This group is characterized by perichondral prismatic calcification forming a honeycomb mosaic in most of the cartilaginous endoskeleton (Janvier, 1996) and by paired male intromittent organs derived from pelvic radials (claspers) (Zangerl, 1981). They are further characterized by paired fins and nostrils, two-chambered hearts and skin covered with placoid scales with hard enamel. However, body and teeth shape are highly variable between orders, reflecting adaptations to different habitat, lifestyle and feeding habits (Compagno, 1999; Pollerspöck and Straube, 2020). Species that prey molluscs and crustaceans have dense flattened teeth for crushing, contrarily to those that prey fish that have needle-like teeth for gripping, and from those that feed on larger prey that have pointed lower teeth for gripping and triangular upper teeth with serrated edges for cutting. Morphology of teeth and jaws is also a very important taxonomical character for determination of the taxa and identification of species (Gajić and Dando, 2012).

The majority of chondrichthyan species are apex predators, being near to or at the top of marine food chains and, consequently, pivotal to preserve the balance of the ecosystems they are a part of (Cortés, 1999; Stevens *et al.*, 2000; Freitas *et al.*, 2022). Nowadays, this very speciose lineage of predators plays an essential role as part of the top-down control of coastal and oceanic ecosystem structures and functions (Heithaus *et al.*, 2008; Ebert and Winton, 2010; Ferretti *et al.*, 2010; Burkholder *et al.*, 2013). Many of those species have acquired extreme and very specific life-histories, resulting in elevated sensitivity to fishing mortality (Stevens *et al.*, 2000; García *et al.*, 2008; Bradley and Gaines, 2014).

Most of the deep-water Chondrichthyes are considered K-selected species characterised by slow growth rates, late maturity, high longevity, low fecundity, very low productivity, higher maternal investment and longer reproductive cycles compared with shallow species (OSPAR, 2000; Stevens *et al*., 2000; Denney *et al*., 2002; Large *et al*., 2003; ICES, 2007; Rigby and Simpfendorfer, 2015). Their reproductive strategies are very diverse and characterized by internal fertilization and genital tracts specialized for uterine gestation (Litscher and Wassarman, 2018). The strategies can be classified according to the nutrition of the embryos. Lecithotrophic includes oviparity and yolk sac viviparity, where the only nourishment comes from their yolk sack. Contrarily, matrotrophic modes include an additional nourishment source at some point of the embryo development, unfertilized eggs or the formation of a placenta (Musick *et al*., 2005; Conrath and Musick, 2012; Walker, 2020). As such, egg-laying, aplacental and placental live birth occur among deep-water taxa. In general, chondrichthyans grow slowly, invest in few and well-developed young (Priede *et al*., 2006; Rigby and Simpfendorfer, 2015), and more than 50 % of them give birth live young as compared to 2-3 % of the bony fish of the class Ostheichthyes (Litscher and Wassarman, 2018).

Chondrichthyes as target or as bycatch species, have been exploited over the years, for their meat, fins and shark products, such as liver oil, fins, and gills, with high market value (Clarke et al., 2006, Ebert and Stehmann, 2013; Consales and Marsili, 2021).

Chondrichthyans are vulnerable to human impact, with the ability to define the species turnover of benthic communities and, therefore, influence the ecosystem´s functioning by regulating other predators' populations (Thrush *et al.,* 1991; Lucas and Stobo, 2000; Acevedo-Gutiérrez, 2002; Lucifora *et al.*, 2012). The primary threat is fishing because commercial demand for meat and fins is high and because the majority of chondrichthyan-based fishery is unmanaged (Fowler *et al.* 2005). Presently, more than one-third of chondrichthyan fish species are threatened by overfishing (Dulvy *et al*., 2021). However, species of this group are not all equally susceptible to extinction. As stated by Garcia *et al.* (2008), the risk of extinction is strongly related to the reproductive mode, being matrotrophically viviparous species the ones to tend towards a higher extinction risk. Garcia *et al.* (2008) suggested that the species most prone to get extinct are Lamniformes and Squaliformes. Several works state that the changes in the diversity of fishes in the Northeastern Atlantic is due to the impact fishing has in the vulnerability of chondrichthyans (Rogers *et al.,* 1999, Stevens *et al.,* 2000, Dulvy *et al.,* 2014).

Regulation is one of most important determinants of Chondrichthyes populations and therefore the risk of overexploitation and extinction is density dependence in survival of very young individuals (Dulvy and Forrest, 2010). As such, juvenile survival rather than fecundity is a crucial factor contributing to population growth rate, especially in longer-lived species (Frisk *et al*., 2001).

Fisheries using demersal trawls (e.g., Pajuelo *et al.*, 2016), longlines or gillnets have been bycatching chondrichthyans, over the years. In relation to pelagic sharks, they are globally bycaught, in a large scale, in longlines dedicated to the fishing of tuna and billfish (Stevens *et al.,* 2000). In the Northeast Atlantic, studies also performed by Dulvy *et al.* (2000) indicated that after a long period of exploitation, this may affect specific population parameters as communities of skate tend to decrease in abundance and size.

Fisheries are not the only threat that species of Chondrichthyes face, habitat fragmentation, climate change, pollution and consequent environmental contamination are also on the list. One of the reasons for this to happen is because these species dwell in a large range of habitats, from surface coastal waters to deep-sea bottoms, facing various pressures and stressors.

Loss and degradation of habitat are extremely worrying especially for those species which inhabit regions closest to human activity (IUCN, 2021). The main causes of this disturbance are commercial development, agriculture, aquaculture, natural system modifications, human disturbance, energy production, mining, invasive species, transportation and service corridors (Dulvy *et al*., 2021). Climate change is also of concern for threatened chondrichthyans, namely through the reduction of coral cover due to bleaching and disease affecting the health of coral reef-associated species and to changes in sea-water temperature that makes native habitats less suitable (Dulvy *et al*., 2021).

Pollution is considered a non-lethal stressor affecting threatened chondrichthyans. As stated by Consales and Marsili (2021), this group is the most at risk, as the majority are at the top of the food chain, due to the persistent and bio accumulative effect of contaminants. Moreover, pollution pressures have been allocated to species based on the risks affecting the area they inhabit, rather than the specimen’s own susceptibility to suffer from pollution (Mudd and Patterson 2010; Sheppard *et al.,* 2010; Consales and Marsili, 2021).

In different parts of the world, mitigation measures were applied to achieve the protection and recovery rates of the populations of vulnerable species and, until this day, include the implementation of marine protected areas, shark sanctuaries and changes in fishing effort (Baum *et al.,* 2003; Shephard *et al.,* 2012; Ward-Paige *et al.,* 2012).

However, a massive gap remains between the number of populations exploited versus those assessed for sustainable management (Dulvy *et al*., 2017). It is clear that there is no single silver bullet for better management, and that multiple approaches are needed to safeguard against depletion (Dulvy *et al*. 2017). Adoption of protective measures will also depend on the reconciliation of shark protection with the perception of public safety (Ferretti *et al*., 2015 *in* Jorgensen *et al*., 2022).

1.1. Deep-water Chondrichthyes

Deep-water chondrichthyans have been defined as sharks, rays and holocephalans that spend most of their lifecycle at depths below 200 m. This depth is generally recognised as the continental and insular shelf edge, and, therefore, deep-water species are those occurring on or over the continental and insular slopes and beyond, including the abyssal plains and oceanic seamounts. Of the global chondrichthyan fauna, 530 species are considered deep-water species. The deep-water chondrichthyans are divided between 254 shark species (47.9 %), 236 batoid species (44.5 %) and 40 species of holocephalans (7.5 %) (Kyne and Simpfendorfer, 2010).

Most available life history data on sharks, batoids, and chimaeras are from shallow waters. Difficulties in deep-sea sampling due to dispersal, depth of occurrence, taxonomic uncertainty and other factors limit current knowledge. (Kyne and Simpfendorfer, 2010).

The interest in fishing deep-sea species is increasing, leading to the mortality of deep-sea chondrichthyans, since the ability of deep-sea fishes to sustain fisheries is quite unknown. However, the slow growth, late maturity age and low longevity of deep-sea species are pointed out as the reasons for their limited ability to support the fishing pressure (Koslow *et al.,* 2000; Cailliet *et al.,* 2001). Some species of deep-sea Chondrichthyes can easily be driven to extinction by a really low fishing mortality rate, which in some cases, is believed to have already happened (Graham *et al.,* 2001; Devine *et al.,* 2006; Morato *et al.,* 2006). According to Garcia *et al.* (2008), for the extinction of deep-sea chondrichthyans to potentially happen, it is sufficient that, applied to continental shelf and oceanic species, the mortality in fishing reaches 58 % and 38 %, respectively.

Hence, the interest about the global status of chondrichthyans has grown recently, nevertheless, in several regions across the globe, the complete understanding of the population and conservation status of numerous species of chondrichthyans is yet to be utterly achieved (Dulvy *et al*., 2014; Cortés, 2016; Pardo *et al*., 2016).

2. Madeira and nearby Seamounts

The exclusive economic zone (EEZ) of Madeira includes a complex of seamounts. Madeira-Tore geological complex is in the North-eastern Atlantic Ocean, enclosing a number of seamounts extending from the Madeira archipelago (33° N latitude) to the Portuguese mainland EEZ (38° N). Portugal has defined the area as a potentially critical under the Marine Strategy Framework Directive (MSFD), aiming to create new large-scale Marine Protected Areas (MPAs) in the North Atlantic (Biscoito *et al*., 2017).

In general, seamounts are underwater topographic features which rise from the surrounding seafloor. Usually, they have a conical form and volcanic origin associated to tectonic activity (Wessel, 2007), with rough, rocky bottoms and steep slopes (Gubbay, 2003). Seamounts' environment promotes adequate conditions for the colonization, shelter, and growth of diverse fauna (Amorim *et al*., 2009), hence attracting many species from the surrounding open ocean, such as deep-water fish species, and harboring frequently special epibenthic communities formed by sponges and deep-water corals. Because of this, seamount ecosystems provide diverse habitats and normally host rich pelagic and benthic communities, playing an important role on the ecology and biodiversity of the oceans. The high concentration of marine life found on seamounts made these areas attractive and important for commercial fisheries, to whose impacts they are highly vulnerable. Seamounts are ubiquitous features in the world oceans, more than 100.0 large seamounts according to Wessel (2007), but scientific knowledge about their biodiversity and functioning is still scarce, since few of them have been studied in any detail (about 250-280 seamounts have been sampled according to Rogers *et al*., 2015). The limited knowledge extends also to the effects of exploitation on seamount communities, both on the short and long-term, making their management even more difficult.

The interest in the conservation and sustainable exploration of seamounts and associated biological communities boosted the need for a better understanding of these ecosystems and the threats to which they are subject. Recent efforts were carried out aiming to study in some detail two seamount complexes located in Portuguese waters, the Madeira-Tore and the Great Meteor (Biscoito *et al*., 2017; Delgado *et al*., 2017; Freitas *et al*., 2021). The results provided baseline information for sustainable use and management measures of the Portuguese marine environment and to the development of the strategies for the continuous assessment of the environmental status of Portuguese marine waters towards the achievement and maintenance of their good environmental status. In this regard, several studies have been conducted aiming to increase the knowledge of fish diversity in these seamounts at different depth strata down to 2500 m and allowed to provide updated species checklists (Biscoito *et al*., 2017; Delgado *et al*., 2017; Freitas *et. al*., 2021). Despite these scientific efforts, anthropogenic activities and their impacts on most seamounts are still insufficiently documented and evaluated (Campos *et al*., 2019).

Overfishing on seamounts is of particular concern, considering the high vulnerability of seamount-aggregating species present in relation to other species (Morato and Clark, 2007). As such, sustainable exploitation must be promoted in these areas in order to preserve the living resources at medium and long terms.

3. Global Fishing

The expansion of human activities around the world is threatening the living resources of the oceans. The current rate of biodiversity loss is several orders of magnitude higher than the regular historical extinction rates, only comparable to the five great extinctions of Earth’s history (Cardillo *et al*., 2005), which were unchained by natural disasters of global scale. In spite of it, few extinctions of marine species are reported to date in absolute numbers, which is even more shocking when comparing to the ones registered on land (Cardillo *et al*., 2005; Reynolds *et al*., 2005; Pearson *et al*., 2010; Comeros-Raynal *et al*., 2012; Ripple *et al*., 2019;). The increase in human exploitation and scarce resources for marine species reports may forewarn of increasing loss of marine biodiversity (Myers and Worm, 2005; Worm *et al*., 2005), leading to substantial reductions in the abundance of target species, carrying changes in the structure and species composition of fish communities (Jennings *et al*., 1999; Ferretti *et al*., 2010). Such responses may imply differential community alterations and abundance trends caused by different life-histories of overexploited species.

Fishing pressure has steadily increased over the last century to meet increasing needs, which has resulted in sudden and critical declines of predatory communities (Ferretti et al., 2008; Coll et al., 2009 Ferretti et al., 2010; Graham et al., 20100; Da-Rocha et al., 2011; Langangen et al., 2011; Storai et al., 2011; Dulvy et al., 2014; Correia et al., 2016).

The incidental capture of non-target species is commonly known as bycatch, and it is one of the major concerns for sustainable fishing. Traditionally, bycatch has been considered the portion of the catch, which is discarded dead or dying, nevertheless, the decision of discarding species depends on the fishery, region and time of the year, the latter, on an economic and personal fisher's consideration. Excessive physical damage, lack of demand, room for more valuable species or exceeding quotas established by management are the drivers of discarding. The detrimental effects lie in the survival probabilities of the discarded individual and the level of discarding. The magnitude of the global impact of fisheries still remains poorly understood and highly contentious, insights from ecosystem modelling and stock assessments suggest improvement on few well-studied exploited ecosystems (Wilkin, 1994; Pauly *et al*., 2000; Olsen *et al*., 2004; Da-Rocha *et al*., 2011; Pitcher and Cheung, 2013). This scope is based on roughly just 295 populations of 147 fish species, hence, far from representing the majority of world´s fisheries (Newton *et al*., 2007; Worm *et al*., 2009; Hutchings *et al*., 2009; Costello *et al*., 2012; Ricard *et al*., 2012).

The very first estimate of annual discards was done covering the years 1980-1993 on a global scale, with about 27 million tons of reported discard per annum, unveiling it as a quarter of the total landed catches (Alverson *et al*., 1994). A later study covering the period 1998-2001 estimated annual discarding to be 7.3 million tons with a large uncertain range, the explanation may lie in a reduction of reported bycatch, based on differences in methodology and changes in targeting/retention practices, incentives for bycatch trading and other socio-economic drivers (Megalofonou *et al*., 2005). In responses to awareness and first management steps, fisheries have found new commercial use of bycatch, largely unmanaged, lack measures and can potentially be illegal, unreported and unregulated fishing (IUU) (Camhi *et al*., 2009) developing to so-unwanted unsustainability. Based on the results of previous studies, a more holistic definition of bycatch (Davies *et al*., 2009) has been defined, which considers bycatch as either unused and unmanaged. The first term refers to the discarded portion of the catch, whilst the second refers to the portion of catch for which no specific management measures are in place, aiming for sustainability. A managed species is protected under clear and defined measures to assure a sustainability goal. Therefore, based on this new definition of bycatch, it was estimated for the same period to be 38.5 million tons per annum (Lobo *et al*., 2010; Pitcher and Cheung, 2013; Oliver *et al*., 2015; FAO, 2018; Roda *et al*., 2019).

Overfishing and habitat destruction have unequivocally disturbed species all over, elasmobranchs among the most affected (Heupel *et al*., 2009; Simpfendorfer and Kyne, 2010; Ferretti *et al*., 2010; Polidoro *et al*., 2012). FAO has reviewed the state of knowledge of shark and ray stocks worldwide and made recommendations for management needs (FAO2018). The Convention on International Trade in Endangered Species (CITES) warned about the inherent vulnerability and rapid expansion of shark and ray fisheries (McClenachan *et al*., 2012; FAO, 2018; Pérez Roda *et al*., 2019). FAO and the International Council for the Exploration of the Sea (ICES) had called upon the scientific community to compile all available information on elasmobranch landings and put together local Shark Plans of Action (SPOAs) with a first meeting ending in 2009 (Zhou *et al*., 2019). Regarding the finning trade, the European Union (EU) approved the legislation to ban finning in European waters and by European vessels outside of European waters (Reg. No. 1185/2003) with an amendment in 2011 (2011/0634), regarding fins to be landed still attached to the body. Until the approval, the legislation allowed to land a maximum fraction of 5% fins of the weight of the total catches, and was considered too permissive as the percentage was larger than the current fin-to-total-body weight ratio on a wide range of pelagic shark species (Santos and Garcia, 2008; Cortés *et al*., 2010).

Although implementations for management of elasmobranch fisheries are inevitable, it has not been the case for the vast majority of the fisheries. Rather, overwhelming patterns of absence of management provokes rapid declines tackling even decades to recover, if still possible, for low valued stocks (Ward-Paige *et al*., 2010; Beard *et al*., 2011; Oliver *et al*., 2015).

The elaboration of the IUCN Red List, based on the IUCN Red List Categories and Criteria, of the undoubtedly 1041 chondrichthyan species, a quarter have been listed as threatened due to overexploitation, with larger animals being the most vulnerable and threatened as mentioned above, with five out of the seven most threatened families being rays (Megalofonou *et al*., 2005; Ferretti *et al*., 2008; Ferretti *et al*., 2010; Sprogis *et al*., 2018).

Previous studies have identified bycatch patterns of mega-fauna based on regions, gear types and fisheries involved (Trent *et al*., 1997; Kaplan *et al*., 2007; Clarke, 2009; Lobo *et al*., 2010; Oliver *et al*., 2015; Shaaban *et al*., 2018). Further, composition and magnitude of bycatch is also affected by the selectivity and other gear characteristics, i.e., gillnets and longlines are considered more selective than trawl nets. In artisanal fisheries, the elasmobranch catch is generally fully utilized, whereas commercial fisheries show contrasting discarding practices, from having large discarding to high rates of retention aiming to fulfill lacks of targeted species, restricted policies or the lucrative finning trade (Hilborn, 2007).

The exploitation of deep-sea species has been growing since the last decades of the 20th century (Merret and Haedrich, 1997). It is estimated that there are 100 million sharks being caught per year by fishing vessels from all around the world (Worm *et al*., 2013). Hence, in 2015 the global shark market was estimated to generate roughly 1 billion USD dollars (Dent and Clarke, 2015).

4. Study area and state-of-the-art

4.1. Study area

The archipelago of Madeira is located between 32º37’52” N and 32º52’08” N and 16º39’19” W and 17º15’54” W, 754 km off the West coast of Africa and 980 km to the southeast of Europe. This archipelago is part of the Macaronesian ecoregion, together with the archipelagos of the Azores to the north, and Salvage and Canary Islands to the south (*sensu* Spalding *et al.*, 2007). In addition, according to more recent multi-taxa studies, Madeira is integrated into the Webbnesian marine ecoregion (i.e., Madeira-Salvage-Canaries, see Freitas *et al.*, 2019). However, for the purpose of giving the geographical distribution of the species included in this manuscript, the archipelagos of the eastern-central Atlantic (Azores - Madeira - Salvage - Canary Islands - Cape Verde) will be considered as "Macaronesia" in a broad sense *sensu lato,* as a "traditional" biogeographical unit.

The archipelago, of volcanic origin, of Miocene age, the island of Madeira being the largest and youngest one with no more than 7 million years, is characterized by having a very narrow shelf, followed by a very steep slope down to the abyssal plain (Schmincke, 1973; Geldmacher *et al.,* 2000; Klügel *et al.,* 2009). Despite Madeira's vast (EEZ), which is 500 times larger than its terrestrial area, its fishery resources are not very abundant since the surrounding ocean is considered oligotrophic and upwelling events are sporadic and very restricted (Parsons *et al.,* 1984; Caldeira *et al.,* 2002; Ribeiro, 2008).

4.2. Madeira deep-sea fishery and fisheries management

Fishing has been part of Portugal's culture for the last centuries, representing a high income for coastal communities, traditionally artisanal and subsistence, using vessels with less than 12 m in length (DGPA, 1998; Torres *et al.*, 2016).

The Madeiran fisheries are artisanal and small-scale, mostly composed of small vessels. The active commercial fishing fleet has decreased gradually in number of vessels from the nineties onwards. Out of the 86 local fishing vessels that landed in regional ports in 2020, 71 % were small vessels with less than 12 m and only 5 % were bigger than 24 m length. These small-scale fisheries are dominated by mid-water drifting longlines targeting black and intermediate scabbard fishes (respectively *Aphanopus carbo* Lowe, 1839 and *Aphanopus intermedius* (Parin, 1983) and by the pole and line vessels that target tuna, together accounting for approximately 89 % of the total of the exploited marine resources landed in the archipelago in 2020. The remaining 11 % corresponded to the landings of small pelagic species (6 %), shellfish (3 %) and demersal species (2 %) (Freitas *et al*. submitted (2)). The fishing fleet of Madeira operates regularly in Madeiran waters near the islands with occasional large-scale trips to more productive areas like Madeira seamounts. Commercial fishing in the region has been declining since 1990 in terms of the number of active fishing vessels. (Freitas *et al*., 2021).

Fishing activity in Madeira has been done ever since the early days of the discovery, starting with the deep-sea shark fishery, which later gave origin to the black and intermediate scabbard fishes fishery (Biscoito *et al.*, 2011), one of the most important fisheries nowadays in Madeira. In fact, the first specimen of *A. carbo* was caught by accident in 1839, when a drifting longline for deep-sea sharks was set out a little further from the coast, at a greater depth (Leite, 1988 in Freitas and Biscoito, 2007). This fishery using drifting longlines, takes place between 800 and 1200 m of depth, on the slopes of Madeira proper and adjacent islands and seamounts. Apart from this well-established commercial fishery, only few attempts of deep-sea fisheries, at experimental and scientific level, were done and very scarce information on the fish fauna occurring on the islands' slopes is available. The deep-sea fish fauna of Madeira (NE Atlantic) has been object of study by several ichthyologists over the last 150 years, e.g. R. T. Lowe (1802-1874), J. Y. Johnson (1820-1900) and G. E. Maul (1909-1997) who were responsible for the description of many new or little-known deep-sea species, mostly recovered from the stomachs of black scabbardfish. Although the meso- and bathypelagic fish fauna has been surveyed during several research cruises, almost none has dealt with the deep demersal fish fauna, mostly because the rugged nature of the islands' sea floor makes bottom trawling a very tricky collecting method.

The deep-sea fishery targeting the black and intermediate scabbardfish off the Madeira archipelago mentioned above represents one of the world's long-standing exploitation of meso- and bathypelagic fish species (Biscoito *et al*., 2011; Delgado *et al*., 2013). During at least 150 years this fishery continued as an artisanal sustainable activity, but during the last decades of the twenty century the increase of the fishing effort and yields may have changed this situation (Vasconcelos *et al.*, 2020). At present it is still one of the most important activities of the Madeira fishing fleet considering both its yields and economic value. Landings in 2017 achieved around 2.163 tons, which yielded 7.6 million €, however this represents a serious decrease since the fishery landings peak in 1998 (4.203 tons). New important regional fisheries at the North-eastern Atlantic also targeting this resource emerged in the 1980's in Sesimbra, off mainland Portugal, using a bottom longline (set longline- LLS) and French deep-sea trawl fishery west of the British Isles (Nakamura and Parin, 1993; ICES, 2012). Concerning the target species of these deep-water fisheries, catches off Madeira are composed by the sympatric species: *A. carbo* and *A. intermedius* in an 80 % : 20 % ratio. Catches from south -i.e. Canaries area- present a higher abundance of the intermediate scabbardfish (*A. intermedius*), whereas catches north of Madeira made by the Sesimbra fishery, off Portugal mainland, are solely constituted by the black scabbardfish (*A. carbo*) (Biscoito *et al*., 2011).

In Madeira this by-catch usually represents around 5 % of total catches in number (Severino *et al*., 2009; Veiga *et al*., 2013). Farias *et al*. (2013) proposed a distribution and hypothetical migratory cycle of *A. carbo* in the northeast Atlantic. These authors stated that spawning of black scabbardfish occurs around Madeira and the Canary archipelagos during the last quarter of the year. According to their migratory hypothesis, eggs, larvae, and possibly juveniles move north to areas from south of Icelandic and Faroe Islands to the west of the British Isles where they remain for some years to feed and grow. Then, they move south to the area off mainland Portugal, where they reach the size of first maturity but do not reproduce, and later move further south to the spawning grounds. Apparently, *A. intermedius* distributes southward, being a subtropical and tropical species in the Atlantic Ocean, with the Azores, Madeiraand the Canaries being the superposition area of both species (Parin, 1990; Biscoito *et al*., 2011). The fishing gear used by the Madeira fleet for the capture of these deep-sea fishes is a horizontal drifting longline usually set well above the bottom, in the water layer between 800 and 1300 m deep (Morales-Nin and Sena-Carvalho, 1996). The fishing gear used in this way does not contact the seafloor, causing no damage to its vulnerable ecosystems. Nevertheless, the intensive fishing of the target species caused a decrease in their relative abundance in the usual fishing grounds, leading to an extensive geographical expansion of the fishery reaching as far as the Southern Azores Seamount Chain and the Canaries Economic Exclusive Zone. Changes in the fishing pattern of the fleet, for example the increase of soak time, were also registered along the last decades (Delgado *et al*., 2018)

In the archipelago of Madeira, most of the deep sea chondrichthyans are caught in artisanal fisheries dedicated to black scabbardfish and intermediate scabbardfish *(A. carbo* Lowe, 1839 and *A. intermedius,* Parin, 1983, respectively) using horizontal drifting longlines, since the seventeenth century (Merrett and Haedrich, 1997). Despite the efforts made over the last years to study deep-sea fish fauna of this north-eastern archipelago, as well as seamount fish fauna, the majority did not cover species captured in depths below 600 m (Tracey *et al*., 2004). As stated by Freitas *et al*. (2021), the existing data are obtained by the sampling effort associated with fishing activities, which makes evident the need to understand the dynamics of seamount-aggregating elasmobranch species (Menezes *et al*., 2009; Christiansen *et al*., 2015; Vieira *et al*., 2018). A recent study examined the landings of commercial elasmobranch species in 1990-2020 acknowledging that, in this period, 2.316 tons of elasmobranchs were landed, an equivalent to nearly €

2.1 million in first sale value. Of this value, it was noticeable the annual landing from 2003 to 2013, with annual landing values higher than 70 tons.

These fisheries present a by-catch mainly constituted by deepwater sharks (Freitas *et al.*, 2018), specially *Centrophorus squamosus* that represented in 2019 around 38 % of the total bycatch of these species (DRP, 2020, Freitas *et al.,* submitted (3)) Hence, the *C. squamosus* was the most landed species coinciding with the gastronomic importance that this species has in the region (Freitas *et al*., 2021, Freitas *et al.*, submitted (3)).

In the Macaronesian archipelagos, the European Union fisheries management, under the EU Common Fishery Policy (CFP) and the fisheries partnership agreement with Cape Verde, are responsible for the regulation of shark fisheries. Therefore, it is mandatory for Macaronesian regions to annually report catch data for each shark species caught in association with fisheries to the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Lehr, 2015).

Since 2015, the European Union (EU) imposed a Total Allowable Catch (TAC) of zero tons for deep-water shark species and, therefore, leading to a massive decrease in global landing of these species, annually, and in 2021 the Council Regulation (EU) 2021/91 of 28 January 2021, officially prohibited the landing of deep-water sharks in the archipelago of Madeira.

In Madeira, Azores and Canary archipelagos a regulation is in force, delimited by the European amendments of Western Waters Regulation (EC 1954/ 2003) that limits the vessels registered in the ports of the islands of fishing inside the (EEZ) up to 50 or 100 nm and not the previous 200 nm. However, this does not apply to EU Community vessels, which conventionally fish in those waters as far as these do not exceed the fishing effort in effect (Freitas *et al*., 2021).

Preventive actions of management of deep-sea fisheries are essential to maintain stocks and biodiversity, in view of the sustainability of the species that dwell in deep-sea habitats. The absence of these actions could potentially lead to the loss of high trophic level predators and consequent ecosystem level changes (Simpfendorfer and Kyne, 2010). Proper conservation strategies could involve the closure of fishing areas with proven high catch values of Chondrichthyes and for that, the knowledge of the biological parameters of these species is required (Freitas *et al*., 2022). The reliable data retrieval would depend on on-board observer programs or remote electronic monitoring (REM) systems.

The high transparency in the report of chondrichthyan catches will allow reliable estimates of catches in the region to be obtained (Bonfil, 1994). Due to the impacts this group face, Chondrichthyes are a priority for conservation measures taking place worldwide. Populations of these species are globally decreasing and, as it is present in the Red List of the International Union for Conservation of Nature (IUCN), 37% of the overall known shark and ray species are already threatened with extinction (IUCN, 2021). In the archipelago of Madeira, considering the 67 valid species of cartilaginous fish reported, 8 were classified as Vulnerable, 9 as Endangered, and 7 as Critically Endangered, according to the IUCN European Red List of marine fishes (Nieto *et al*., 2015; Biscoito *et al*., 2018).

4.3.State-of-the-art

In the Macaronesian ecoregion, since 2011 shark catches have been decreasing and showing signs of stabilization (Gonzáles-Mantilla *et al*., 2021). This could be, in part, explained by the diminished fishing fleet operating in the waters of the Macaronesia and the regulations implemented by the European Common Fisheries Policy (CFP) regarding the shark landings and commercialization, by reducing quotas and the possibility to retain certain species of sharks and rays on board (Gonzáles-Mantilla *et al*., 2021).

In Macaronesian archipelagos deep-water fishing resources are considered of high economic value, however, only a few species are commercially exploited of the overall species inhabiting these regions (Costa *et al*., 2018). Also, the exploitation of species inhabiting Macaronesian waters occurs deeper since the islands' colonization (Vieira, 1995). In this region, deep-sea diversity is estimated to reach 1,029 fish species, living in extreme conditions, in low productivity environments, that include the minimal access or no access to sunlight, and minor nutrient concentrations (Haedrich, 1996; Merret and Haedrich, 1997; Costa *et al*., 2018). The EEZ of Madeira also comprises several areas with recognized high species richness and unique ecosystems. An example is the Selvagens Islands which are known to be one of the least disturbed islands in the Atlantic Ocean, where fishing is not allowed (Almada *et al*., 2015;). Friedlander et al. (2016) also stated that these islands are known to be unique and one of the last intact ecosystems of the eastern Atlantic Ocean. Madeira Archipelago also counts with four Marine Protected Areas, which is indicative of the interest and concern in preserving marine ecosystems surrounding this area (Freitas *et al*., 2004).

The first reference to cartilaginous fish from Madeira in the scientific literature, was given by Bowdich (1825) (*Sphyrna zygaena*, *Dalatias licha* and *Squalus acanthias*). Lowe (1843–1860), in his reference work "A History of the Fish of Madeira", listed only four species of sharks and rays, nonetheless, on the overall of his scientific production (1833–1860), 26 species were recorded by him. Recently Carneiro *et al.* (2014) on the checklist of marine fish from Portugal, including the archipelagos of the Azores and Madeira, recording 76 cartilaginous fish species from Madeira. However, in many cases these records are not based on specific references or specimens in collection (Biscoito *et al.,* 2018). More recently, an updated checklist of all cartilaginous fishes of the archipelago of Madeira, based on occurrences and validated by specimens in natural history museum collections, confirmed 67 species of sharks, rays and chimaeras for this area (Biscoito *et al*., 2018), which represent 5% of the total valid chondrichthyan species described globally (Weigmann, 2016). Moreover, it was verified that 24 of the reported species are threatened according to the IUCN European Red List of Marine Fishes (Nieto *et al*., 2015).

In recent years some research surveys allowed to explore a greater bathymetric range (up to 2500 m depth) and to record for the first time some species of Chondrichthyes for this area, namely *Hydrolagus affinis* (de Brito Capello, 1868) (Freitas *et al*., 2011) and *Chimaera opalescens* (Luchetti *et al*., 2011), increasing the knowledge about deep-water species of the archipelago of Madeira (Freitas *et al*., 2017). Furthermore, studies using genetics and taxonomy have been performed aiming to clarify uncertainties over identification of some Chondrichthyes and trying to discern species with problematic morphological identification (e.g., *Deania* spp.) (Stefanni *et al*., 2021; Marrero *et al*., submitted 1).

Seamounts around Madeira and Azores archipelagos are of special interest and fit in Portugal's plans to classify them as Marine Protected Areas (MPAs) in the next years under the European Marine Strategy Framework Directive (EU-MSFD). These areas often play an important role in species biogeography and connectivity between key stone habitats (Koslow *et al*., 2016). However, the knowledge about seamount fishes continues to be scarce, as well as the interactions between living communities that seamounts sustain (Brewin *et al.*, 2007).

Aims and specific objectives

The main goals of this thesis are firstly to clarify and update the taxonomy of deep-sea cartilaginous fishes occurring within the 200 nautical mile (EEZ) of Madeira. Secondly, to assess the fisheries impact on the biology and population dynamics of Chondrichthyes in Madeira archipelago, aiming to develop suitable management strategies to preserve these species, specifically the populations under pressure by the Madeiran drifting longline artisanal fishery.

To accomplish the previous aims, the thesis has been organised in order to reach the following specific objectives:

(i) provide an updated checklist of the cartilaginous fishes occurring within the Exclusive Economic Zone of Madeira, based either on specimens in collection or on reliable published information;

(ii) confirm two new records of Chondrichthyes for the Madeira archipelago extending the previously known range of distribution of these species, and also provide its vertical distribution;

(iii) clarify uncertainties over the identification of *Deania calcea* and *Deania hystricosa* through visual identification of skin denticles and molecular markers;

(iv) contribute to the knowledge of chondrichtyes communities, chondrichtyes diversity and occurrence of certain species around these seamounts, and provide baseline information for sustainable use and management measures of these areas;

(v) deliver a reliable overview of Madeira’s elasmobranch fisheries and their evolution over a time period of 31 years (1990-2020) by estimating the annual landings and auction values, identifying the main elasmobranch fish species landed, characterizing the elasmobranch fishing fleet and determining temporal trends in elasmobranch landings;

(vi) verify the effects of the long-term exploitation on the biology and population dynamics of *Centrophorus squamosus* through a comparative study over a 20-year period, and present suitable management strategies to preserve this species, specifically the populations under pressure by the Madeiran black scabbardfish longline artisanal fishery;

(vii) provide the first report on the length-weight relationships and condition factor of eight chondrichthyan species and contribute to the development of a proper management plan for the conservation of these species.

Thesis outline and structure

The present thesis contains five parts and comprises fifteen chapters.

The Part I is composed by chapter 1 and comprises the general introduction, the aims, and an integrative description of all chapters.

The Part II deals with systematics and distribution of deep-sea Chondrichthyes in Madeira archipelago and includes five chapters. Chapter 2 comprises an updated checklist of Chondrichthyes of the archipelago of Madeira and confirms the presence of 67 species in this area. Chapters 3 and 4 report two new records of chimaeras for the Madeira EEZ. These records not only enlarge the previously known area of distribution of these species, but also confirm its depth distribution down to 2500 m.

In chapter 5, a clarification on identification of *Deania calcea* and *Deania hystricosa* is performed using skin denticles and molecular markers.

In chapter 6 - Taxonomic status of deep-sea sharks *Deania calcea* and *D. hystricosa* (Centrophoridae), the genetic differences measured between these species were study

The Part III includes the deep sea Chondrichthyes from the seamounts around Madeira archipelago and comprises three chapters.

In chapter 7 Records of some rare deep-sea fishes caught in the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira (East-Central Atlantic), records of some rare deep-sea fishes and aspects of their life history traits are presented. This chapter also includes a first approach to the estimation of the length-weight relationships of 11 deep-water, data-deficient species for which prior information, estimated from data collected, did not exist in FishBase.

In chapter 8 - Biodiversity in seamounts: The Madeira-Tore and Great Meteor. BIOMETORE 5 cruise report the main results and a preliminary list of the species collect in scientific cruises to Seine and Unicorn seamounts are presented.

In chapter 9 - Sharks, rays and chimaeras of the Seine and Unicorn seamounts (NE Atlantic Ocean), updates the checklist of sharks, rays and chimaeras for the Seine and Unicorn seamounts, summing up 20 species.

The Part IV concerns to the deep sea Chondrichthyes fisheries and biology and includes five chapters. In chapter 10 - Long term overview of elasmobranch fisheries in an oceanic archipelago: the case study of Madeira Archipelagoa, a reliable overview of Madeira's elasmobranch fisheries and their evolution over a period of 31 years is presented.

In chapter 11 - Long-term population status of the commercially exploited shark Centrophorus squamosus in an oceanic archipelago, a comparative study for the species *Centrophorus squamosus* was performed analysing the biological parameters of the species over 22 years. In chapter 12 - Length-weight relationships for eight Chondrichthyes from the north-eastern Atlantic Ocean, the length-weight relationships (LWRs) for eight Chondrichthyes are present for the first time for the Madeira waters. These LWRs are very useful to provide a baseline for conservation strategies particularly in species susceptible to overexploitation as elasmobranchs.

In chapter 13 - Assemblages of deep-sea fishes on the middle slope off Northwest Africa (26°–33° N, eastern Atlantic), the structure and composition of deep-sea fish assemblages living on the middle slope off NW Africa (26–33° N) were investigated and also the impact of deepest trawls on biodiversity.

In chapter 14 - Deep-sea sharks as by-catch of an experimental fishing survey for black scabbardfishes (*Aphanopus* spp.) off the Canary Islands (NE Atlantic), thee deep sea sharks associated as by-catch of the Madeiran midwater drifting longline fishery for scabbardfishes (*Aphanopus* spp.) were investigated within the Canary Islands Exclusive Economic Zone, whose fishing grounds have been exploited during the past 15 years. Nine species of chondrich¬thyans were identified, belonging to five families: Pseudotriakidae, Centrophoridae, Etmopteridae, Somniosidae and Chimaeridae.

Part V comprises the main results and final discussion of all chapters, and provide some recommendations for the exploitation of deep-sea commercial species in the archipelago of Madeira in order to prevent overexploitation.

Of the fifteen chapters that compose the thesis, fivehave been published by the candidate as first author, five as co-author in peer reviewed journals, three have been recently submitted for publication, and finally two concern the introduction and general discussion of this manuscript:

PART I - GENERAL INTRODUCTION

Chapter 1: General introduction

PART II – SYSTEMATICS AND DISTRIBUTION

Chapter 2: Annotated checklist of the fishes of the archipelago of Madeira (NE Atlantic): I – Chondrichthyes

Biscoito M, Ribeiro C, **Freitas M** (2018). Annotated checklist of the fishes of the archipelago of Madeira (NE Atlantic): I – Chondrichthyes. **Zootaxa** 4429(3): 459-494. https://doi.org/10.11646/zootaxa.4429.3.2

MF went in research campaigns to obtain the specimens, carried out the sampling and morphological identification. Also is a scientific diver whose observations were included in the paper. Went to several Museums with the first author to analyse and identify specimens. Help to conceived, design and write the study and contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 3: First record of *Hydrolagus affinis* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and the Seine seamount (North Atlantic Ocean)

Freitas M, Almeida AJ, Delgado J, González JA, Santana JI, Biscoito M (2011). First record of *Hydrolagus affinis* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and the Seine seamount (North Atlantic ocean). **Acta Ichthyologica et Piscatoria** 41(3): 255-257. https://doi.org/10.3750/AIP2011.41.3.14

MF carried out the sampling, morphological identification, conceived and designed the study. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 4: First records of *Chimaera opalescens* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and North-West African coast

> **Freitas M**, Vieira S, Costa L, Delgado J, Biscoito M, González JA (2017). First records of *Chimaera opalescens* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and North-West African Coast. **Acta Ichthyologica et Piscatoria** 47(1): 81-84. https://doi.org/10.3750/AIEP/02114
>
> MF carried out the sampling, morphological identification, conceived and designed the study. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 5: Molecular systematics of the long-snouted deep- water dogfish (Centrophoridae, *Deania*) with implications for identification, taxonomy, and conservation

> Stefanni S, Catarino D, Ribeiro PA, **Freitas M**, Menezes GM, Neat F, Stanković D (2021). Molecular systematics of the long-snouted deep-water dogfish (Centrophoridae, *Deania*) with implications for identification, taxonomy, and conservation. **Frontiers in Marine Science**, 7: 1-14. https://doi.org/10.3389/fmars.2020.588192
>
> MF went in research campaigns to obtain the specimens, carried out the sampling, morphological identification of the Madeira specimens, the data treatment of madeira specimens and contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 6: Taxonomic status of the rough long nose dogfish *Deania hystricosa* (Centrophoridae)

> Marrero M, Hernández M, Martin, MV, Casañas I, **Freitas M**, Pascual-Alayón PJ (**submitted 1**). Taxonomic status of deep-sea sharks *Deania calcea* and *D. hystricosa* (Centrophoridae). **Regional Studies in Marine Science**

PART III –DEEP SEA CHONDRICHTHYES FROM MADEIRA SEAMOUNTS

Chapter 7: Records of some rare deep-sea fishes caught in the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira (East-Central Atlantic)

> Delgado J, Carvalho D, **Freitas M**, Biscoito M, Gouveia EP (2017). Records of some rare deep-sea fishes caught in the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira (east-central Atlantic). **Acta**

Ichthyologica et Piscatoria 47(1): 91-96. https://doi.org/10.3750/AIEP/02088

MF went in research campaigns to obtain the specimens, carried out the sampling, morphological identification of the chondrichthyes and contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 8: Biodiversity in seamounts: The Madeira-Tore and Great Meteor. BIOMETORE 5 cruise report

Biscoito M, Araújo G, Henriques P, Martins F, Sousa R, **Freitas M**, Delgado J (2017). Biodiversity in seamounts: The Madeira-Tore and Great Meteor. BIOMETORE 5 cruise report. **Bocagiana**, 244: 1-9

MF carried out the sampling and the morphological identification of the Chondrichthyes. Data treatment of his group including and contributed to reach the final version.

Chapter 9: Sharks, rays and chimaeras of the Seine and Unicorn seamounts (NE Atlantic Ocean)

Freitas M, Sousa R, Ideia P, Gaspar M, Delgado J, Costa AL, Santos A, Biscoito M (2021). Sharks, rays and chimaeras of the Seine and Unicorn seamounts (NE Atlantic Ocean). **Marine Biodiversity Records**, 14: 1-10. https://doi.org/10.1186/s41200-021-00218-4

MF went in research campaigns to obtain the specimens, carried out the sampling and morphological identification. Conceived and designed the study. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

PART IV - DEEP SEA CHONDRICHTHYES FISHERIES AND BIOLOGY

Chapter 10: Long term overview of elasmobranch fisheries in an oceanic archipelago: the case study of Madeira Archipelago

Freitas M, Gaspar M, Ideia P, Delgado J, Sousa R (**submitted 2**). Long-term overview of elasmobranch fisheries in an oceanic archipelago: the case study of Madeira archipelago. **Marine Policy**

MF conceived and designed the study. Contributed to data analyses. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 11: Long-term population status of the commercially exploited shark *Centrophorus squamosus* in an oceanic archipelago

> **Freitas M**, Ideia P, Costa AL, Faria G, Kaufmann M, Delgado J, Sousa R (**submitted 3**). Long-term population status of the commercially exploited shark *Centrophorus squamosus* in an Ocean archipelago. **Regional Studies in Marine Science**
>
> MF carried out the sampling since 1996. Contributed to data treatment and analyses. Conceived and designed the study. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 12: Length-weight relationships for eight Chondrichthyes from the north-eastern Atlantic Ocean

> **Freitas, M.**, Ideia, P., Biscoito, M., Kaufmann, M., & Sousa, R. (2022). Length-weight relationships for eight Chondrichthyes from the north-eastern Atlantic Ocean. **The Egyptian Journal of Aquatic Research**, 49, 87–90. https://doi.org/10.1016/j.ejar.2022.01.002
>
> MF went in research campaigns to obtain the specimens, carried out the sampling and morphological identification. Conceived and designed the study. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

Chapter 13: Assemblages of deep-sea fishes on the middle slope off Northwest Africa (26°–33° N, eastern Atlantic)

> Pajuelo, J. G., Seoane, J., Biscoito, M., **Freitas, M.**, González, J. A. (2016). Assemblages of deep-sea fishes on the middle slope off Northwest Africa (26°–33° N, eastern Atlantic). **Deep-Sea Research Part I**, 118: 66-83. https://doi.org/10.1016/j.dsr.2016.10.011
>
> MF carried out the sampling and the morphological identification of the Chondrichthyes. Data treatment of his group including and contributed to reach the final version.

Chapter 14: Deep-sea sharks as by-catch of an experimental fishing survey for black scabbardfishes (*Aphanopus* spp.) off the Canary Islands (NE Atlantic)

> **Freitas M**, Costa L, Delgado J, Jiménez S., Timóteo V, Vasconcelos J, González JA (2018). Deep-sea sharks as by-catch of an experimental fishing survey for black scabbardfishes (*Aphanopus* spp.) off the Canary Islands (NE

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MF conceived and designed the study. Carried out the sampling and morphological identification and data analisys. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein

PART V - GENERAL DISCUSSION

Chapter 15: General discussion

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PART II

SYSTEMATICS AND DISTRIBUTION

Chapter 2

Annotated checklist of the fishes of the archipelago of Madeira (NE Atlantic): I – Chondrichthyes

CHAPTER 2 - Annotated checklist of the fishes of the archipelago of Madeira (NE Atlantic): I – Chondrichthyes

Abstract

As part of an annotated checklist of fishes of the archipelago of Madeira, a list with all cartilaginous fishes recorded from the archipelago is presented. The list contains 67 species of sharks, rays and chimaeras, whose presence in the area the authors consider confirmed. Another 14 species previously referred for the area are now considered dubious records and five species are withdrawn from the list. *Centrophorus uyato* is here recorded for the first time from Madeira. Three species (*Mitsukurina owstoni*, *Odontaspis noronhai* and *Chimaera opalescens*) are so far only present in Madeira within Macaronesia. The 67 confirmed species are based on occurrences, substantiated by specimens in natural history museum collections or other published evidence. For all species, the first reference is given, as well as other relevant references for the archipelago and remaining Macaronesia.

Keywords

Pisces, cartilaginous fishes, checklist, Madeira Archipelago, NE Atlantic Ocean.

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Introduction

The archipelago of Madeira is located between 32°37'52" N and 32°52'08" N and 16°39'19" W and 17°15'54" W, 754 km off the West coast of Africa and 980 km to the southeast of Europe. The archipelago is part of the biogeographic region of Macaronesia, which includes the Azores, the Canary Islands and the Cape Verde (Báez & Sánchez-Pinto 1983; Beyhl *et al.* 1995).

The archipelago includes the inhabited islands of Madeira and Porto Santo and the Desertas and Selvagens Islands; these last two are nature reserves, the permanent human presence being restricted to wardens and scientists. They are all of volcanic origin, being Madeira the youngest with no more than 7 million years and they are characterized by having a very narrow shelf followed by a very steep slope down to the abyssal plain (Geldmacher *et al.* 2000). The oceanic area in which the archipelago is located is considered oligotrophic (Parsons *et al.* 1984), and upwelling events are sporadic and very localized (Caldeira *et al.* 2002).

The first reference to the cartilaginous fish from Madeira in the scientific literature, was given by Bowdich (1825) (*Sphyrna zygaena*, *Dalatias licha* and *Squalus acanthias*). Lowe (1843-60), in his reference work *A History of the Fishes of Madeira,* lists only four species ofsharks and rays, but on the overall ofhis scientific production (1833-1860), 26 species were recorded. Johnson (1885) in his *Handbook for Madeira* mentioned 24 species of sharks and 14 of rays, still he did not detailed. Maul (1948) in his systematic list of the fishes recorded from Madeira, listed 46 species of cartilaginous fish. More recently, Wirtz *et al.* (2008) on an annotated checklist ofthe coastal fishes of Madeira with new records, listed 35 cartilaginous species, although some were considered doubtful. Carneiro *et al.* (2014) on the checklist of marine fishes from Portugal, including the archipelagos of the Azores and Madeira, record 76 cartilaginous fish species from Madeira, but in many cases these records are not based on specific references or specimens in collection. According to Fishbase (Froese & Pauly 2017), the list of cartilaginous species from Madeira sums up to 60 species, but among them some are questionable.

Since its foundation in 1929, the Funchal Natural History Museum, largely due to the efforts of G. E. Maul (1909-1997), who established a link between the Museum and the local fishermen and monitored over more than 50 years the Funchal fish market, gathered a large collection of cartilaginous fish species. Maul's work was continued by the authors and it became clear that not only over twenty species occurring in Madeiran waters have escaped other authors' attention, but also some species listed in the literature were dubious or erroneous records. It is then justified to present an updated checklist of the cartilaginous fishes occurring within the 200-mile exclusive economic zone of Madeira, based either on specimens in collection or on reliable published information.

Material and methods

For the purpose of the present paper, the study area is the well-established 200-mile Exclusive Economic Zone (EEZ) of Madeira (Fig. 1), an area ofapproximately 446,000 km^2 mostly covering deep (abyssal) oceanic waters. Although Portugal has presented to the United Nations Commission on the Limits of the Continental Shelf a proposal to extend the limits of its continental shelf (EMEPC 2009), the authors have opted to consider the EEZ as the boundary of the study area due, on one side, to the difficulty to establish the limits of the waters of the archipelago in the new context of the aforementioned extension and on the other, to the fact that the status ofthe waters over the extension area will remain intemational waters and at depths covered by the extension of the platform few species of cartilaginous fish could be considered strictly benthic.

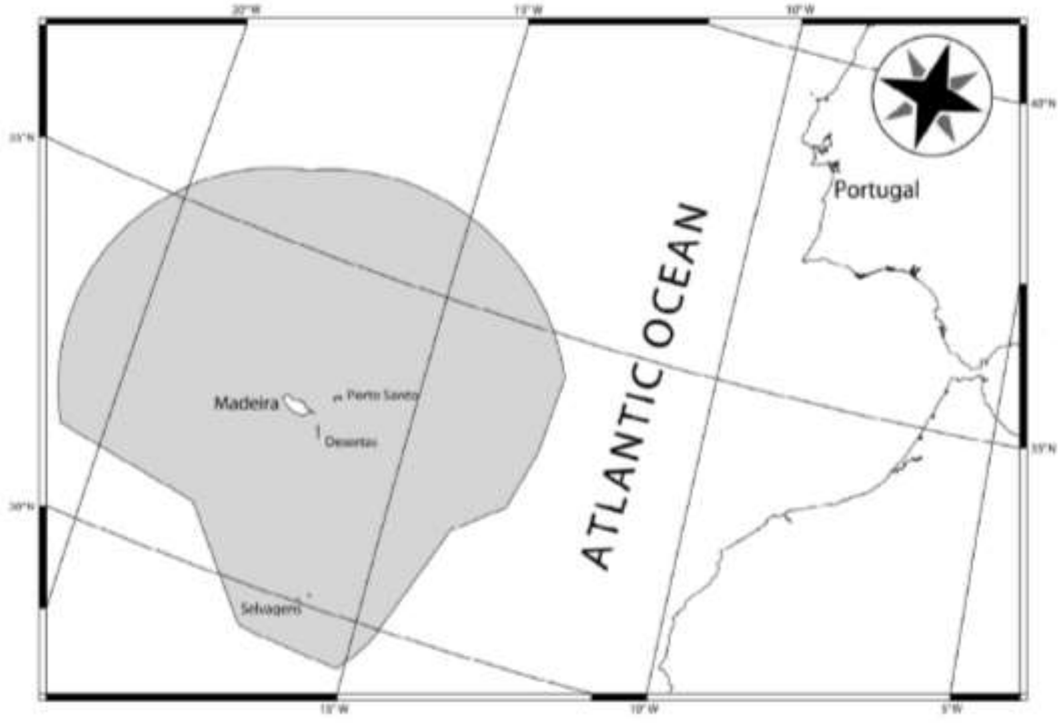

Figure 1. The archipelago of Madeira, showing the 200-mile Exclusive Economic Zone (in grey), which is the area covered by the present checklist.

ln order to produce the present checklist, an extensive bibliographic review was done, covering the last 300 years, from Bowdich (1825) until Biais *et al.* (2017). Whenever possible, information from museum collections was also gathered. These included the Funchal Natural History Museum (MMF), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), the American Museum of Natural History, New York (AMNH), the California Academy of Sciences, San Francisco (CAS), the National Natural History Museum, Paris (MNHN), The Natural History Museum, London (BMNH) and the Field Museum of Natural History, Chicago (FMNH). Other sources used: Direção de Serviços de Investigação da Direção Regional das Pescas (DSI) (Madeira Fisheries Research Laboratory).

This list is organized taxonomically, following the classification and nomenclature of Eschmeyer *et al.* (2017) for sharks and chimaeras and Last *et al.* (2016c) for rays.

The species were grouped in three categories: A) the accepted checklist. Species whose presence in the study area was published in a reliable source and/or are present in a museum collection, following the recommendations of Bello *et al.* (2014). Oceanic species with confirmed wide distributions around the study area (e.g. *Carcharodon carcharias*), were also included in this category, based only on catalogue-type literature or photographs. B) doubtful records in need of confirmation. This category contains all the species that, in spite having been referred by authors as occurring in the area, neither specimens in museum collections were found, nor reliable observations were recorded and therefore cannot be accepted as being part of the checklist, until specimens from Madeira are collected and deposited in museum collections. C) species to withdraw from the list. This category contains all the species that, in spite having been referred in the literature as occurring in the area, their records were either imprecise, not based on collected specimens, eventually unlike to occur in the area of Madeira or may configure misidentification. Species in this category are withdrawn from the list of Chondrichthyans from Madeira.

The vernacular Madeiran and English names are also given for each species, when available. Species present in MMF collection are marked with an asterisk (*) and a solid black triangle (Δ) means the type locality is Madeira, *sensu lato*.

For each species, all references for the study area available to the authors are given, starting by the first record.

MMF specimens are currently deposited at the Funchal Marine Biology Station and from 1999 onwards, from each specimen, ethanol fixed tissue samples have also been preserved.

Results

Up to the present and following the criteria adopted, 67 species of Chondrichthyes belonging to 24 families are recorded from the archipelago of Madeira, in the sense of the study area (see above). Of these, *Centrophorus uyato* is here recorded for the first time. Fourteen species are considered doubtful records and without confirmed specimens in hand should not be considered as forming part of the fauna of the study area. Five species do not meet any of the criteria adopted and are therefore excluded from the fauna of the study area, for the sake of precision in biodiversity knowledge. Concerning the item Macaronesia distribution, only three of the species present in the following checklist were just recorded from Madeira.

A. Accepted checklist

CLASS ELASMOBRANCHII

ORDER HEXANCHIFORMES

Family Chlamydoselachidae

* *Chlamydoselachus anguineus* Garman, 1884 - No common name in Madeira; Frilled shark.

Collet 1890: 219-20 / Belloc 1934: 150 / Noronha & Sarmento 1934: 137 / Nobre 1935: 411 / Fowler 1936:24 / Noronha & Sarmento 1948: 77 / Maul 1948: 137 / Albuquerque 1954-56: 74 / Boeseman 1973: 10 / Cadenat & Blache 1981: 15 / Compagno 1984a: 14-15 / Boeseman 1984: 76 / Sanches 1986: 5 / Lloris *et al.* 1991: 224 / Carneiro *et al.* 2014: 12 / Delgado *et al.* 2017.

Distribution in Macaronesia. Madeira and the Azores (Porteiro *et al*. 2010; Carneiro *et al*. 2014). Also present in the Canary Islands (J.A. González, pers. comm. 2013).

Remarks. there are six specimens in MMF collection, the oldest dating back to 1940. Maul (1948) refers as rare.

Family Hexanchidae

* *Heptranchias perlo* (Bonnaterre, 1788) - Bico-doce; Sharpnose seven-gill shark.

Lowe 1838: 194 I Günther 1870: 398 (as *Notidanus cinereus*).

Nobre 1935: 414 (as *Heptanchus cinereus*).

Fowler 1936: 27 / Noronha & Sarmento 1948: 94 / Maul 1948: 137 / Nunes 1953: 63 / Albuquerque 1954-56: 77 / Boeseman 1973: 9 / Boeseman 1984: 72 / Sanches 1986: 50 / Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Santos et *al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996; 2005; Menezes *et al*. 2004).

Remarks. There are two specimens in MMF collection (MMF36031, MMF42318), the oldest dating back from 1961. Maul (1948) refers as frequent, all year.

* *Hexanchus griseus* (Bonnaterre, 1788) - Albafar; Bluntnose sixgill shark

Lowe 1838: 194 (as *Notidanus griseus*).

Belloc 1934: 151 / Noronha & Sarmento 1934: 96, 140 / Fowler 1936: 26 / Noronha & Sarmento 1948: 91 / Maul 1948: 137 / Nunes 1953: 52 / Albuquerque 1954-56: 75 / Boeseman 1984: 73 / Sanches 1986: 49 / Carneiro *et al*. 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005).

Remarks. there are three specimens in MMF collection (one mounted on exhibition), the oldest dated from 1951 and the most recent from 2007. Although Maul (1948) refers as rare, there are regular observations of interaction between this species and deep bottom fish traps.

ORDER ORECTOLOBIFORMES

Family Rhincodontidae

Rhincodon typus Smith, 1828 - Tubarão-baleia, pintado; Whale shark

Wirtz *et al*. 2008: 3 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Monteiro *et al*. 2008; Wirtz *et al*. 2013).

Remarks. the species has been observed underwater by divers, including ichthyologists, in coastal waters of the island of Madeira and by Madeiran tuna fleet fishermen. Although there are no specimens in collection from the area, the oceanic character and actual distribution range and the unmistakable external characters of this species, validates its inclusion in this checklist.

ORDER LAMNIFORMES

Family Alopiidae

*$^{\Delta}$ *Alopias superciliosus* Lowe, 1841 - Peixe-rato-de-natura; Bigeye thresher

Lowe 1841: 39 (as *Alopecias superciliosus*).

Springer 1973a: 17 / Cadenat & Blache 1981: 145-149 / Compagno 1984a: 231-232 / Quéro 1984a: 91 /

Sanches 1986: 60 / Lloris *et al*. 1991: 220 / Wirtz *et al*. 2008: 3 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Arruda 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Cadenat & Blache 1981).

Remarks. Madeira is the type locality, but the holotype is unknown. There is one formalin preserved specimen in MMF collection, dated from 2012 (MMF 42302), caught on the black scabbard fish longline. Although this species has economic importance in many regions of the world (Nieto *et al*. 2015), in Madeira it is not used for consumption (Nunes 1953). ln 1996 during the project ARQMAD-02-P96 of the DSI, one specimen of this species was caught SW of Porto Moniz, Madeira, while hauling a bottom longline at 800-900 m depth.

* *Alopias vulpinus* (Bonnaterre, 1788) - Peixe-rato; Thresher

Lowe 1838: 194 (as *Carcharias vulpes*).

Lowe 1852: 253 / Belloc 1934: 140 / Nobre 1935: 438-439 (as *Alopias vulpes*).

Noronha & Sarmento 1934: 122 and 135 (as *Alopecias vulpes*).

Fowler 1936: 43 / Maul 1948: 138 / Albuquerque 1954-56: 85 / Springer 1973a: 17 / Cadenat & Blache 1981:143-144 / Sanches 1986: 59 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Arruda 1997; Porteiro *et al*. 2010) and Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. one mounted specimen in the MMF exhibition. Maul (1948) refers as frequent all year.

Family Cetorhinidae

* *Cetorhinus maximus* (Gunnerus, 1765) - Peixe-frade; Basking shark

Johnson 1885: 202 / Noronha & Sarmento 1934: 110, 144 / Nobre 1935: 440 (as Selache maxima).

Noronha & Sarmento 1948: 106 / Maul 1948: 138 / Nunes 1953: 138 / Albuquerque 1954-56: 901 / Springer 1973a: 16 / Sanches 1986: 58 / Carneiro *et al.* 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996; Wirtz *et al*. 2013).

Remarks. in the MMF collection there are a skin dated from 1937 (MMF 606) and a stranded specimen preserved in formalin dated from 2000 (MMF 31368). To our knowledge this was the last documented occurrence of the species in Madeira. Maul (1948) refers the species as occasional visitor.

Family Lamnidae

Carcharodon carcharias (Linnaeus, 1758) - Tubarão-branco, Great white shark

Lichtenstein 1844: 2 (as *Squalus carcharias*).

Albuquerque 1954-1956: 89 / Springer 1973a: 13 / Compagno 1984a: 238-242; 2001: 100 / Quéro 1984b: 84 / Sanches 1986: 56 / Lloris *et al*. 1991: 223 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005).

Remarks. although there are no specimens in MMF collection, the species is included in the present checklist since it was visually identified several times in Madeira EEZ, including by one of the authors (MB). The DSI reported a capture in 1982 of one specimen in a tuna longline at a depth of168-200 m, SW of Porto Santo. Wirtz *et al*. (2008) did not include it in their checklist since it was not considered a coastal fish (recorded only from the open ocean).

* *Isurus oxyrinchus* Rafinesque, 1810 - Marracho; Shortfin mako

Günther 1870: 390 / Noronha & Sarmento 1934: 115 (as *Lamna spallanzanii*).

Maul 1948: 138 / Nunes 1953: 158 / Noronha & Sarmento 1948: 111 (as *Lamna oxyrinchus*).

Albuquerque 1954-56: 87 (as *lsurus oxyrhynchus* sic).

Fowler 1936: 33 / Springer 1973a: 14 / Cadenat & Blache 1981: 157-160 / Quéro 1984b: 85 / Sanches 1986: 57 / Wirtz *et al*. 2008: 21 / Carneiro *et al*. 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Porteiro *et al*. 2010), the Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al*. 2013).

Remarks. Maul (1948) refers as doubtful record (see Remarks on next species), but there is one mounted specimen (no date) in MMF exhibition and two formalin preserved specimens dated from 2011 (MMF 41667) and 2015 (MMF 44383).

* *Lamna nasus* (Bonnaterre, 1788) - Marracho; Porbeagle

Lowe 1838:1941 / Belloc 1934: 138 / Noronha & Sarmento 1934: 115 and 140 / Nobre 1935: 430 (as *Lamna cornubica*)

Fowler 1936: 32 / Albuquerque 1954--56: 86 (as *Isurus nasus*)

Noronha & Sarmento 1948: 111 / Maul 1948: 137 / Nunes 1953: 158 / Springer 1973a: 13 / Sanches 1986: 55 I Compagno 1984a: 248-249 I Wirtz *et al*. 2008: 2 I Carneiro *et al*. 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002) and Cape Verde (Reiner 1996, 2005).

Remarks. although there are no preserved specimens collected in Madeira, these waters are inside the species' distribution area (Ebert & Stehmann 2013). Moreover, a recent study on migration patterns of porbeagle shark in the Northeast Atlantic, confirmed the occurrence of this species to Madeiran waters, with one of the tagged sharks being spotted off Madeira (Biais *et al.* 2017). Wirtz *et al*. (2008) refer that it was erroneously noted as common by Maul (1948), due to a typographical error. This remark was originally meant for *Isurus oxyrhynchus* and the reference to a doubtful presence, for *L. nasus*. (pers. comm. of G. E. Maul to M. Biscoito).

Family Mitsukurinidae

* *Mitsukurina owstoni* Jordan, 1898 - No common name in Madeira; Goblin shark (Fig. 2)

Cadenat & Blache 1981: 138-141 / Quéro 1984b: 82 / Sanches 1986: 54 / Lloris *et al*. 1991: 232 / Compagno 1984a: 223-224; 2001: 69-70 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. recorded only from Madeira.

Remarks. in MMF there are two formalin preserved specimens, the first dated from 1956 (MMF 8196) and the other one dated from 2004 (MMF 36064). To our knowledge, the latter was the last specimen of this species to be caught in Madeiran waters. It was caught in a bottom long line at Funchal Bay at 2500 m of depth, in the framework of project PESCPROF-1.

Figure 2. *Mitsukurina owstoni* (MMF 8196). Female, 3100 mm TL, caught at Madeira in 1956 by the black scabbard fish fishermen.

Family Odontaspididae

* *Odontaspis ferox* (Risso, 1810) -Tubarão-da-areia; Smalltooth sand tiger

Maul 1955: 1 (as *Carcharias ferox*).

Springer 1973b: 11 / Compagno 1984a: 219-221; 2001: 64-66 / Quéro 1984b: 80 / Springer 1990: 81-82 / Lloris *et al*. 1991: 234 / Sanches 1986: 52 / Carneiro *et al*. 2014: 10.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Menezes *et al*. 2004).

Remarks. there are two specimens in the MMF collection, a skin (MMF 2478) and a mounted specimen on exhibition (MMF 2678), both obtained in 1941. Maul (1948) refers only the presence of the genus *Odontaspis*, as *O. noronhai* was already in the collection, but not yet described, and conspired it very rare.

*$^{\Delta}$ *Odontaspis noronhai* (Mau], 1955) - No common name in Madeira; Bigeye sand tiger shark (Fig. 3)

Maul 1955: 3 as *Carcharias noronhai.*

Springer 1973b: 11 / Cadenat & Blache 1981: 131-132 / Compagno 1984a: 221-222 / Quéro 1984b: 81 / Springer 1990: 82 / Lloris *et al.* 1991: 204 / Sanches 1986: 53 / Carneiro *et al.* 2014: 10.

Distribution in Macaronesia. Recorded only from Madeira.

Remarks. Madeira is type locality. The holotype is a mounted female specimen, caught off Câmara de Lobos, Madeira, between 600-1600 meters of depth in 13/04/1941 (MMF 2691). A formalin preserved specimen (MMF 3376) is also present in MMF collection, but collection details are unknown. Maul (1948) stated the genus *Odontaspis* as very rare.

Figure 3. *Odontaspis noronhai*, Holotype (MMF 2691). Mounted specimen on permanent exhibition at MMF.

ORDER CARCHARHINIFORMES

Family Carcharhinidae

Carcharhinus falciformis (Müller & Henle, 1839) - No common name in Madeira; Silky shark (Fig. 4)

Lowe 1839: 90 in part (as *Carcharius falcipinnis*).

Lowe 1843: 93 (as *Charcharias falcipinnis*).

Noronha & Sarmento 1934: 110 and 137 (as *Carcharias faclcipinis* sic).

Compagno 1973: 24; 1984b: 470-472 / Sanches 1986: 69 / Lloris *et al.* 1991: 223 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Arruda 1997), Canary lslands (Brito et al. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Wirtz *et al.* 2013).

Remarks. the record of this species has been controversial. Lowe (1839) describes *C. falcipinnis* as new to science, due to the absence of comparative material, and gives the vernacular Madeiran name of "Faqueita" which is currently used for *C. galapagensis* / *C. obscurus* ("Faquêta"). Later Lowe (1843) considered that his species was as synonym of *C. melanopterus* (Quoy & Gaymard, 1824). This is very doubtful, not only because *C. melanopetrus* has not yet been recorded from the Atlantic Ocean, but also because Lowe himself did not mention the conspicuous black fin tips in the original description. Compagno (1973) considers *C. falcipinnis* in part as synonym of *C. falciformis*. Wirtz *et al.* (2008) state that this species needs confirmation and Carneiro *et al.* (2014) accept its presence in Madeira based on the known wide geographical distribution given by Ebert and Stehmann (2013). The holotype of *C. falcipinnis* is not known, but recently one of the authors (MB) examined a mounted specimen in The Natural History Museum collection (BMNH 1851.4.9.14), from Madeira and presented by R. T. Lowe in 1851, labelled as *C. obscurus*, and concluded, based mainly on the origin of first dorsal fin in relation to the pectoral fin's free rear tip (the first well behind the latter), that it is *C. falciformis*, thus confirming the presence of the species in Madeira.

Figure 4. *Carcharhinus falciformis* (BMNH 1851.4.9.14). Specimen from Madeira presented to The Natural History Museum, London, by the Rev. Richard Thomas Lowe in 1851.

* *Carcharhinus galapagensis* (Snodgrass & Heller, 1905) - Faquêta; Galapagos shark

Compagno 1984b: 473-474 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Brum & Azevedo 1995; Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. one mounted specimen in MMF (MMF 023409) collection dated from ca. 1940, in poor state of preservation. Carneiro *et al.* (2014) mention the presence of this species in the Azores and Madeira but pointed out that according to Ebert & Stehmann (2013), the species *C. obscurus* is very closely related with *C. galapensis* and difficult to distinguish from each other. Recent molecular studies suggested that these two species might in fact be a single one, with one of the two forms being found far from landmasses (*C. galapagensis*) and the other one (*C. obscurus*) occurring in association with continental shelves and upper slopes. Studies are currently on-going to determine the relationship between these two species (Ebert & Stehmann 2013). For the time being we have opted to maintain this species in the Madeiran checklist, with the reserve stated above.

* *Carcharhinus limbatus* (Müller & Henle, 1839) - Tubarão, Anequim; Blacktip shark

Lowe 1841: 38; 1843: 93 / Noronha & Sarmento 1934: 133, 137; 1948: 132 (as *Carcharias microps*).

Fowler 1936: 48 (as *Eulamia limbatus*).

Maul 1948: 138 (as *Charcharias limbatus*).

Albuquerque 1954-56: 104 / Compagno 1973: 24; 1984b: 481-483 / Branstetter 1984a: 106 / Sanches 1986: 70 / Lloris *et al.* 1991: 223 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Arruda 1997), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. Lowe's specimen is unknown. One formalin preserved specimen in MMF collections dated from 2008 (MMF 39543). Although Wirtz *et al.* (2008) considered a very doubtful record, the existence of a preserved specimen in MMF collections confirms the presence of the species in the area of Madeira.

* *Carcharhinus longimanus* (Poey, 1861) - No common name in Madeira; Oceanic whitetip shark.

Maul 1955: 4 / Compagno 1973: 24; 1984b: 484-486 / Cadenat & Blache 1981: 265-267 / Branstetter 1984a:107 / Sanches 1986: 71 / Lloris *et al.* 1991: 223 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel, 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. Five specimens in MMF collections (one mounted specimen and formalin preserved specimens), first collected in 1938 and last one in 1953. The occurrence of the species in Madeiran waters is rare.

* *Carcharhinus obscurus* (Lesueur, 1818) - Faqueta; Dusky shark (Fig. 5)

Lowe 1839: 90 in part (as *Charcharius falcipinnis*).

Günther 1870: 366 / Belloc 1934: 131 / Noronha & Sannento 1948: 106 / Maul 1948: 138 (as *Carcharias obscurus*).

Fowler 1936: 49 (as *Eulamia obscurus*).

Albuquerque 1954-56: 103 / Compagno 1973: 25; 1984b: 489-4 / Cadenat & Blache 1981: 268-270 / Sanches 1986: 72 / Lloris *et al.* 1991: 223 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Arruda 1997), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. A skin sample in MMF collection identified by G. E. Maul, but with no indication about collection date and location and two specimens preserved in BMNH (1895.5.8.143 and 2015.11.11.1), the former from the Selvagens Islands and the latter from Madeira, possibly sent by R. T. Lowe and with an indication on the label as a possible syntype of *C. falcipinnis* Lowe, 1839. Both specimens were seen by one of the authors (MB) and bear all *C. obscurus* diagnostic characters given by Ebert & Stehmann (2013).

Figure 5. *Carcharhinus obscurus* (BMNH 1895.5.8.143). Male specimen (855 mm TL), caught at Selvagem Grande in 1895 and presented to The Natural History Museum, London, by Cecil Baring and Ogilvie Grant.

On the validity of this species, see remarks on *C. galapagensis* above. Maul (1948) refers as rare, pelagic at surface and coastal.

* *Prionace glauca* (Linnaeus, 1758) - Tintureira; Blue shark

Lowe 1838: 194 / Belloc 1934: 131 / Noronha & Sarmento 1934: 131, 137; 1948: 129 / Nunes 1953: 235 (as *Carcharias glaucus*).

Fowler 1936: 54 / Albuquerque 1954-56: 100 (as *Glyphis glaucus*).

Compagno 1973: 30, 1984b: 521-524 / Branstetter 1984a: 113 / Cadenat & Blache 1981: 237-239 / Sanches 1986: 74 / Lloris *et al.* 1991: 236 / Wirtz *et al.* 2008: 3 / Carneiro *et al.* 2014: 12 / Almada *et al.* 2015: 4.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010), Canary Islands (Brito *et al.* 2002; Brito Hemández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. Seven specimens in MMF collections. Maul (1948) refers as frequent, pelagic from surface. Frequently seen on the south coast of Madeira, where small individuals have been seen nearshore (MF personal observation).

Family Pentanchidae

* *Apristurus laurussonii* (Saemundsson, 1922) - No common name in Madeira; Iceland catshark or Madeira catshark

Cadenat & Maul 1966: 60 / Compagno 1984b: 270 / Quéro 1984c: 96-97 / Cadenat & Blache 1981: 186 / Sanches 1986: 63 / Lloris *et al.* 1991: 221 (as *Apristurus maderensis*).

Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Saldanha & Biscoito 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014) and Canary Islands (Brito *et al.* 2002; Brito Hemández & Sancho Rafel 2003).

Remarks. Nakaya & Sato (1998) considered *A. maderensis* Cadenat & Maul (1966) as a junior synonym of *A. laurussonii*. Two formalin preserved specimens in MMF collections: MMF 18750, the holotype, collected in 1961 in a longline for the black scabbardfish *Aphanopus* spp., and MMF 36797, collected more recently in 2005 at Porto Santo.

* *Galeus melastomus* Rafinesque, 1810 - Leitão-do-mar; Blackmouth catshark

Lowe 1838: 194 (as *Scyllium artedi*)

Lowe 1843-1860: 93-97 / Günther 1870: 406 / Belloc 1934: 129 (as *Pristiurus melanostomus*).

Noronha & Sarmento 1934: 114, 143 (as *Pristiurus artedi*).

Nunes 1953: 156 / Albuquerque 1954-56: 95 (as *Galeus melanostomus*).

Fowler 1936: 40 / Noronha & Sarmento 1948: 110 / Maul 1948: 138 / Springer 1973c: 20 I Cadenat & Blache 1981: 167-171 / Sanches 1986: 64 / Menezes *et al.* 2009: 2690 / Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos et *al.*1997; Arruda 1997; Carneiro et *al.* 2014) and the Canary Islands (Brito et *al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. four formalin preserved specimens in MMF collections, the first dated from 1968 and the last one from 2004. Maul (1948) refers as frequent all year-round and the same author (1976) refers that although it is well known from Madeira, it is not often taken.

Family Pseudotriakidae

* *Pseudotriakis microdon* Brito Capello, 1868 - Mona; False catshark

Noronha 1926: 385 I Noronha & Sarmento 1934: 115 and 143 (as *Pseudotriacis microdon* sic)

Noronha & Sarmento 1948: 112 I Maul 1948: 138 I Nunes 1953: 160 I Albuquerque 1954-56: 96 I Cadenat & Blache 1981: 199-202 I Compagno 1984b: 378-379 I Quéro 1984c: 101 I Sanches 1986: 65 I Lloris *et al.* 1991: 236 I Menezes *et al.* 2009: 2690 I Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004).

Remarks. one formalin-preserved specimen caught on 19.11.1951, at Câmara de Lobos in a bottom long line (MMF 3270) and one mounted in MMF exhibition (no MMF number). There is also a skin from Madeira preserved in BMNH (1921.6.8.1.). Maul (1948) refers as rare.

Family Sphyrnidae

* *Sphyrna zygaena* (Linnaeus, 1758) - Tubarão-martelo, Cornuda; Smooth hammerhead

Bowdich 1825: 75 I Lowe 1838: 195 (as *Squalus zygaena*).

Lowe 1838: 195 I Lowe 1843-60: 83-86 I Günther 1870: 381 (as *Zygaena malleus*).

Noronha & Sarmento 1934: 107, 146 I Nobre 1935: 425 (as *Zygaena zygaena*).

Fowler 1936: 64 I Noronha & Sarmento 1948: 103 I Nunes 1953: 101 I Albuquerque 1954-56: 109 I Gilbert 1973: 32 I Sanches 1986: 76 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997, Porteiro *et al.* 201O), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. five formalin-preserved specimens in MMF collections, first dated from 1984 and the last one from 2013. Maul (1948) refers as frequent all year-round. Common in the island of Madeira and rarer in Porto Santo. Juveniles have been seen nearshore at Funchal during summer (MF personal observation).

Family Triakidae

* *Galeorhinus galeus* (Linnaeus, 1758) - Cação, Tope shark

Lowe 1838: 194 (as *Galeus vulgaris*).

Noronha & Sarmento 1934: 102 and 139 I Nobre 1935: 424 (as *Galeus galeus*).

Belloc 1934: 130 (as *Galeus canis*).

Fowler 1936: 57 1 Noronha & Sarmento 1948: 97 I Maul 1948: 138 I Nunes 1953: 81 I Albuquerque 1954-56: 98 I Compagno 1973: 27 I Cadenat & Blache 1981: 210-212 I Branstetter 1984b: 118 I Sanches 1986: 66 I Lloris *et al.* 1991: 228 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 201O), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. there are five registers in MMF collections, including skin, jaws and formalin preserved specimens, the first dated from 1944 and the last one from 2013. Maul (1948) refers as frequent all year, coastal, confirmed by recent observations.

* *Mustelus mustelus* (Linnaeus, 1758) - Caneja; Smooth-hound

Vinciguerra 1882-83: 608 (as *Mustelus vulgaris*).

Roule 1919: 115 (as *Galeorhinus mustelus*).

Belloc 1934: 130 (as *Mustelus laevis*).

Nobre 1935: 428 I Fowler 1936: 61 I Noronha & Sarmento 1948: 97 I Maul 1948: 138 I Albuquerque 1954-56:105-106 I Compagno 1973: 28, 1984b: 419 I Cadenat & Blache 1981: 221-222 I Branstetter 1984b: 119 I Sanches 1986: 67 I Lloris *et al.* 1991: 233 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997 stated that the first and only known record of the species to the Azores is based on Belloc (1934) and point that its occurrence in the region needs further documentation), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004; Wirtz *et al.* 2013).

Remarks. Vinciguerra (1882-83) states that the two specimens from Madeira were young and difficult to recognize the species' external characters. He assigned them to *M. vulgaris* Müller & Henle, 1839, based on the position of the dorsal fin insertion in relation to the internai margin of pectoral fin (over the middle of the internal margin of pectoral fin). Although *M. vulgaris* Müller & Henle, 1839 in partis now considered as a synonym of *M. asterias* Cloquet, 1819 (Compagno 1973), the character pointed by Vinciguerra clearly falls under *M. mustelus*. Fowler (1936) and Maul (1948) follow this reasoning, the latter consubstantiated with specimens in the MMF collection, re-determined by us. On this point we do not agree with Compagno (1973) who considers Fowler's (1936), Noronha

& Sarmento's (1948) and Maul's (1948) records of *M. mustelus* as *M. asterias* (see remarks under the latter in the next category).

ln MMF collections there are thirteen records of *M. mustelus*, including formalin preserved specimens, skin and jaws, the first dated from 1944 and the last one dated from 2013. Maul (1948) refers the species as frequent all year and coastal. Commonly seen around the island of Madeira all year-round, with juveniles being seen in schools nearshore.

ORDER SQUALIFORMES

Family Centrophoridae

* *Centrophorus granulosus* (Bloch & Schneider, 1801) - Ramudo; Gulper shark

Günther 1870: 420-421 I Belloc 1934: 146 I Nobre 1935: 448 I Fowler 1936: 73 I Noronha & Sarmento 1948:122 I Maul 1948: 138 I Nunes 1953: 200 I Albuquerque 1954-56: 120 I Cadenat & Blache 1981: 54-56 I Krefft & Tortonese 1973: 38 I Compagno 1984a: 37-38 I McEachran & Branstetter 1984: 130 I Sanches 1986: 80 I Lloris *et al.* 1991: 223 I Carneiro *et al.* 2014: 13.

Maul 1948: 139 I Carneiro et al. 2014: 13 (as *Centrophorus lusitanicus*).

Freitas & Biscoito 2007: 5 I Carneiro et *al. 2014*: 13 (as *Centrophorus niaukang*).

Distribution in Macaronesia. Madeira, Azores (Santos et *al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Menezes *et al.* 2012), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004).

Remarks. According to White *et al.* (2013) *C. lusitanicus* Bocage & Capello, 1864 and *C. niaukang* Teng, 1959 are considered junior synonyms of *C. granulosus*. Both *C. lusitanicus* and *C. niaukang* had been recorded from Madeira (Maul 1948; Freitas & Biscoito 2007). White *et al.* (2013) did not see the specimens in MMF collection (20 records, from 1940 until 2004) and doubts remain about the synonymy of the Madeiran specimens previously identified as *C. niaukang* with *C. granulosus*, a subject currently under study.

*$^{\Delta}$*Centrophorus machiquensis* Maul, 1955 - Quelmo (Fig. 6)

Maul 1955: 5 I Krefft & Tortonese 1973: 39 I McEachran & Branstetter 1984: 131 I Lloris *et al.* 1991: 223 Cadenat & Blache 1981: 58-63 (as *Centrophorus* "forme" *uyato - machiquensis*).

Figure 6. *Centrophorus machiquensis,* Holotype (MMF 3767). Female, 1050 mm TL, caught off Machico, Madeira, in 1941. Drawing made from the mounted holotype by Helena Encarnação.

Distribution in Macaronesia. recorded with certitude only from Madeira. May also be present in the Canary Islands (A. Brito pers. comm.).

Remarks. Madeira is the type locality. The holotype is a mounted specimen on exhibition in the Funchal Natural History Museum (MMF 3767) and there are a skin and several formalin preserved specimens in MMF collections, from 1941 until 1996.

The taxonomic status of this species has been questioned by Krefft & Tortonese (1973), McEachran & Branstetter (1984), Compagno (1984b) and (Muñoz-Chapuli & Ramos (1989), all pointing in the direction of a synonymy with *C. granulosus*. Cadenat & Blache (1981) also questioned the validity of *C. machiquensis*, as they found not possible to separate *C. machiquensis* from *C. uyato* (Rafinesque, 1810). A revision of the latter is currently under way (White *et al*. 2013) and these authors recommend that *C. machiquensis* should be treated as a synonym of *C. uyato*, for the time being.

The authors have decided to retain *C. machiquensis* as a valid species, based on morphological and ecological characters, separating it from *C. granulosus* and from *C. uyato* and this matter is being treated elsewhere. See also remarks under *C. uyato*.

* *Centrophorus squamosus* (Bonnaterre, 1788) - Xara-branca; Leafscale gulper shark

Lowe 1852: 253 I Belloc 1934: 147 I Cadenat & Blache 1981: 63-68 I McEachran & Branstetter 1984: 132 I Compagno 1984a: 43-44 I Sanches 1986 I Lloris et *al.* 1991: 223 I Carneiro et *al.* 2014:13.

Johnson 1868: 713-714 (as *Machephilus dumerilli*).

Günther 1870: 422 (as *Centrophorus dumerilii*).

Fowler 1936: 78 I Noronha & Sarmento 1948: 132 I Maul 1948: 139 I Nunes 1953: 244 I Albuquerque 1954-56: 122 I Krefft & Tortonese 1973: 44 (as *Lepidorhinus squamosus*) I Martins & Ferreira, 1995 I Freitas & Biscoito 2001 I Severino et *al.* 2009 I Delgado *et al.* 2017.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Menezes *et al.* 2012) and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Apart from the holotype of *M. dumerilli* Johnson, 1868 in the BMNH collections (1865.5.20.15) and one fluid preserved specimen in the AMNH (1-73241 collected on 20.10.1972), there are several formalin preserved specimens, jaws and skins in MMF collections (first dated from 1917 and last one from 1965). Maul (1948) refers as frequent all year, occurring offshore and indeed this is the commonest Centrophorid species in the bycatch of the black scabbardfish longline fishery in Madeira.

Centrophorus uyato (Rafinesque, 1810)-No common name in Madeira; Little gulper shark - NEW RECORD (Fig. 7)

Distribution in Macaronesia. Madeira and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004).

Remarks. the usage of this name and validity of *C. uyato* is being debated for a long time, as it is pointed out by Muñoz-Chapuli & Ramos (1989), White *et al.* (2013) and Veríssimo *et al.* (2014). The authors have opted to preserve the present designation, based on the key provided by Veríssimo *et al.* (2014).

This new record is based on a preserved specimen in BMNH 1862.4.22.29, a 436 mm TL juvenile female caught at Madeira and presented by J. Y. Johnson. A thorough morphological comparison between this Madeiran specimen and specimens from *C. machiquensis* is being done to support the validity of the latter, unless the revision that is under way (White *et al.* 2013; Veríssimo *et al.* 2014) brings sound evidence that *C. machiquensis* is not a valid species. See also remarks under *C. machiquensis*.

Figure 7. *Centrophorus uyato* (BMNH 1862.4.22.29). Juvenile female (436 mm TL) from Madeira presented to The Natural History Museum, London, by J. Y. Johnson in 1862.

* *Deania calcea* (Lowe, 1839)-Gata; Birdbeak dogfish

Lowe 1839: 92 as *Acanthidium calceus.*

Lowe 1849: 19 I Garman 1913: 216 I Albuquerque 1954-56: 123 (as *Acanthidium calceus*).

Lowe 1843: 93 I Günther 1870: 423 I Belloc 1934: 145 I Nobre 1935: 454 (as *Centrophorus calceus*).

Capello 1872: 88 (as *Centrophorus crepidalbus*).

Fowler 1936: 79 I Mau] 1948: 139 I Nunes 1953: 217 I Krefft & Tortonese 1973: 42 I Nunes 1974 I Cadenat & Blache 1981: 69-72 I McEachran & Branstetter 1984: 137 I Sanches 1986 (as *Deania calceus*) Compagno 1984a: 65-66 I Carneiro *et al.* 2014: 13.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997), the Canary lslands (Brito *et al.* 2002) and Cape Verde (Hanel & John 2014).

Remarks. Madeira is the type locality. One preserved specimen in BNHM collections (1861.5.19.33), skin samples in MNHN (IC-AA-0025, collected by J. Cadenat in 1960 at 32º 30' N; 14° 0' W). Two preserved specimens in MMF collections (MMF 40030, MMF 42319). Maul (1948) refers as frequent all year, occurring offshore. A detailed comparative study including genetic analysis, of the species of *Deania* from off Portugal mainland, Madeira, Azores, Morocco, Mauritania, Cabo Verde and Namibia is being done by one of the authors (MF).

* *Deania hystricosa* (Garman, 1906) - Sapata; Rough longnose dogfish

Cadenat & Blache 1981 (as *Deania maufi*).

Compagno 1984a: 66-67 (as *Deania histricosa* sic) Carneiro *et al.* 2014: 13 1 Delgado *et al.* 2017.

Distribution in Macaronesia. Madeira and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Several formalin preserved specimens in MMF collections collected in 2004 and 2005. Type material of *D. maufi* in MNHN (1969-296, 298, 299, 300). This is the largest and probably the commonest of the three *Deania* species occurring in Madeira and is caught as a by-catch of the black scabbard fish fishery. See other remark under *D. calcea*.

* *Deania profundorum* (Smith & Radcliffe, 1912) - Sapata; Arrowhead dogfish

Freitas & Biscoito 2007: 5-6 I Carneiro *et al.* 2014: 13 1 Delgado et *al.* 2017.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Porteiro *et al.* 2010), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004).

Remarks. eight formalin preserved specimens in MMF collections (first dated from 1968 and last one from 2013). One specimen preserved in BMNH collections (1986.11.7.1). See other remark under *D. calcea*.

Family Dalatiidae

* *Dalatias licha* (Bonnaterre, 1788) - Gata, Trabolha; Kitefin shark

Bowdich 1825: 74 (as *Scymnus licha*).

Lowe 1838: 194 (as *Scymnus nicaeensis*).

Günther 1870: 425 I Collet 1890: 219 I Roule 1912: 17 I Noronha & Sarnento 1934: 144 (as *Scymnus lichia*).

Krefft & Tortonese 1973: 46 (as *Scymnorhinus licha*).

Fowler 1936: 86 I Noronha & Sarmento 1948: 107 I Maul 1948: 139 I Nunes 1953: 148 I Albuquerque 1954-56: 132 I McEachran & Branstetter 1984: 136 I Compagno 1984a: 63-64 I Sanches 1986: 90 I Lloris *et al.* 1991:225 I Carneiro *et al.* 2014: 14 I Delgado *et al.* 2017.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al*. 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005).

Remarks. skin, oil, jaws and formalin preserved specimens in MMF collections (dated from 1940, 42 and 44). The DSI in the framework of the project ARQMAD-02-P96, 1996 caught this species using bottom long-lines at a depth 600-700 m, SW of Porto Moniz, Madeira. Maul (1948) referd it as frequent all year, from offshore.

* *Squafiofus laticaudus* Smith & Radcliffe, 1912 - Tubarão-anão; Spined pygmy shark

Noronha 1926: 386 I Noronha & Sarmento 1934: 144; 1948: 22 (as *Squaliolus sarmenti*)

Maul 1948: 139 I Albuquerque 1954-56: 135 (as *Euprotomicrus sarmenti*).

Lloris et *al.* 1991: 239 (as *Squaliodus laticaudus* sic).

Krefft & Tortonese 1973: 48 I Cadenat & Blache 1981: 108-111 I McEachran & Branstetter 1984: 145 I Compagno 1984a: 108-109 I Sanches 1986: 94 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Silva *et al.* (1998) report as the first record of the species to Azores; Santos *et al.* (1997) reported as a new record, referring to Silva *et al.* (1998) specimen; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005).

Remarks. Noronha's specimen is deposited in FMNH collections (58862 - *Squaliolus sarmenti*: Off Câmara de Lobos, Funchal, Madeira, eastern Atlantic, depth about 500-800 fathoms). Also, a preserved specimen in AMNH (1-15731) and thirteen records, including stomach content and formalin preserved specimens in MMF collections (from 1940 to 2004). Maul (1948) refers as rare, from offshore.

Family Etmopteridae

* *Etmopterus princeps* Collett, 1904 - Lixinha-da-fundura; Great lanternshark

Freitas & Biscoito 2007: 4 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Saldanha & Biscoito 1997 [reported as new record to Azores]; Santos *et al.* 1997; Porteiro *et al.* 2010), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Menezes *et al.* 2004; Reiner 2005).

Remarks. seven formalin preserved specimens in MMF collections (first dated from 1984 and the last one from 2004).

* *Etmopterus pusillus* (Lowe, 1839) - Xarinha-preta; Smooth lanternshark

Lowe 1834: 144 (as *Centrina nigra*. Specific name preoccupied).

Lowe 1839: 91 (as *Acanthidium pusillum*).

Günther 1870: 425 I Collet 1890: 219 I Noronha & Sarmento 1934: 112 and 144 (as *Spinax pusillus*).

Noronha & Sarmento 1934: 139 I Nobre 1935: 459 I Fowler 1936: 81 I Noronha & Sarmento 1948: 108 I Maul 1948: 139 I Nunes 1953: 148 I Albuquerque 1954-56: 119 I Krefft & Tortonese 1973: 43 I McEachran & Branstetter 1984: 140 I Compagno 1984a: 82-83 I Sanches 1986: 87 I Lloris et *al.* 1991: 22 I Carneiro et *al.* 2014: 13.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Saldanha & Biscoito 1997; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Menezes *et al.* 2004; Reiner 2005).

Remarks. Madeira is the type locality (Syntype: BMNH 1855.11.19.27). Several preserved specimens: USNM 94519 and sixteen records including stomach contents and formalin preserved specimens in MMF collections. Maul (1948) refers as rare, occurring offshore. This is a common species caught as by catch in the black scabbard fish fishery. Maul's statement can only be justified due to the usual discard of the caught specimens on board since there is no commercial use of this species.

* *Etmopterus spinax* (Linnaeus 1758) - Lixinha-da-fundura; Velvet belly

Noronha & Sarmento 1934: 114 (as *Spinax spinax*).

Nobre 1935: 457 I Fowler 1936: 80 I Noronha & Sarmento 1948: 111 I Maul 1948: 139 I Nunes 1953: 157 I Albuquerque 1954-56: 118 I Krefft & Tortonese 1973: 42 I McEachran & Branstetter 1984: 141 I Sanches 1986: 86 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira archipelago, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Hanel & John 2014 as questionable).

Remarks. Three specimens in MMF collection (MMF 47153, 47155 & 47163), caught at Unicorn Seamount. Maul (1948) refered this species as rare, occurring offshore.

Family Somniosidae

* *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864 - Xara-preta; Portuguese dogfish

Günther 1870: 423 (as *Centrophorus coelolepis*).

Capello 1872: 88 I Belloc 1934: 144 I Noronha & Sarmento 1934: 134 and 137 I Fowler 1936: 74 I Noronha & Sarmento 1948: 133 I Maul 1948: 139 I Nunes 1953: 245 I Albuquerque 1954-56: 126 I Krefft & Tortonese 1973:40 I Cadenat & Blache 1981: 95-97 I McEachran & Branstetter 1984: 134-35 I Compagno 1984a: 55-56 I Sanches 1986: 82 I Lloris et *al.* 1991: 224 I Carneiro et *al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Saldanha & Biscoito 1997; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Hanel & John 2014).

Remarks. Several preserved specimens: USNM 94520, MNHN IC-AB0244, MNHN1965-123, and nine records including skin, mounted and formalin preserved specimens in MMF collections (dated from 1944-2017). Maul (1948) refers as frequent all year, occurring offshore.

* *Centroscymnus owstonii* Garman, 1906 - Xara-preta-de-natura; Roughskin dogfish

Günther 1870: 423 (as *Centrophorus coelolepis*).

Regan 1906: 437 (as *Centroscymnus cryptacanthus*).

Fowler 1936: 75 I Maul 1948: 139 I Albuquerque 1954-56: 128 I Krefft & Tortonese 1973: 41 I Cadenat & Blache 1981: 93-95 I Sanches 1986: 83 I Lloris *et al.* 1991:224 (as *Centroscymnus cryptacanthus*).

Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Porteiro *et al.* 2010) and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Günther's specimen (BMNH 1865.5.20.14), is indeed the first record from Madeira, although at the time he has identified it as *C. coelolepis*. This specimen, who was donated by J. Y. Johnson, was later used by Regan in 1906 to describe *Centroscymnus cryptacanthus*, now considered a junior synonym of *C. owstonii* Garman 1906 (Compagno 2001). Several formalin preserved specimens in MMF collections from Madeira, Porto Santo, Seine, and Unicorn Seamounts. Maul (1948) refers as rare, occurring offshore.

* *Centroselachus crepidater* (Barbosa du Bocage & de Brito Capello, 1864) - Sapata-de-natura; Longnose velvet dogfish

Günther 1870: 421-22 1 Noronha & Sarmento 1934: 128, 137 I Nobre 1935: 451 (as *Centrophorus crepidater*).

Noronha & Sarmento 1948: 126 (as *Centroselachus crepidator*).

Kreftt & Tortonese 1973: 41 I McEachran & Branstetter 1984: 135 I Compagno 1984a: 56-57 I Sanches 1986: 84 I Lloris *et al.* 1991: 224 (as *Centroscymnus crepidater*).

Fowler 1936: 75 I Maul 1948: 139 I Nunes 1953: 218 I Albuquerque 1954-56: 128 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Porteiro *et al.* 2010) and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Four records, including mounted and formalin preserved specimens in MMF collections (dated from 1931, 1940 and 2004) and one specimen preserved in USNM (94522). Maul (1948) referred it as rare, occurring offshore.

* *Scymnodon ringens* Barbosa du Bocage & de Brito Capello, 1864 - Boca; Knifetooth dogfish

Capello 1872: 88 (as *Scymnodon ringeus* sic).

Fowler 1936: 76 I Maul 1948: 139 I Albuquerque 1954-56: 125 I Kreft & Tortonese 1973: 44 I Cadenat & Blache 1981: 87-88 I McEachran & Branstetter 1984: 142 I Sanches 1986: 88 I Lloris *et al.* 1991: 238 I Carneiro *et al.* 2014: 14 I Delgado *et al.* 2017.

Distribution in Macaronesia. Madeira and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. a skin, mounted and formalin preserved specimens in MMF collections dated from 1941 and 1944. Maul (1948) referred it as rare, occurring offshore.

* *Somniosus microcephalus* (Bloch & Schneider, 1801) - No common name in Madeira; Greenland shark

Freitas & Biscoito 2007: 6 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Porteiro *et al.* 2010; Menezes *et al.* 2012) and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. two records (MMF 23429 and 36218), one head and one formalin preserved specimen in MMF collections, dated from 1983 and 2007.

* *Somniosus rostratus* (Risso, 1827) - Trabolha-de-natura; Little sleeper shark

Maul 1955: 7 I Krefft & Tortonese 1973: 47 I Cadenat & Blache 1981: 84-85 I McEachran & Branstetter 1984: 144 I Compagno 1984a: 106-107 I Sanches 1986: 93 I Lloris *et al*. 1991: 239 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Porteiro *et al.* 2010) and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Maul (1955) reported two specimens caught in January 1942 in about 1000 m of depth, according to fisherman. Four records, including stuffed skin, jaws, mounted specimens and formalin preserved specimen in MMF collections dated from 1942, 1951 and 2004. Noronha (1926) had already mentioned the presence of the species in Madeiran waters, although only based on visual observations.

* *Zameus squamulosus* (Günther, 1877) - Xara-preta-de-focinho-comprido; Velvet dogfish

Noronha 1926: 385 I Noronha & Sarmento 1934: 137 I Maul 1948: 139 I Albuquerque 1954-56: 127 (as *Centroscymnus obscurus*).

Krefft & Tortonese 1973: 45 I Cadenat & Blache 1981: 88-90 I Compagno 1984a: 98-99 I Lloris *et al.* 1991: 238 (as *Scymnodon obscurus*).

Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Porteiro *et al.* 2010; Menezes *et al.* 2012), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Menezes *et al.* 2004).

Remarks. Three specimens (MMF 0040, 0605 and 20161) and an oil sample (MMF 0438) in MMF collections. Maul (1948) referred it as rare, occurring offshore.

ORDER TORPEDINIFORMES

Family Torpedinidae

* *Torpedo marmorata* Risso, 1810 - Tremedeira; Spotted torpedo

Lowe 1838: 195 I Lowe 1843: 94 I Noronha & Sarmento 1934: 131 I Albuquerque 1954-56: 185-186 I Stehmann & Bürkel 1984a: 160 I Sanches 1986: 122 I Lloris *et al.* 1991: 240 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 14 I Almada *et al.* 2015: 4.

Lowe 1843: 93 (as *Torpedo picta*).

Noronha & Sarmento 1934: 145 (as *Torpedo marmoratus*).

Distribution in Macaronesia. Madeira, Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al*. 2013).

Remarks. Five records in BMNH (1862.4.22.14, 1861.5.19.52, 1855.11.29.23, 1862.4.22.13, 1898.1.26.43-44) and two formalin preserved specimens in MMF collections (dated from 1964, MMF 020632 and 2011, MMF 41393).

* *Tetronarce nobiliana* (Bonaparte, 1835) -Tremelga; Electric ray

Lowe 1838: 195 I Günther 1870: 449 I Noronha & Sarmento 1934: 131 and 145 (as *Torpedo hebetans*).

Fowler 1936: 121-122 I Maul 1948: 139 I Noronha & Sarmento 1948: 130 I Albuquerque 1954--56: 186 (as *Torpedo nobiliana*).

Krefft & Stehmann 1973a: 56 I Stehmann & Bürkel 1984a: 160 I Sanches 1986 I Lloris *et al.* 1991: 240 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira and Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al*. 2010).

Remarks. Lowe's specimen (BMNH 1852.8.30.22, Holotype of *T. hebetans*) was confirmed as *T. nobiliana* by the first author. One specimen in MMF collection (MMF 47181), caught at Seine Seamount.

* *Torpedo torpedo* (Linnaeus, 1758) - Tremelga; Common torpedo

Noronha & Sarmento 1948: 130 I Maul 1948: 139 I Nunes 1953: 236 I Sanches 1986: 121 I Carneiro *et al.* 2014: 14.

Distribution in Macaronesia. Madeira, Azores (Carneiro et *al.* 2014), the Canary lslands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and the Cape Verde (Reiner 1996, 2005. Wirtz *et al.* (2013) made a remark that the photo given by Reiner (2005) is *Torpedo marmorata* and therefore the presence of this species in Cape Verde needs confirmation).

Remarks. Five records in MMF collections (dated from 1951 to 1965). Maul (1948) refers as frequent all year, coastal.

ORDER RAJIFORMES

Family Rajidae

* *Dipturus intermedius* (Parnell, 1837) - No common name in Madeira; Flapper skate (Figs. 8 and 9) Günther 1870: 468 (as *Raja macrorhynchus* sic).

Ebert & Stehmann 2013: 317-321 (as *Dipturus* sp. cf. *intermedia*).

Figure 8. *Dipturus intermedius* (BMNH 1860.8.30.7). Juvenile male (442 mm DL) from Madeira presented to The Natural History Museum, London, by the Rev. Richard Thomas Lowe in 1860.

Figure 9. *Dipturus intermedius* (BMNH 1860.8.30.7). Detail of tail showing lateral thorns directed forward, a distinguishing character of the species.

Distribution in Macaronesia. Madeira

Remarks. One mounted specimen collected in Madeira by R. T. Lowe (BMNH 1860.8.30.7), named as *D. macrorynchus*, was identified as *D. intermedius* by MB. One specimen registered in MMF collection dated from 1943 (MMF 2869), collected with bottom trawl off the west coast of Funchal, could not be located. The Madeiran specimen in the Natural History Museum (London), bears two thorns along the lower edges of tail, at level of dorsal fins, distinctly inclined towards the head (Fig. 9), a character of *Dipturus intermedia* (Iglésias et *al.* 2010; Last *et al.* 2016b). It is most probable that this species also occurs in the Azores and the Canary lslands, but we were not able to see specimens from there and records in the literature are referred to *Dipturus batis* (see remarks in doubtful records).

Dipturus oxyrinchus (Linnaeus, 1758) - No common name in Madeira; Longnosed skate

Lowe 1839: 92 (as *Raja oxyrhyncus* sic).

Lowe 1843: 94 I Lowe, 1849: 201 Noronha & Sarmento 1934: 124 and 143 (as *Raia oxyrhynchus*).

Fowler 1936: 112 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Lloris *et al.* 1991: 236 (as *Raja oxyrinchus*).

Albuquerque 1954-56:169 (as *Raja oxyrhynchus*, sic.)

Stehmann 1973: 63 I Stehmann & Bürkel 1984a: 177 I Sanches 1986: 107 (as *Raja* (*Dipturus*) *oxyrinchus*).

Wirtz *et al.* 2008: 4 I Ebert & Stehmann 2013: 225 I Carneiro *et al.* 2014: 15.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010) and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. No specimens or other material from Madeira were found in natural history museum collections. Carneiro *et al.* (2014) refer as existing in MMF collection, but the specimen in question was collected in Portugal mainland. Maul, 1948 refers as rare, coastal. Despite no specimens in collection have been found, the collection of two specimens off the North coast of Madeira during the ARQMAD 02-P96 Cruise in 1996 (DSI unpubl. data) lead us to leave this species in the checklist.

Leucoraja fullonica (Linnaeus, 1758) - Raia; Shagreen ray

Günther 1870: 467 I Fowler 1936: 115 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Albuquerque 1954-56: 166 I Lloris et *al.* 1991: 236 (as *Raja fullonica*).

Garman 1913: 328 I Noronha & Sarmento 1934: 123 and 143 (as *Raia fullonica*).

Stehmann 1973: 64 I Stehmann & Bürkel, 1984a: 1791Sanches, 1986: 108 (as Raja (Leucoraja) fullonica).

Wirtz *et al.* 2008: 4 I Erbert & Stehmann 2013: 335 I Carneiro *et al.* 2014: 15.

Distribution in Macaronesia. Madeira and Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010).

Remarks. One mounted specimen in BMNH collections (1860.8.30.4), from Madeira donated by R. T. Lowe.

Leucoraja circularis (Couch 1838) - No common name in Madeira; Sandy skate

Günther 1870: 462 (as *Raja circularis*).

Belloc 1934: 174 I Noronha & Sarmento 1934: 123 (as *Raia circularis* sic).

Distribution in Macaronesia. Madeira and Canary lslands (Brito Hernández & Sancho Rafel 2003).

Remarks. this record is based on a mounted specimen in BMNH collections (1860.8.30.3), obtained from Madeira and donated by R. T. Lowe. Based on the external characters (e.g., spines organization on body and number of teeth rows), this specimen has been confirmed by us (MB) as *L. circularis*.

Raja brachyura Lafont, 1873 - Raia; Blonde ray

Günther 1870: 459 (as *Raja undulata*) and 460 (as *Raja asterias*).

Stehmann 1973: 59 I Stehmann & Bürkel 1984a: 184 I Sanches 1986: 100 I Lloris et *al.* 1991: 236 I Wirtz *et al.* 2008: 4 I Carneiro *et al.* 2014: 15.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010) and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Three specimens in BMNH collections (1862.4.22.34, 1864.8.22.2, 2013.3.25.2). Günther (1870) gives *R. undulata* Lacepède 1802 for Madeira, based on a specimen donated by R. T. Lowe (BMNH 2013.3.25.2). This specimen was later labelled as *R. asterias* and *R. brachyura*. The latter identification was confirmed by the authors (MB). This species is reported to have been caught to the North of Madeira, Porto Santo and Desertas lslands, in the framework of project ARQMAD (1995-97), using bottom longlines at 100 m depth (DSI unpubl. data). ln spite being mentioned as present in MMF collection (Wirtz *et al.* 2008; Carneiro *et al.* 2014), no registered specimens were found in that museum. A specimen was collected off Madeira's north coast in 2011 and lived for one month in the Aquarium of Porto Moniz (Carolina Ornelas, pers. comm.).

Raja clavata Linnaeus, 1758 – Raia; Thornback ray (Fig. 10)

Günther 1870: 456 I Noronha & Sarmento 1934: 123 and 143 I Fowler 1936: 110 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Nunes 1953: 198 I Albuquerque 1954-56: 160 I Stehmann 1973: 59 I Stehmann & Bürkel 1984a: 185 I Sanches 1986: 102 I Lloris *et al.* 1991: 236 I Wirtz *et al.* 2008: 4 I Carneiro *et al.* 2014: 15.

Garman 1913: 326 (as *Raia clavata*).

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010) and Canary Islands (Lloris *et al.* 1991).

Remarks. Wirtz *et al.* (2008) and Ebert & Stehmann (2013) refer that specimens of *Raja clavata* from Madeira may be assigned to *R. maderensis* Lowe, 1838 (see remarks under the latter). One of the specimens from Madeira sent to the Natural History Museum by R.

T. Lowe (BMNH 1860.8.30.5) and used by Günther (1870) was observed by one of the authors (MB) and based on their morphological characters, confirmed as *R. clavata*.

* *Raja maderensis* Lowe, 1838 - Raia-da-Madeira; Madeira ray (Fig. 11)

Lowe 1838: 195 I Lowe 1843: 94 I Garman 1913: 325 I Belloc 1934: 171 (as *Raia maderensis*)

Duméril 1865: 545 I Günther 1870: 459 I Capello 1872: 88 I Noronha & Sarmento 1934: 123 and 143 I Fowler 1936: 113 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Stehmann 1973: 60 I Stehmann & Bürkel 1984a: 186 I Sanches 1986: 103 I Lloris *et al.* 1991: 236 I Wirtz *et al.* 2008: 4 I Carneiro *et al.* 2014: 15 I Last *et al.* 2016b: 322.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997) and the Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Madeira is the type locality of this species. Holotype not found. A specimen preserved in BMNH (1862.4.22.35), a female specimen in alcohol in MNHN (MNHN-IC-0000-1792) and eight records including formalin preserved specimens and other material in MMF collections (dated from 1964 to 2013). Maul (1948) refers as coastal and frequent all year-round and the same author (1976), refers as relatively common in about 100 m depth in Madeiran waters. The validity of this species has been questioned (Chevolot *et al.* 2007; Serra-Pereira *et al.* 2011; Bali *et al.* 2016). Based on genetics, Chevolot *et al.* (2007) concluded that Azorean specimens identified as *R. maderensis*, might in fact be *R. clavata*. Bali *et al.* (2016) did not study specimens from Madeira and admit that, in spite their data point to the synonymy of *R. maderensis* with *R. clavata*, the existence of an endemic *R. maderensis* could not be ruled out. The material of both species (*R. maderensis* from Madeira and Azores and *R. clavata* from Madeira and UK), observed by the authors (MB) in BMNH as well as recent observations and genetic analyses of fresh specimens of *R. maderensis* from Madeira by the authors (MF), show consistent differences between the two species, regarding not only colour pattern, but also teeth shape and genetic divergence. We therefore consider both species valid, as Last *et al.* (2016b). The specimens from the Azores (BMNH 1903.6.27.38 and 1983.9.8.1) confirm the presence of this species in that archipelago. At least 10 specimens collected off Madeira's north coast between 2005 and 2014 lived from a few months to 9 years in the Aquarium of Porto Moniz (Carolina Ornelas, pers. comm.).

Figure 10. *Raja clavata* (BMNH 1860.8.30.5). Juvenile female (144 mm DL) from Madeira presented to The Natural History Museum, London, by the Rev. Richard Thomas Lowe in 1860.

Raja montagui Fowler 1910 - Raia-pregada; Spotted ray

Günther 1870: 458 (as *Raja maculata*)

Noronha & Sarmento 1934: 123 and 143 (as *Raia maculata*)

Maul 1976:7

Distribution in Macaronesia. Madeira and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Günther's specimen (BMNH 1860.8.30.2), presented by R. T. Lowe, is a mounted half-grown female and its identity was confirmed by the authors (MB). This species is not present in MMF collections, despite what is said by Carneiro et al. (2014).

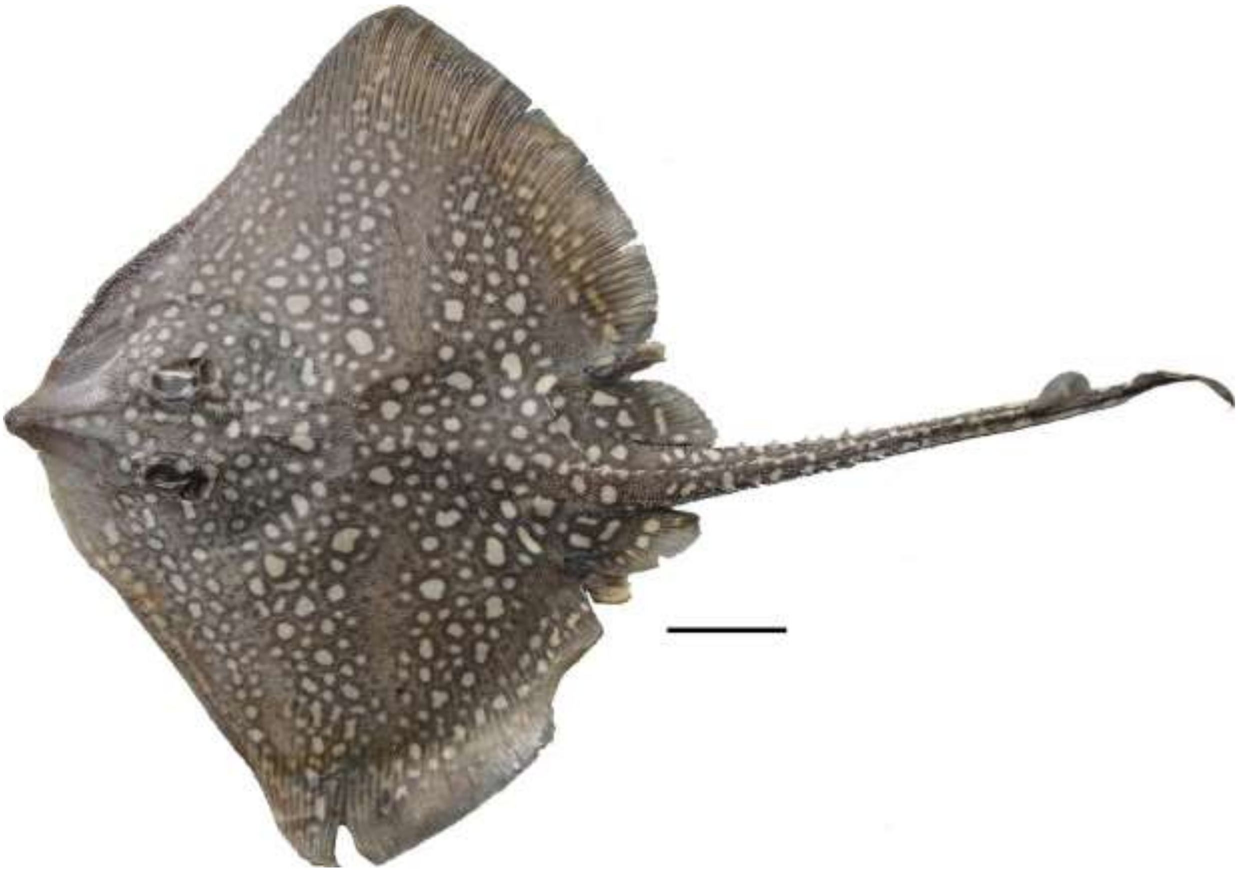

Figure 11. *Raja maderensis* (MMF 42926). Juvenile male (371 mm DL), caught off the south coast of Madeira. Funchal fish market, 18.12.2013. Scale bar 50 mm.

* *Rostroraja alba* (Lacepede, 1803) - No common name in Madeira; Bottlenosed skate

Lloris et al 1991: 236 (as *Raja alba*).

Carneiro *et al*. 2014: 15.

Distribution in Macaronesia. Madeira and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. two preserved specimens in MMF collection (MMF 23650 and MMF 36215), both collected on Desertas islands, first dated from 1984 and the last one dated from 2004.

ORDER MYLIOBATIFORMES

Family Dasyatidae

Bathytoshia lata (Garman, 1880) - Ratão; Roughtail stingray (Fig. 12)

Günther 1870, 477 (as *Trygon thalassia*).

Fowler 1936: 126 I Albuquerque 1954-56: 174 I Krefft & Stehmann 1973b: 71 I McEachran & Capapé 1984: 198 I Sanches 1986 I Lloris *et al.* 1991: 225 I Wirtz *et al.* 2008: 4 I Ebert & Stehmann 2013: 396 I Carneiro *et al.* 2014: 16 (as *Dasyatis centroura*).

Last et al. 2016a: 532.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Porteiro *et al*. 2010), Canary lslands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and the Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. a female specimen from Madeira (BMNH 1931.5.6.) was confirmed by the first author. Wirtz *et al*., 2008 stated as not present in the MMF collection, but this record is confirmed by numerous underwater photos.

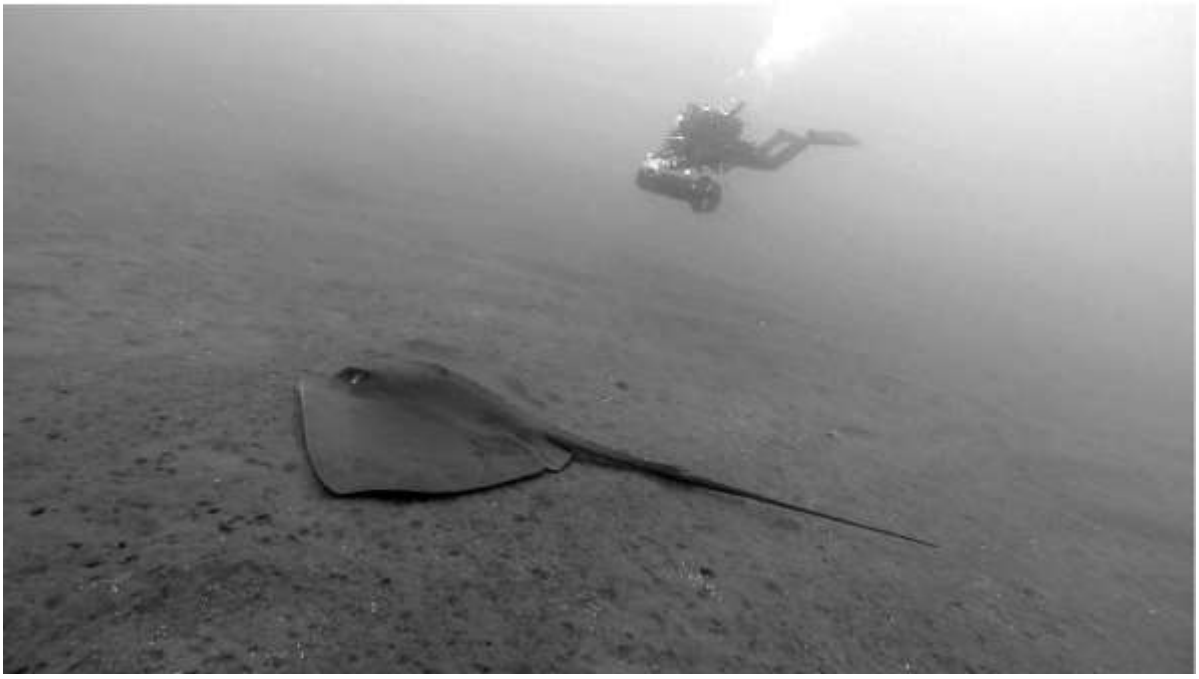

Figure 12. *Bathytoshia lata*. Underwater photograph of a specimen with approximately 1000 mm DL, taken at Cais do Carvão, Funchal, on 02/09/2016. Photographed by Pedro Neves.

* *Dasyatis pastinaca* (Linnaeus, 1758) - Ratão; Common stingray

Lowe 1838:196 I Noronha & Sarmento 1934: 125 and 145 (as *Trygon pastinaca*).

Fowler 1936: 128 I Noronha & Sarmento 1948: 122 I Maul 1948: 140, 42 I Nunes 1953: 201 I Albuquerque 1954-56: 172 I Krefft & Stehmann 1973b: 70 I McEachran & Capapé 1984: 199 I Sanches 1986: 174 I Lloris *et al.* 1991: 225 I Wirtz *et al*. 2008: 41 Ebert & Stehmann 2013:397 I Carneiro *et al*. 2014: 16 I Almada *et al*. 2015: 4.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al*. 2010), Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al*. 2013; Hanel & John 2014).

Remarks. specimen preserved in BMNH collections (1898.1.26.45-46) and three formalin preserved specimens in MMF collections (dated from 1993 and 94). Maul (1948) refers as frequent all year and coastal, which is confirmed by the authors.

* *Pteroplatytrygon violacea* (Bonaparte, 1832) - No common name in Madeira, Pelagic stingray

Biscoito & Wirtz 1994: 2 (as *Dasyatis violacea*).

Wirtz *et al.* 2008: 4 (as *Pteryplatytrygon violacea* sic) Ebert & Stehmann 2013: 399 I Carneiro *et al*. 2015: 16.

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Arruda 1997; Porteiro *et al*. 2010), Canary lslands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Hanel & John 2014).

Remarks. three formalin preserved specimens in MMF collections (MMF 25298-25300), all dated from 1990.

* *Taeniurops grabatus* (Geoffroy St. Hilaire, 1817) - Ratão; Round stingray

Biscoito & Wirtz 1994: 2 I Wirtz *et al*. 2008: 5 I Carneiro *et al*. 2014: 16 I Almada *et al*. 2015: 4 (as *Taeniura grabata*).

Distribution in Macaronesia. Madeira, Azores (Santos *et al*. 1997; Arruda 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Monteiro *et al.* 2008; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. one formalin preserved specimen in MMF collections (MMF 28784) dated from 1997.

Family Gymnuridae

* *Gymnura altavela* (Linnaeus, 1758) - Uje-manta; Spiny butterfly ray

Lowe 1839: 92 I Lowe 1843: 94 (as *Trygon altavela*).

Günther 1870: 486 I Noronha & Sarmento 1934: 124 and 143 I Nobre 1935: 487 I Fowler 1936: 131 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Albuquerque 1954-56: 174 (as *Pteroplatea altavela*) Krefft & Stehmann 1973b: 72 I McEachran & Capapé 1984: 204 I Sanches 1986: 116 I Lloris *et al.* 1991 I Wirtz *et al.* 2008: 5 I Ebert & Stehmann 2013: 401 I Carneiro *et al.* 2014: 16.

Distribution in Macaronesia. Madeira and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. two formalin preserved specimens in MMF (MMF 14040, 22137) collections (dated from 1958 and 1966). A specimen was collected off Madeira's north coast in 2005 and lived for seven years in the Aquarium of Porto Moniz (Carolina Ornelas, pers. comm.). Commonly seen by divers in Madeira, including authors (CR and MF).

Family Myliobatidae

* *Myliobatis aquila* (Linnaeus, 1758) - Ratão-águia; Common eagle ray

Günther 1870: 489 I Noronha & Sarmento 1934: 124 I Nobre 1935: 489 I Fowler 1936: 134 I Noronha & Sarmento 1948: 122 I Maul 1948: 140 I Nunes 1953: 199 I Albuquerque 1954-56: 177 I Krefft & Stehmann 1973b: 74 I McEachran & Capapé 1984: 206 I Sanches 1986: 117 I Lloris *et al.* 1991: 233 I Wirtz *et al.* 2008: 5 I Ebert & Stehmann 2013: 405 I Carneiro *et al.* 2014: 16 I Almada *et al.* 2015: 4. Belloc 1934: 175 (as *Leiobatus aquila*).

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. one preserved specimen in BMNH (1898.1.26.47), five formalin and ethanol preserved specimens in MMF collection (dated from 1960 to 2006). Although Maul (1948) referd it as coastal and rare, it is commonly observed in Madeira and Porto Santo. At least 12 specimens collected off Madeira's north coast between 2005 and 2014 lived from a few months to 10 years in the Aquarium of Porto Moniz (Carolina Ornelas, pers. comm.).

Aetomylaeus bovinus (Geoffroy St. Hilaire, 1817) - Dormideiro; Buli ray

Lowe 1838: 196, 1843-60: 99 (as *Myliobatis aquila*).

Günther 1870: 490 1 Noronha & Sarmento 1934: 124 (as *Myliobatis bovina*).

Nobre 1934: 490 1 Fowler 1936: 135 I Maul 1948: 140 I Nunes 1953: 199 I Albuquerque 1954-56: 178 (as *Pteromylaeus bovina*).

Krefft & Stehmann 1973b: 74 I McEachran & Capapé 1984: 206 I Sanches 1986: 118 I Lloris *et al.* 1991: 236 I Wirtz *et al.* 2008: 5 I Ebert & Stehmann 2013: 407 I Carneiro *et al.* 2014: 16 I Almada *et al.* 2015: 4 (as *Pteromylaeus bovinus*).

Distribution in Macaronesia. Madeira, Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. Lowe (1843-60) gives a detailed description of this species leaving no doubt that he is referring to *A. bovinus* and not *M. aquila*. Günther (1870) refers at least three specimens from Madeira, two ofthem sent by R. T. Lowe. Although there are no specimens in the MMF collections, this record was confirmed by underwater photos (Wirtz *et al.* 2008 and the authors).

Family Mobulidae

* *Mobula birostris* (Walbaum, 1792) - Manta; Giant manta

Maul 1948: 140 I Nunes 1953: 241 I Albuquerque 1954-56: 183 I Sanches 1986: 120 I Wirtz *et al.* 2008: 5 I Carneiro *et al.* 2014: 16 (as *Manta birostris*).

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014), Canary lslands (Brito *et al. 2002*; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Monteiro *et al.* 2008; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. one mounted specimen in MMF exhibition. Maul, 1948 refers as frequent in some seasons, coastal at surface and occurring offshore.

* *Mobula mobular* (Bonnaterre, 1788) - Jamanta, urjemanta; Devi] fish

Johnson 1885: 202 (as *Dicerobatis giorna*).

Noronha & Sarmento 1934: 133 (as *Dicerobatis giornae*).

Nobre 1935: 491 I Noronha & Sarmento 1948: 132 I Maul 1948: 140 I Nunes 1953: 241 I Albuquerque 1954-56: 181 I Krefft & Stehmann 1973c: 77 I Sanches 1986: 119 I Wirtz *et al.* 2008: 5 I Ebert & Stehmann 2013: 415 I Carneiro et *al.* 2014: 16.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013 refer the record needs confirmation; Hanel & John 2014 refer there is no record for the area).

Remarks. Maul (1948) mentions the presence of the species in MMF collections. Indeed, there is a register in the catalogue (MMF 546), but unfortunately it could not be located. Other natural history museums checked did not have Madeira specimens. ln spite of this and taking into consideration the distribution area given by Ebert & Stehmann (2013), which makes the presence of this species in Madeira highly probable, we opt to consider it as present in Madeiran waters.

CLASS HOLOCEPHALI ORDER CHIMAERIFORMES

Family Chimaeridae

* *Chimaera opalescens* Luchetti, Iglésias & Sellos 2011 - No common name

Freitas *et al.* 2017: 84

Distribution in Macaronesia. Madeira.

Remarks. Six formalin preserved specimens in MMF collection (dated from 1961 to 2015), previously identified as *C. monstrosa* were re-identified (Freitas *et al.* 2017).

* *Hydrolagus affinis* (de Brito Capello, 1868) - Ratazana-da-fundura; Smalleyed rabbitfish

Freitas *et al.* 2011: 256 I Carneiro *et al.* 2014: 16.

Distribution in Macaronesia. Madeira, Azores (Porteiro *et al.* 2010; Menezes *et al.* 2012; Carneiro *et al.* 2014) and the Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. four formalin preserved specimens in MMF collections dated from 1956 to 2004.

B. Doubtful records in need of confirmation

Family Carcharhinidae

Carcharhinus plumbeus (Nardo, 1827) - No common name in Madeira; Sandbar shark

Lloris *et al.* 1991: 223 I Branstetter 1984a: 109 I Carneiro *et al.*2014: 12.

Distribution in Macaronesia. possibly Madeira archipelago, Azores (Arruda 1997), Canary Islands (Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013).

Remarks. According to Ebert & Stehmann (2013) the occurrence of *C. plumbeus* in Madeira is possible. Since neither specimens nor other material in natural history museum collections were found, nor reliable observations were recorded, at this point, the presence of this species is considered as subject to confirmation.

Galeocerdo cuvier (Péron & Lesuer, 1822) -Tubarão-tigre; Tiger shark

Branstetter 1984a: 111 I Lloris *et al.* 1991: 228 I Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. Possibly Madeira archipelago, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010), Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005; Monteiro *et al.* 2008; Wirtz *et al.* 2013)

Remarks. no specimens or other material from Madeira were found in natural history museum collections. Carneiro *et al.* (2014) noted that Ebert & Stehmann (2013) indicated the presence of the species in Madeira based on its geographical distribution. Since the species has been reported from the remaining Macaronesian archipelagos and it has been collected in the Azores, the occurrence of the species in Madeiran waters is also expected, but at this point, the presence of this species is considered as subject to confirmation.

Rhizoprionodon acutus (Rüppell, 1837) - Tubarão-bicudo; Milk shark

Compagno 1973: 31 I Cadenat & Blache 1981: 244-247 I Compagno 1984b: 525-26 I Branstetter 1984a: 114 I Sanches 1986: 75 I Lloris *et al.* 1991: 237 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. possibly Madeira archipelago and Cape Verde (Reiner 1996, 2005; Menezes *et al.* 2004; Wirtz *et al.* 2013).

Remarks. no specimens or other material from Madeira were found in natural history museum collections. Wirtz *et al.* (2008), considered this record from Madeira as very doubtful. Carneiro *et al*. (2014) state that *R. acutus* was indicated as native from Madeira by Compagno (1984b), but its presence was not confirmed. At this point, the presence of this species is considered as subject to confirmation.

Family Scyliorhinidae

Scyliorhinus canicula (Linnaeus, 1758) - Pata-roxa; Small-spotted catshark

Lichtenstein 1844: 2 (as *Squalus catalus*).

Fowler 1936: 38 I Albuquerque 1954-56: 93 I Carneiro et al 2014: 11.

Distribution in Macaronesia. Possibly Madeira archipelago, Azores (Santos *et al.* 1997) and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. no specimens or other material from Madeira were found in natural history museum collections. According to Maul (1976), it does not seem to live in Madeiran waters. At this point, the presence of this species is considered as subject to confirmation.

Family Triakidae

Mustelus asterias Cloquet, 1819-Caneja; Starry smooth-hound

Compagno 1973: 28; 1984b: 402 I Branstetter 1984b: 119 I Sanches 1986: 68 I Lloris *et al.* 1991: 233 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 11.

Distribution in Macaronesia. possibly Madeira archipelago and Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Noronha & Sarmento (1934: 103), recorded *Mustelus vulgaris* Müller & Henle 1839. Since part of Müller & Henle's species is considered as a synonym of *M. mustelus* and another part as a synonym of *M. asterias* and Noronha & Sarmento (1934) do not give any diagnostic characters, it is impossible to assign this record to any ofthe species in question. Compagno (1973) records *M. asterias* from Madeira, based on Fowler (1936: 61, as *M. mustelus*) and Noronha & Sarmento 1948: 97, 138, as *M. mustelus*), influencing the subsequent records, all based in literature. As demonstrated in the remarks under *M. mustelus* in the present paper, Fowler's and Noronha's records were based on Vinciguerra's (1882-83) specimens, which in turn should be considered as *M. mustelus*. Since no specimens or other material from Madeira were found in natural history museum collections, at this point, the presence of this species is considered as subject to confirmation.

Family Sphyrnidae

Sphyrna lewini (Griffith & Smith, 1834) - Tubarão-martelo; Scalloped hammerhead

Quéro 1984d: 123 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 12.

Distribution in Macaronesia. possibly Madeira archipelago, Azores (Arruda 1997, but not considered a valid record by Santos *et al.* 1997), Canary Islands (Brito *et al.* 2002; Brito Hemández & Sancho Rafel 2003) and Cape Verde (Wirtz *et al.* 2013, stating the need of confirmation).

Remarks. No specimens or other material from Madeira were found in natural history museum collections. At this point, the presence of this species is considered as subject to confirmation.

Family Oxynotidae

Oxynotus centrina (Linnaeus, 1758) - No common name in Madeira; Angular roughshark

Lowe 1838: 194 (as *Centrina Salviani*).

Noronha & Sarmento 1934: 137 1 Nobre 1935: 444 (as *Centrina centrina*).

Ebert & Stehmann 2013: 122.

Distribution in Macaronesia. possibly Madeira archipelago, Canary Islands (Brito *et al.* 2002; Brito Hemández & Sancho Rafel 2003) and Cape Verde (Reiner 1996, 2005).

Remarks. Since no specimens or other material from Madeira were found in natural history museum collections, at this point, the presence of this species is considered as subject to confirmation.

Oxynotus paradoxus Frade, 1929 - No common name in Madeira; Sailfin roughshark

Quéro 1984d: 127 I Carneiro et *al.* 2014: 14 I Ebert & Stehmann 2013: 124.

Distribution in Macaronesia. possibly Madeira archipelago, Azores (Santos *et al.* 1997; Azevedo *et al.* 2003; Carneiro *et al.* 2014), Canary Islands (Ebert & Stehmann 2013) and Cape Verde (Hanel & John 2014, but with no specimens).

Remarks. since no specimens or other material from Madeira were found in natural history museum collections, at this point, the presence of this species is considered as subject to confirmation.

ORDER PRISTIFORMES

Family Pristidae

Pristis pristis (Linnaeus, 1758) - No common name in Madeira; Common sawfish

Noronha & Sarmento 1934: 110 and 143 (as *Pristis antiquorum* Latham).

Nobre 1935: 467 I Noronha & Sarmento 1948: 105 I Maul 1948: 139 I Nunes 1953: 134 I Albuquerque 1954-56: 144 I Krefft & Stehmann 1973d: 51 I Stehmann & Bürkel 1984b: 154 I Sanches 1986: 96 I Lloris *et al.* 1991: 236 I Wirtz *et al.* 2008: 3 I Carneiro *et al.* 2014: 15.

Distribution in Macaronesia. possibly Madeira archipelago, Canary Islands (Lloris *et al.* 1991; Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and questionably Cape Verde (Reiner 1996, 2005; Wirtz *et al.* 2013, Hanel & John 2014).

Remarks. No specimens or other material from Madeira was found in major natural history collections. Although Maul (1948) refers it as very rare, we opt to consider the presence of this species as in need of confirmation.

ORDER RAJIFORMES

Family Rajidae

Dipturus batis (Linnaeus, 1758) - No common name in Madeira; Blue skate

Nobre 1935: 475 I Albuquerque 1954-56: 168 (as *Raia batis*).

Fowler 1936: 111 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Nunes 1953: 198 (as *Raja macrorynchus*).

Stehmann 1973: 62 I Stehmann & Bürkel 1984a: 175 I Sanches 1986: 106 (as *Raja* (*Dipturus*) *batis.*

Lloris *et al.* 1991: 236 (as *Raja batis*).

Ebert & Stehmann 2013: 317-321 (as *Dipturus* sp. cf. *flossada*).

Carneiro *et al.* 2014: 15.

Distribution in Macaronesia. possibly Madeira archipelago, Azores (Porteiro *et al*. 2010) and Canary Islands (Brito *et al*. 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Iglésias *et al.* (2010) have demonstrated that *Dipturus batis* (Linnaeus, 1758) is a composite species and provisionally split it into *Dipturus* sp. cf. *flossada* and *Dipturus* sp. cf. *intermedia*. Last *et al.* (2016b) retained *D. batis* and considered Dipturus sp. cf. *flossada* (Risso, 1826) as ajunior synonym. Older records from Madeira refer this species as *Raja macrorynchus* Rafinesque, 1810 (Fowler 1936; Noronha & Sarmento 1948; Maul, 1948; Nunes 1953). This species is here considered as ajunior synonym of *D. batis* (see remarks on next section).

Ebert & Stehmann (2013) and Last *et al.* (2016b) note that both species (*D. batis* and *D. intermedius*) appear to live sympatrically in most of their distribution area, although not occurring with the same abundance, therefore we have opted to place *D. batis* as a doubtful record, until specimens from Madeira come to hand.

Raja miraletus Linnaeus, 1758 - No common name in Madeira; Brown ray

Garman 1913: 323 I Fowler 1936: 116 I Maul 1948: 140 (as *Raia quadrimaculata*)

Albuquerque 1954-56: 153 I Stehmann 1973: 58 I Stehmann & Bürkel 1984a: 187 I Sanches 1986: 98 I Lloris *et al.* 1991: 236 I Wirtz *et al*. 2008: 4 I Ebert & Stehmann 2013: 370 I Carneiro *et al*. 2014: 15

Distribution in Macaronesia. possibly Madeira archipelago, Canary lslands (Brito et al. 2002 as dubious record) and Cape Verde (Reiner 1996, 2005).

Remarks. Garman (1913) refered the presence in Madeira of *R. quadrimaculata* Risso, 1827, now considered a junior synonym of *R. miraletus* (Eschmeyer *et al*. 2017), based on Günther's (1870: 462) *Raja circularis*, who in turn gave Madeira based on a specimen

(BMNH 1860.8.30.3) sent by R. T. Lowe. As pointed out above, Lowe's specimen was observed by one of us (MB) who concluded that in fact it belongs to *Leucoraja circularis*. Since no specimens or other material could be found in natural history museum collections, the presence of this species in Madeira is considered as in need of confirmation.

Family Gymnuridae

$^{\Delta}$*Gymnura hirundo* (Lowe, 1843) - Raia-borboleta; Madeira butterfly ray

Lowe 1843: 94 I Günther 1870: 487 I Noronha & Sarmento 1934: 124 and 143 I Fowler 1936: 133 I Noronha & Sarmento 1948: 122 I Maul 1948: 140 1 Albuquerque 1954-56: 175 (as *Pteroplatea hirundo*).

Nunes 1953: 199 (as *Pteroplates hirundo* sic).

Krefft & Stehmann 1973b: 73 I Wirtz *et al*. 2008: 5 I Carneiro *et al.* 2014: 16.

Distribution in Macaronesia. Possibly Madeira archipelago.

Madeira Material: Madeira is the type locality, but the holotype is unknown. Several specimens in BMNH labelled as *G. hirundo* from Japan and China were all observed by us (MB) and not confirmed as belonging to the present species. Two specimens in MMF collection previously identified by G. E. Maul as *G. hirundo*, were re- identified by the authors as *G. altavela*. Several authors questioned the validity of this species (Compagno 1999; Wirtz *et al*. 2008; Eschmeyer *et al*. 2017; Yokota *et al*. 2016) and with further studies it may well be considered as a synonym of *G. altavela*. Since no specimens of this species have been found in museum collections, we opt to place it as in need of confirmation.

Family Mobulidae

Mobula tarapacana (Philippi, 1892) - Manta-cornuda; Chilean devil ray

Carneiro *et al*. 2014: 16.

Distribution in Macaronesia. possibly Madeira archipelago, Azores (Porteiro *et al.* 2010), Canary Islands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003) and Cape Verde (Reiner 2005; Wirtz *et al.* 2013; Hanel & John 2014).

Remarks. No specimens from Madeira could be found in natural history collections. Wirtz *et al.* (2008) mention that *M. mobular* sightings may eventually be *M. tarapacana.* A similar situation seems to occur in the Canary lslands (Brito *et al.* 2002). Until a solid proof of the occurrence of this species in Madeiran waters appears, we consider the presence of this species as in need of confirmation.

Family Chimaeridae

Chimaera monstrosa Linnaeus, 1758 - Quimera; Rabbit-fish

Maul 1948: 140 I Albuquerque 1954-56: 189 I Stehmann & Bürkel 1984c: 213 I Sanches 1986: 127 I Lloris *et al.* 1991: 224 I Carneiro *et al.* 2014: 16.

Distribution in Macaronesia. Madeira, Azores (Santos *et al.* 1997; Arruda 1997; Porteiro *et al.* 2010; Carneiro *et al.* 2014) and the Canary Islands (López Abellán *et al.* 1994; Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. According to Freitas *et al.* (2017), the presence of this species in the waters of the archipelago of Madeira needs confirmation.

C. Species withdrawn from the list of Chondrichthyans from Madeira

Family Triakidae

Mustelus canis (Mitchill, 1815) - No common name in Madeira; Dusky smooth-hound

Fowler 1936: 61 I Noronha & Sarmento 1948: 97 I Maul 1948: 138 I Albuquerque 1954-56: 106 and 107 I Nunes 1953: 82.

Distribution in Macaronesia. Recorded only from Madeira.

Remarks. Fowler's (1936) reference to Madeira is based on Lowe (1838: 194) and Günther (1870: 385) who recorded *Mustelus laevis,* now considered as a synonym of *M. mustelus* (Linnaeus, 1758) (Compagno 1973; Eschmeyer *et al.* 2017). No specimens or other material from Madeira were found in natural history museum collections. According to Compagno (1984b), *M. canis* is restricted to the western Atlantic Ocean and Gulf of Mexico, therefore this species should be excluded from the list of Chondrichthyans of Madeira.

Mustelus punctulatus Risso, 1827 - No common name in Madeira; Black-spotted smooth-hound

Branstetter 1984b: 121 I Wirtz *et al*. 2008: 3.

Distribution in Macaronesia. recorded only from Madeira.

Remarks. The origin of this record seems to be the map given by Branstetter (1984b). Wirtz *et al*. (2008) considered this a very doubtful record from Madeira. ln the eastern Atlantic, this Mediterranean species seems to occur only in continental coasts, from Gibraltar to the Western Sahara (Compagno 1984b). Since no specimens or other material from Madeira were found in natural history museum collections, at this point, this species should be excluded from the list of chondrichthyans of Madeira.

Family Echinorhinidae

Echinorhinus brucus (Bonnaterre 1788) - No common name in Madeira; Longnose spurdog

McEachran & Branstetter 1984: 138 I Sanches 1986: 91.

Distribution in Macaronesia. All references to Macaronesia seem to be based on literature and apparently no specimens have been caught in the area or at least were not deposited in museum collections (Santos *et al.* 1997; Brito *et al.* 2002; Carneiro *et al.* 2014; Hanel & John 2014).

Remarks. Since there are neither reliable references nor specimens in collection, this species should be excluded frorn the list of Chondrichthyans ofMadeira.

Family Squalidae

Squalus acanthias Linnaeus, 1758 - No common name in Madeira; Piked dogfish

Bowdich 1825: 74-75 (as *Spinax acanthias*).

Noronha & Sarmento 1934: 135 (as *Acanthias acanthias*).

Belloc 1934: 140 I Fowler 1936: 69 I Albuquerque 1954-56: 115 I Cadenat & Blache 1981: 47-48 I McEachran & Branstetter 1984: 146 I Sanches 1986: 78 I Lloris et al, 1991: 239 I Carneiro *et al.* 2014: 13.

Distribution in Macaronesia. Azores (Santos *et al.* 1997; Arruda 1997) and Canary lslands (Brito *et al.* 2002; Brito Hernández & Sancho Rafel 2003).

Remarks. Bowdich (1825) seems to be the original source of all subsequent references of this species to the archipelago of Madeira. ln his account (pp.74-75) he said "Two dead sharks (the *Spinax acanthias* and *Scymnus licha*) lay on the beach;" (referring to the beach of Porto Santo). It is improbable that two fishes (*Squalus acanthias* and *Dalatias licha*), occurring in such different habitats had been abandoned together by fisherman. The report of *D. licha* indicates that we are probably in the presence of a discard of the fishery for the black scabbard fish, where this species is sometimes caught as a by catch. On the other hand, there are no records of a *Squalus* being caught the same way until now. Moreover, the name *spinax* has been used in the past to identify members of the genus *Etmopterus* (Etmopteridae), which in the present case makes sense, as these species occur in the same habitat and are usually caught the same way as *D. licha*. Not having access to the specimens seen by Bowdich, one cannot confirm his identifications, but in view of the above and since no specimens or other material from Madeira were found in natural history museum collections in Funchal and elsewhere, we propose that this species should be excluded from the list of Chondrichthyans of Madeira.

Family Rajidae

Raja macrorynchus Rafinesque, 1810 - No common name

Günther 1870: 468 (as *Raja macrorhynchus* sic) (misidentification).

Fowler 1936: 111 I Noronha & Sarmento 1948: 121 I Maul 1948: 140 I Nunes 1953: 198.

Distribution in Macaronesia. Recorded only from Madeira.

Remarks. The specimen sent from Madeira by R. T. Lowe to the Natural History Museum (BMNH 1860.8.30.7), on which Günther (1870) and subsequent authors based the occurrence of this species in Madeira (labeled as *Raja macrorhynchus* (sic)), was observed by the authors (MB) and identified as *Dipturus intermedius*.

R. macrorynchus is considered a valid species by Eschmeyer *et al.* (2017), but other authors consider it as synonym of *D. batis* (e.g., Ebert & Stehmann 2013). In all, since records in the literature are all based on Lowe's specimen in BMNH, we opted to withdraw this species from the list of Chondrichthyans of Madeira, no matter it is a valid species or a junior synonym.

Discussion

The present checklist confirms the presence of 67 species of cartilaginous fishes in the waters of the archipelago of Madeira, which represent 5% of the total valid chondrichthyan species described globally (Weigmann 2016). Considering the global Macaronesia, this list contains three species (*Odontaspis noronhai*, *Mitsukurina owstoni* and *Chimaera opalescens*) that have not been recorded from the remaining Macaronesian archipelagos. A comparison between the present results and checklists for the Azores (Santos *et al.* 1997; Porteiro *et al.* 2010) showed that the total number of species here recorded is higher than the number recorded from the Azores (60 according to Porteiro *et al.* 2010) whilst is smaller than the recorded from the Canaries (86 according to Brito Hernández & Sancho Rafael 2003).

Of the 67 cartilaginous fish species reported in this annotated checklist, 24 are in the list of threatened species (VU (8), EN (9) and CR (7)) according to the IUCN European Red List of marine fishes (Nieto *et al.* 2015).

Important to refer that according to FishBase (Froese & Pauly 2017) the list of cartilaginous species to Madeira comprises 60 species, four of which are here referred as needing confirmation and one to be excluded (*Mustelus punctulatus*). Therefore, the present checklist represents an increase of 21% on the total number of cartilaginous species previously referred to Madeira in this online database in 2017.

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Chapter 3

First record of *Hydrolagus affinis* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and the Seine seamount (North Atlantic Ocean)

CHAPTER 3 - First record of *Hydrolagus affinis* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and the Seine seamount (North Atlantic Ocean)

Abstract

The smalleyed rabbitfish, *Hydrolagus affinis* (de Brito Capello, 1868) (Chimaeridae), is recorded from the archipelago of Madeira for the first time, based on seven specimens caught between 1200 and 2500 m depth. This record extends the previously known range of distribution of this species, and also confirms its vertical distribution down to 2500 m. Additional material collected from the Canary Islands and the Azores was used for comparison.

Keywords

Chimaeridae, *Hydrolagus affinis*, Madeira, NE Atlantic

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Introduction

The family Chimaeridae comprises two genera, *Chimaera* L. (with a separate anal fin, sharply marked off from the caudal fin by a deep notch) and *Hydrolagus* Gill, 1862 (without a separate anal fin) (Bigelow and Schroeder 1953). *Hydrolagus* is represented by 22 described species (James et al. 2009, Eschmeyer 2010), four of them known from the north-east Atlantic: *Hydrolagus affinis* (de Brito Capello, 1868), *H. lusitanicus* Moura, Figuereido, Borlado-Machado, Almeida et Gordo, 2005, *H. mirabilis* (Collett, 1904), and *H. pallidus* Hardy et Stehmann, 1990.

Hydrolagus affinis was first described from a single specimen caught off Setúbal, east Portugal (Capello 1868). It is a benthopelagic species occurring on continental slopes and deep-sea plains from 300 to 2400 m (Stehmann and Bürkel 1984). Its distribution extends from East Greenland (61º50’N), Rockall Trough, Bay of Biscay and off Portugal to 22º52’N to off northwest Africa, including the Canary and the Cape Verde Islands in the East Atlantic (Stehmann and Bürkel 1984, Hardy and Stehmann 1990, Brito et al. 2002, Møller et al. 2004). It is also distributed from Canada (lat 62º55′N) to Cape Cod in the West Atlantic (Hardy and Stehmann 1990, Møller et al. 2004). The species has also been reported from the Mid-Atlantic Ridge (Lat. 37º18′N), off the Azores (Marques and Porteiro 2000).

Hydrolagus affinis can be separated from the other three congeneric species occurring in the NE Atlantic by a number of morphologic characters, including its uniform darker colouration, purplish-brown at all life stages (Hardy and Stehmann 1990, Moura et al. 2005).

Following several deepwater surveys off the Madeira Islands and the nearby Seine Seamount, this species was caught and is here recorded for the first time.

Two longline surveys of the benthic fauna of the Madeira Islands and the Seine Seamount between 750 m and 2500 m of depth were carried out (Fig. 1). All the specimens studied were caught during these two cruises on board the Portuguese R/V ARQUIPÉLAGO: Recprofmad-1 (October 11 - November 9, 2004) and Chacmad-1 (September 30 - October 21, 2005). On average, bottom longlines were deployed for 4–6 h. Bait used was salted Atlantic chub mackerel (*Scomber colias*).

Voucher specimens were deposited in the collections of the Museu Municipal do Funchal (História Natural) (MMF) and the Museo de Ciencias Naturales de Tenerife (TFMC). Additional material deposited in MMF from the Lucky Strike hydrothermal vent field (off the Azores) was also examined. Finally, unpreserved material sampled in the Canary Islands was included in the present study for comparison purposes.

All specimens were measured to the nearest mm following Didier and Séret (2002).

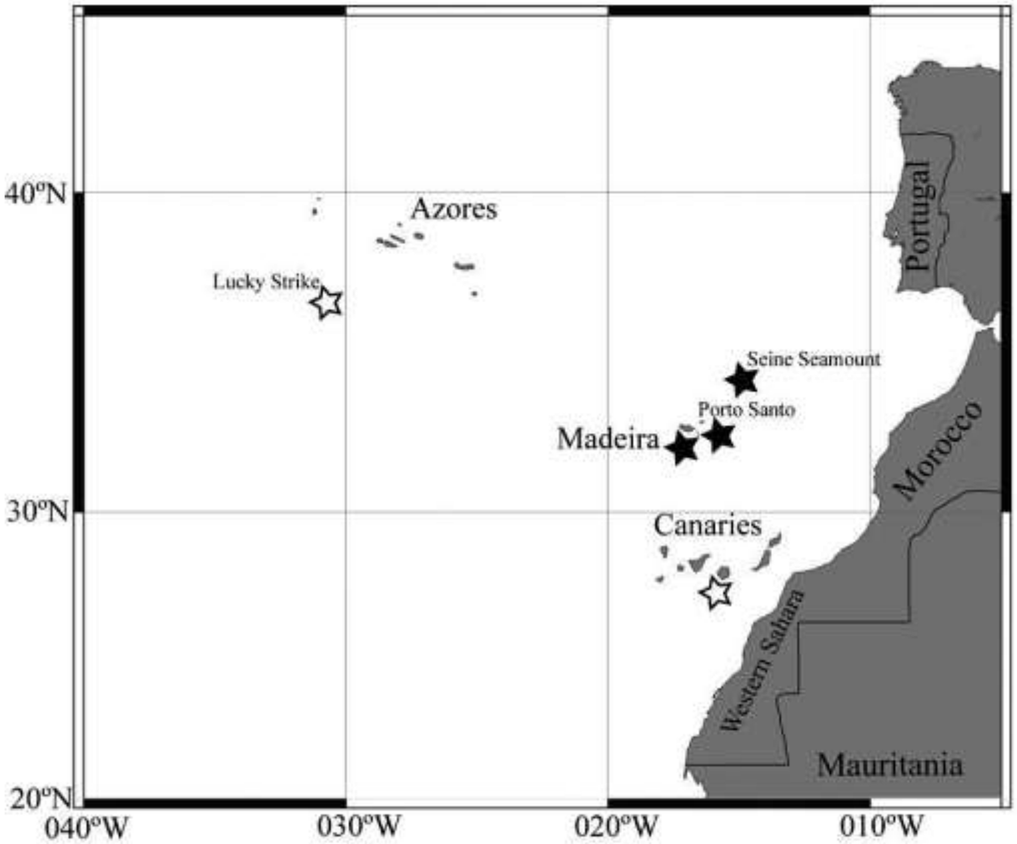

Fig. 1. Collection locations of *Hydrolagus affinis*: new specimens (Madeira and Seine seamount), specimens from Azores and Canary Islands used for comparisons.

Hydrolagus affinis (de Brito Capello, 1868) (Fig. 2)

Material examined: 13 *H. affinis* specimens. Archipelago of Madeira and Seine Seamount: MMF35996, 1023 mm total length (TL), female, Bay of Funchal, Madeira, 32º33′N, 16º50′W, 2500 m, cruise Recprofmad-1, sta. 5, 16 Oct 2004; MMF36085, 1075 mm TL, male, and MMF36089, 1268 mm TL, female, Seine Seamount, 33º45′N 14º22′W, 2500 m, cruise Recprofmad-1, sta. 34, 4 Nov 2004; MMF36786, 1068 mm TL, male, off Ilhéu de Baixo, SE of Porto Santo, 33º01′N, 16º12′W, 1500 m, cruise Chacmad-

1, sta. 10, 6 Oct 2005; MMF8639, 1097 mm TL, female, 16 Jun 1956 andMMF24350, 913 mm TL, female, off Câmara de Lobos, Madeira, 32º37′N 16º59′W, 800–1200 m, 29 Apr 1989; MMF25291, 804 mm TL, male, off Ponta do Sol, Madeira, 32º34′N 17º07′W, 1700 m, 21 Oct 1992. Canary Islands: TFMCBM-VP/01426, 1118 mm TL, female, 1973 m, and TFMCBM-VP/01427, 1100 mm TL, male, 1953 m, 27º37′N 15º53′W, off Arguineguín, SW of Gran Canaria, cruise Recprofcan-4, sta. 3, 16 Oct 2004. Azores: MMF33918, 1100 mm TL, male, 1600 m, 2 Jul 2001, MMF33921, 1360 mm TL, female, 1600 m, 2 Jul 2001. Azores: MMF33923, 1000 mm TL, male, 1700 m, 1 Jul 2001, cruise Ventaco-1; MMF33920, 1160mmTL, male, 1700m, 22 Sep. 2001, cruise Ventaco-2, sta. 3; all from Lucky Strike hydrothermal vent field, Mid-Atlantic Ridge off Azores, 37º18′N 32º16′W.

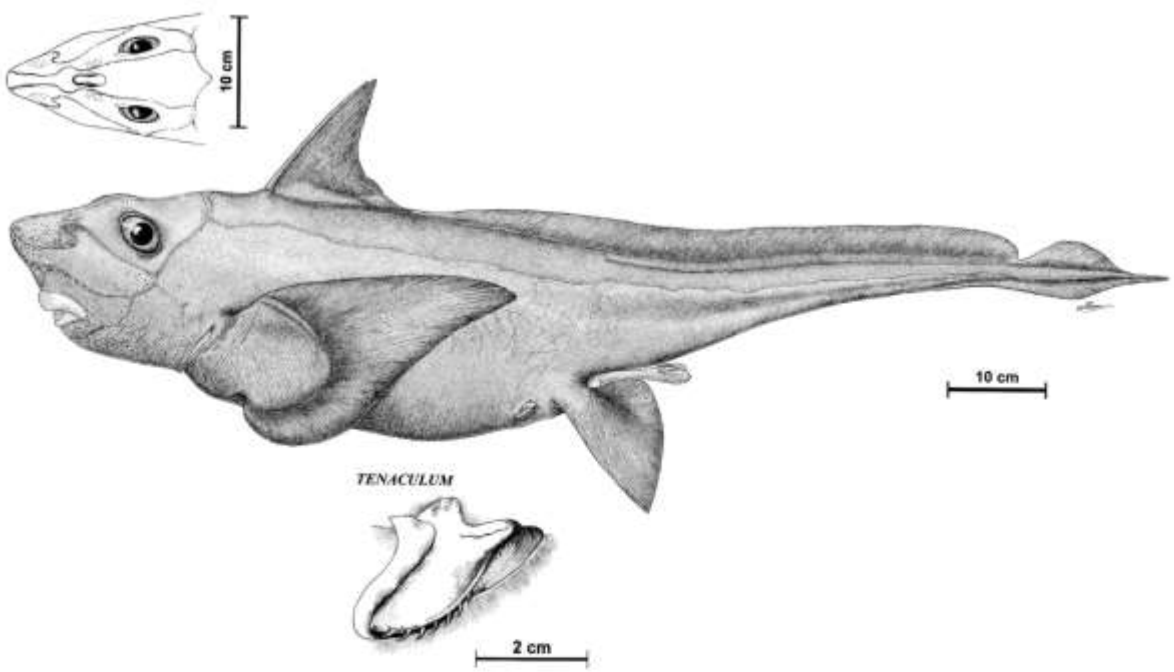

Fig. 2. *Hydrolagus affinis* from Madeira (MMF25291, 1155 mm TL, 804 mm BDL, Ponta do Sol, 1700 m) (courtesy of H. Encarnação)

Table 1 - Selected body proportions of *Hydrolagus affinis* from Madeira Islands and Seine Seamount, the Canary Islands and the Azores (Lucky Strike hydrothermal vent) compared with data from literature hydrothermal vent)

Area	Madeira and Seine Seamount	Canary Islands	Azores (Lucky Strike hydrothermal vent)	NE Atlantic
Reference	PRS	PRS	PRS	H and S
No. of specimens	7	5	4	20

BDL [mm]	675–913	704–770	645–908	151–885
HDL in BDL	25.6–31.0	24.8–29.3	27.0–28.6	19.6–29.4
HDL in TL	17.8–20.7	16.8–21.1	16.1–18.7	—
BDL in TL	64.9–69.6	63.0–67.7	59.6–66.8	—

PRS = presently reported study, H and S = Hardy and Stehmann, 1990, BDL = body length range, HDL in BDL = % head length in body length, HDL in TL = % head length in total length, BDL in TL = % Body length in total length.

Additional material: 3 specimens *H. affinis*, (2 males, 1 female), 1113–1223 mm TL, off Arguineguín, SW of Gran Canaria, 27º37′N 15º53′W, 1943–2292 m, cruise Recprofcan-4, sta. 3 and 4.

Remarks: Selected body proportions of the specimens studied are shown in Table 1 and are compared with data from the literature.

All specimens examined fit Hardy and Stehmann's (1990) redescription. The body length (BDL)/head length (HDL) relation is similar when comparing Canary, Madeiran and Azorean individuals. Also, this Macaronesian BDL/HDL relationship is similar to that obtained from the northeast Atlantic (Hardy and Stehmann 1990) and Greenland (Møller et al. 2004) mate- rial. Some differences observed in specimens from the northeast Atlantic can be explained by the inclusion of very small individuals (sized from 151 mm BDL) in the Hardy and Stehmann's (1990) material.

Moreover, the TL/BDL relation is similar when com- paring Canary, Madeiran and Azorean individuals. Also, this Macaronesian TL/BDL relation is similar to that obtained from Greenland (Møller et al. 2004) material. Some differences observed in specimens from Greenland waters can be explained by the inclusion of very large individuals (more than 913 mm BDL) in the material studied by Møller et al. (2004).

This species commonly occurs on continental slopes and deep-sea plains (Stehman and Bürkel 1984). The results of this study confirm that *H. affinis* also inhabits oceanic islands and seamounts.

Hydrolagus affinis is recorded for the first time from Madeira Island. These records not only enlarge the previously known area of distribution of this species, but also confirm its depth distribution down to 2500 m of depth.

In 2009 a new project called MARPROF (PCT MAC 2007–2013, MAC/2/065) started and new research surveys are planned to continue the exploration of the deep- sea biodiversity in the waters of the Azores, Madeira and the Canary Islands.

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Chapter 4

First records of *Chimaera opalescens* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and North-West African coast

CHAPTER 4 - First records of *Chimaera opalescens* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and North-West African coast

Abstract

This study reports new findings of *Chimaera opalescens* Luchetti, Iglésias et Sellos, 2011, which represent new records of this fish from Madeira and Morocco. The specimens were caught at the depths between 800 and 1221 m. Additional specimens deposited in the Natural History Museum of Funchal (MMF) were also studied as a comparative material and the results are reported herein. The new records of *C. opalescens* extend the previously known area of distribution of this fish further south.

Keywords

Deep-sea fish, new record, archipelago of Madeira, Morocco, NE Atlantic

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Introduction

According to Weigmann (2016) there are 40 valid species of chimaeras representing two genera, *Chimaera* Linnaeus, 1758 and *Hydrolagus* Gill, 1862. The separation of those two genera is based only on the presence or absence of a distinct anal fin (Didier and Séret 2002, Weigmann 2016).

The genus *Chimaera* includes 16 species (Weigmann 2016) two of which, *Chimaera monstrosa* Linnaeus, 1758 and *Chimaera opalescens* Luchetti, Iglésias et Sellos, 2011, are known from the northeast Atlantic Ocean (Luchetti et al. 2011, Weigmann 2016, Eschmeyer et al. 2017).

Chimaera opalescens can be distinguished from its congener by the following combination of characters: body colour beige to tan in adults and bronzy in juveniles, unpaired fins brown to purple, uniformly coloured or with pale or whitish edges, iris black, claspers tripartite divided for one third of their length, not extending beyond pelvic fins in adults, dorsal spine equal or shorter than first dorsal fin, ventral caudal lobe equal or deeper than dorsal caudal lobe and pectoral fins just reaching origin of pelvic-fin when laid backwards, in freshly caught adult specimens (Luchetti et al. 2011). Despite the distinct morphological differences, mainly in the claspers, dorsal spine and fins, it is still commonly misidentified as *Chimaera monstrosa* (see Luchetti et al. 2011, Vieira and Cunha 2014).

Chimaera opalescens was found within the depth range of 900–1975 m (Luchetti et al. 2011, Vieira and Cunha 2014, Weigmann 2016). Its geographic distribution extends from Greenland to the western slope of the British Isles and France, at latitudes between 48° and 59°N (Møller et al. 2004, Luchetti et al. 2011, Holt et al. 2013), the Galicia Bank (Bañón et al. 2016), and south to the Gorringe Bank (36º37.95′N, 11º02.25′W) (Vieira and Cunha 2014).

Chimaera opalescens, presented in this study, constitutes the first record of this fish from the Island of Madeira and northwest African coast, thus extending the southernmost limit of its distribution.

In this study a total of nine specimens of *Chimaera opalescens* from the Island of Madeira and from the northwest African coast were examined (Fig. 1). Six of them came from the black scabbardfish fishery in Madeira (800–1200 m of depth): MMF18538, 745 mm TL, male, 24/08/1961; MMF20455, 625+ mm TL, male, 23/06/1964; MMF23185, 639+ mm TL, male, 03/1977; MMF23947, 863 mm TL, female, 12/02/1986; MMF 42362, 700 mm TL, female, 27/07/2012; MMF44359, 782 mm TL, male, 03/03/2015. Three additional specimens came from the African coast: MMF37259, 775 mm TL, female, NW African slope (30.20ºN, 10.24ºW), 1221 m depth, 20/01/2006; MMF37260 (Fig. 2), 858 mm TL, male, NW African slope (26.05ºN, 15.27ºW), 897 m depth, 23/01/2006; MMF38518, 117 mm TL, newborn, NW African slope (26.18ºN, 15.04ºW), 840 m depth, 18/02/2006.

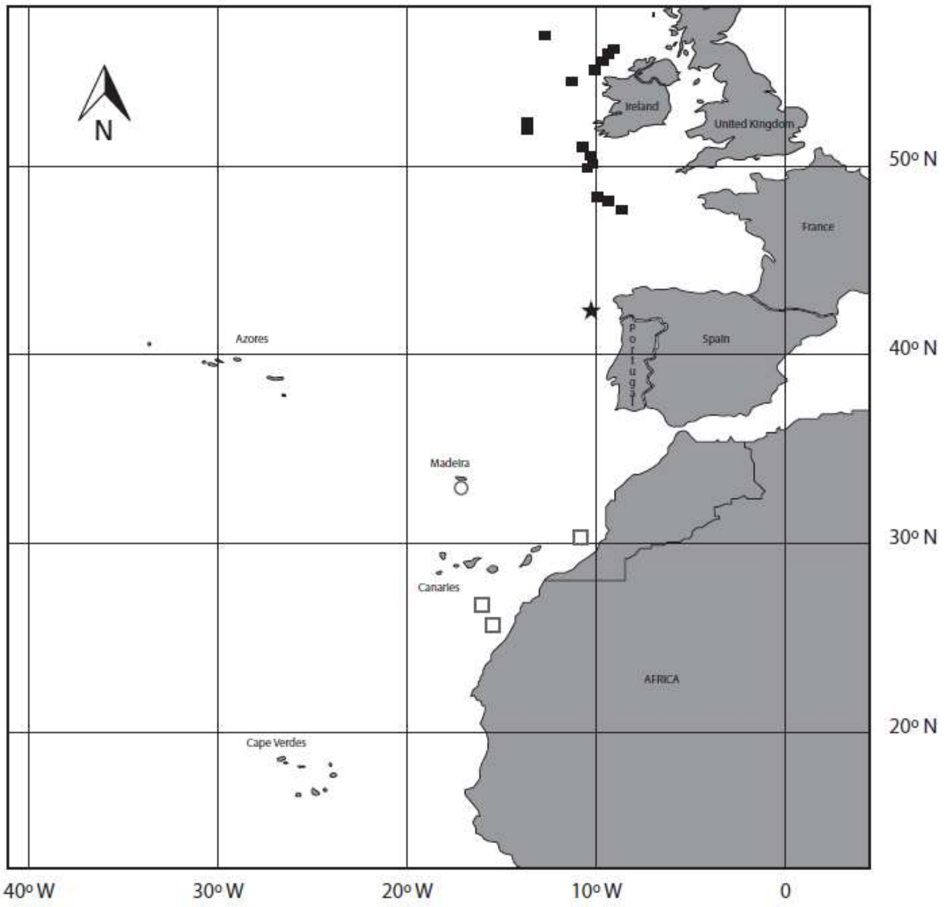

Fig. 1. Collection locations of *Chimaera opalescens*: 30 specimens from British Isles and France (Luchetti et al. 2011), 4 from Galicia bank (Bañón et al. 2016), and 8 from the presently reported study:6 from the Island of Madeira and 3 from the Northwest African coast

The Madeiran specimens were caught as bycatch of the traditional black scabbardfish (*Aphanopus carbo* Lowe, 1839 and *Aphanopus intermedius* Parin, 1983) deep-sea fishery, four of which had been deposited in the collections of the Funchal Natural History Museum and originally identified as *C. monstrosa*.

The northwest African specimens were collected with bottom trawls in the framework of a Scientific Cooperation Protocol between Spain and Morocco (González et al. 2014, González and Biscoito 2015).

All specimens were measured following Didier and Séret (2002) and Luchetti et al. (2011). Abbreviations: TL = total length, PCL = pre-caudal length, PD2 = pre-second dorsal fin length, PD1 = pre-first dorsal fin length, HDL = head length, DSA = dorsal spine length along anterior margin, D1B = first dorsal fin base length, IDS = inter-dorsal space, D2B = second dorsal fin base length, CFI = caudal-filament length, P1A = pectoral-fin anterior margin length, P2A = pelvic-fin anterior margin length, EYL = eye length, EYH = height, CLT = total length of clasper.

Two damaged specimens were not included in the morphological analysis. All voucher specimens were deposited in the collections of the Funchal Natural History Museum (MMF).

Our description of the newly found specimens is consistent with the description of *Chimaera opalescens* given by Luchetti et al. (2011) (Table 1). In Fig. 3 the male sexual characters of one of the studied specimens are shown, in which the denticle arrangement in the frontal and prepelvic tenacula and the shape of the prepelvic tenaculum and claspers, are identical to the description given by Luchetti et al. (2011) for this species.

The presently reported record of *Chimaera opalescens* extends by 10 degrees to the South the previously known range of the species and also reduces the minimum depth (800 m) for the species as compared to the previously published range of 900–1975 m (Weigmann 2016). The species was simply listed with no other details in a paper by Pajuelo et al. (2016) dealing with the assemblages of deep-sea fishes from off northwest Africa. Following the recommendations of Bello et al. (2014), the present account represents the first confirmed record of *C. opalescens* from NW Africa.

Before this study, only two species of the family Chimaeridae were known to occur in Madeira, *Chimaera monstrosa* (see Maul 1949) and *Hydrolagus affinis* (de Brito Capello, 1868) (see Freitas et al. 2011). While re-examining the MMF specimens, originally identified as *C. monstrosa*, we came to the conclusion that they were in fact *Chimaera opalescens*. Since we were not able to locate specimens of *C. monstrosa* from Madeira in museum collections and Maul's (1948) reference is older than the oldest specimen in MMF, the occurrence of *C. monstrosa* in Madeira remains dubious.

Fig. 2. *Chimaera opalescens* from NW African slope (MMF37260, 858 mm TL, male, 26.05ºN, 15.27ºW; 897 m)

Table 1 Comparison between *Chimaera opalescens* from Madeira and NW Africa and species type material. See material and methods for the meaning of abbreviations

Variable	Madeira and NW Africa			British Isles and France		
	Range [mm]	Range [%PCL]	Mean	Range [mm]	Range [%LPC]	Mean
TL	745–863	121.7–148.7	135.6	452–1098	120.4–171.1	147.6
PCL	526–703	100.0	100.0	310–776	100.0	100.0
PD2	171–243	29.0–37.2	33.3	113–286	35.5–39.1	37.5
PD1	102–152	18.3–21.6	20.0	67–157	18.8–25.6	21.5
HDL	97–133	16.2–20.5	18.5	69–146	17.7–23.2	19.7
DSA	80–104	14.4–19.0	16.4	53–132	12.4–19.5	17.1
D1B	42–67	7.1–11.6	9.5	40–84	9.8–13.2	11.4
IDS	21–52	3.4–7.4	4.9	4–55	1.3–7.1	4.7
D2B	299–378	52.8–68.4	58.2	193–494	61.4–65.2	62.9
CFI	140–207	22.9–37.3	28.3	18–235	2.7–50.7	22.3
P1A	127–181	22.9–34.4	27.3	92–205	24.5–31.4	27.6
P2A	73–99	12.0–17.1	14.2	46–120	13.9–17.6	15.2
EYL	26–40	4.1–6.9	5.6	27–51	6.3–9.3	7.9
EYH	16–29	3.0–5.2	3.9	17–34	3.7–6.1	4.8
CLT	51–82	9.7–14.1	11.7	68–73	10.3–11.4	18.0

Material from Madeira and NW Africa (5 males, 2 females) represents the presently reported study; Material from British Isles and France (15 males, 15 females) represents data of Luchetti et al. 2011; TL = total length, PCL = pre-caudal length, PD2 = pre-second dorsal fin length, PD1 = pre-first dorsal fin length, HDL = head length, DSA = dorsal spine length along anterior margin, D1B = first dorsal fin base length, IDS = inter-dorsal space, D2B = second dorsal fin base length, CFI = caudal-filament length, P1A =

pectoral-fin anterior margin length, P2A = pelvic-fin anterior margin length, EYL = eye length, EYH = height, CLT = total length of clasper.

Fig. 3. Male sexual characters of *Chimaera opalescens* (MMF37260, 858 mm TL): claspers (**A**), frontal tenaculum in dorsal view (**B**) and prepelvic tenaculum in ventral view (**C**).

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Chapter 5

Molecular systematics of the long-snouted deep water dogfish (Centrophoridae, *Deania*) with implications for identification, taxonomy, and conservation

CHAPTER 5 - Molecular systematics of the long-snouted deep water dogfish (Centrophoridae, *Deania*) with implications for identification, taxonomy, and conservation

Abstract

According to the most recent taxonomical revision, the deep-sea dogfish genus *Deania* encompasses four species. Three of them, *D. calcea*, *D. profundorum,* and *D. hystricosa*, occur in the North Atlantic. Whilst *D. profundorum* can be identified by the presence of a subcaudal keel, the other two species are not easily visually distinguished. Uncertainties over identification raises concerns over stock units and whether management plans are adequate. In this study we compared onboard visual identification of *Deania* specimens, with morphological inspection of skin denticles under stereo microscope and with independent molecular taxonomical assignment using two molecular markers. Particular emphasis was paid to specimens identified as *D. calcea* and *D. hystricosa* in the NE Atlantic where these species potentially occur sympatrically and may be easily confused. In the past the species have been discriminated on the basis of the size of skin denticles (skin roughness), but our study showed that the crown length of skin denticles covaries with size (and sex), irrespective of species, and therefore this is not a reliable morphological character and should not be used to discriminate between the two species. Phylogenetic analyses did not indicate that *D. hystricosa* to be a distinct lineage from *D. calcea*. Interestingly, however four individuals (specimens from: UK, Azores Is., Madeira Is. and Seine seamount) formed a well-defined sub-clade nested within the *D. calcea* clade, possibly a signature of a past vicariance event or a result of coalescent stochasticity.

Keywords

Deep-sea sharks, fishery by-catch, phylogeny, Atlantic Ocean, deep-sea dogfish, skin denticles.

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Introduction

The vulnerability of sharks to commercial fishing pressure has been well-documented (Baum et al., 2003; Myers and Worm, 2003) and it is widely acknowledged that deep-sea sharks (>200 m depth) are some of the most vulnerable species to fishing pressure (Garcia et al., 2008). Deep-sea sharks have slow growth rates, long life span with late maturation, very low fecundity, and long gestation periods (up to 2 years). Hence deep-sea sharks have population doubling times that can be twice as long as their shallower counterparts (Stevens et al., 2000) and populations can take decades to recover from fishing impacts (Garcia et al., 2008; Simpfendorfer and Kyne, 2009). An International Plan of Action for the Conservation and Management of Sharks adopted in 1999 stipulated that shark-fishing countries should produce national programmes for the conservation and management of sharks. However, only a few countries are currently providing detailed information on deep-sea bycatch, with many lumping species together as “deep-sea sharks” when they report their catches (Ebert and Mostarda, 2015). Furthermore, when species names can be traced back from the original datasets, frequent misidentification and/or taxonomic uncertainties make it difficult to estimate the true impact the fishery is having on deep-sea shark species (e.g., Iglésias et al., 2010; Veríssimo et al., 2014).

Despite their ecological importance and the fact that many are red-listed by the International Union for Conservation of Nature (IUCN, 2020), phylogenetic relationships within deep-sea sharks are still poorly understood and taxonomy is still a challenge (e.g., Veríssimo et al., 2014; White et al., 2017). In this study, we focus on the four-nominal species of the deep-sea squaloid sharks belonging to the genus *Deania* (Jordan and Snyder, 1902) from the family Centrophoridae. The genus *Deania* includes species commonly caught by deep-sea commercial fisheries. The conservation and extinction risk assessed by the IUCN reports that *D. calcea* is categorized as “least concern,” same for all other *Deania* spp. with the exception of *Deania hystricosa* reported as “data deficient” (Nieto et al., 2015; Millar and Dickey-Collas, 2018; IUCN, 2020). *Deania* spp. are bathydemersal species inhabiting continental slopes and seamounts usually between 200 and 2,000 m depth (Bass et al., 1976; Yano, 1991; Compagno, 2005; Weigmann, 2016) depending on the latitude. In terms of distribution, the long snouted deepwater dogfish *Deania calcea* (Lowe, 1839) and the arrowhead dogfish *Deania profundorum* Smith and Radcliffe, 1912 have been described as present worldwide; while the rough longnose dogfish *Deania hystricosa* Garman, 1906 and the longsnout dogfish *Deania quadrispinosa* McCulloch, 1915 have patchy records (Froese and Pauly, 2019).

Identification keys are effective to distinguish *Deania* species from other deep-water sharks, but within the genus it is problematic to discern among the species. Whilst *D. profundorum* can be identified by the presence of a subcaudal keel on the lower surface of the caudal peduncle (Ebert and Stehmann, 2013), the other species lack this feature are not easily distinguished by visual examination. *D. quadrispinosa* can be distinguished from either *D. calcea* or *D. hystricosa* by comparing the distance from exposed origin of first dorsal–fin spine to first dorsal fin rear tip, and the distance from free rear tip to second dorsal–fin spine (Ebert and Mostarda, 2015). According to the literature, separation between D. calcea and*D. hystricosa* is based on the skin denticle size (Compagno, 2005; Ebert and Stehmann, 2013). Moderately large lateral trunk denticles (crown length of about 0.5 mm) correspond to *D. calcea*, while very large denticles (crown length of about 1 mm) correspond to *D. hystricosa* (e.g., Ebert and Stehmann, 2013). Due to these putative differences, some simplified guides for onboard practical identification indicate *D. hystricosa* as the species with very rough skin (Ebert and Fowler, 2015) or “harsh to the touch” as reported in the original description by Garman (1906). Measurement of denticle size while onboard is difficult and impractical, and using the level of “skin roughness” is a subjective criterion. Furthermore, the relationship between body size and skin roughness (denticle size and density) has not yet been investigated. Uncertainties on assigning the correct identification while onboard has raised concern for the correct management of local as well as global fisheries (Ebert and Stehmann, 2013).

In this study we compared onboard visual identification of *Deania* specimens with laboratory inspection of skin denticles under stereo microscope and two molecular markers for an independent taxonomical assignment. Particular emphasis was paid to *D. calcea* and *D. hystricosa* in the NE Atlantic and, by performing a detailed examination of skin denticles on representative specimens belonging to these two putative species, we evaluated the diagnostic performance of skin denticle characters for species discrimination.

Materials and Methods

Sample Collection

A total of 271 *Deania* samples were collected between 2003 and 2010 from various scientific surveys (Figure 1). All specimens were measured, sexed, and identified onboard according to key morphological characters (e.g., Ebert and Stehmann, 2013).

Preliminary identification of the specimens was: 76 *D. calcea*, 42 in doubt between *D. calcea* and *D. hystricosa*, 63 *D. hystricosa*, and 90 *D. profundorum*. A subset of 117 representative samples was selected for further molecular screening (Table 1, Supplementary Table 1). Samples of white muscle tissue were stored in 95% ethanol and maintained at −20◦C until processed for molecular analysis.

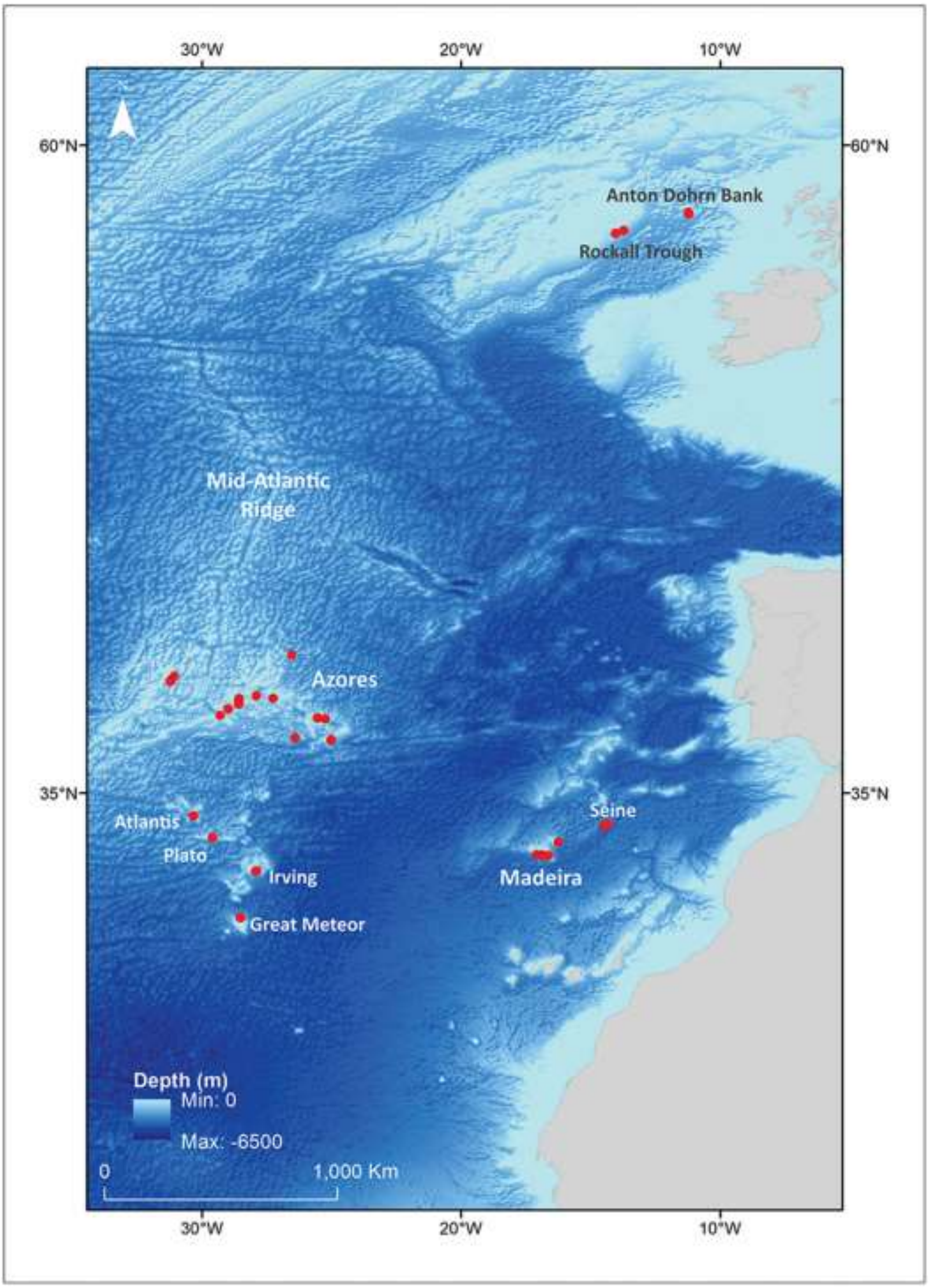

Figure 1 - Sampling areas for *Deania* species in the NE Atlantic (see also **Table 1**) used in the molecular and denticle analyses.

Molecular Analysis

Total genomic DNA was extracted from a small portion of muscle tissue using the E.Z.N.A. R Mag-Bind Tissue DNA Isolation Kit (Omega Bio-tek) following the manufacturer's protocol and using the autonomous extractor KingFisher mL (Thermo -

Electron Corporation, USA). A fragment of ~680 bp of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified in 102 individuals by polymerase chain reaction (PCR) using FishF1 and FishR1 primers (Ward et al., 2005). A ~1,100 bp fragment encompassing the entire mtDNA control region was amplified by PCR in 108 individuals using primers Pro-L and 12S282, which are complementary to the flanking proline tRNA and 12S rRNA genes, (Keeney et al., 2003), respectively. PCR reaction mixtures were similar for both markers and included ~20 ng of DNA template, 0.2µM of each primer, 10 µL of 2x PCR Master Mix (Promega) containing the reaction buffer, dNTPs, MgCl2, and Taq polymerase, and ultra-pure water to a final volume of 20 µL. The PCR thermal profile was 2min at 94◦C, 35 cycles of 30 s at 94◦C, 1min at 50◦C (for COI) or 57◦C (for the control region) and 1.5min at 72◦C, and a final extension step of 7min at 72◦C. A no template control reaction was included in all PCR reactions. PCR products were either purified with ExoSAP-IT (GE Healthcare) or separated by electrophoresis on a 1% agarose gel and excised using the Illustra GFX PCR DNA and Gel Band Purification Kit (GE Healthcare). Sequencing of both strands of each PCR product was performed at BMR Genomics commercial facility (www.bmr-genomics.it) based in Padua, Italy, using the same set of primers.

Sequences were checked using Aliview v. 1.24 (Larsson, 2014) and aligned by eye or using MAFFT v. 7 (Katoh and Standley, 2013). Fifty additional *Deania* COI sequences available in GenBank and BOLD System (Table 1, Supplementary Table 1) were added along with sequences of *Centrophorus squamosus* (COI: JF493080) and *Squalus acanthias* (NC_002012 for both CR and COI) to be used as outgroups. Missing or ambiguous end regions were trimmed to the same length so that all COI sequences in the data set had the same final length of 619 bp, while the length of CR sequences varied from 1,008 to 1,013 bp. Summary statistics (number and frequency of haplotypes, number of polymorphic sites, transitions, transversions, and nucleotide composition), haplotype diversity (h) and nucleotide diversity (π) were computed using DnaSP 5.10 (Librado and Rozas, 2009).

TABLE 1 - List of *Deania* specimens collected for this study and mtCOI and/or mtCR sequences available in literature or public databases.

Ocean	Area	Location	Year	N	Visual ID	Sequencing	Depth (m)	Sex	References
Atlantic	UK	Anton Dohrn Seam.	2006	3	*D. calcea*	2CR, 1COI+CR	650–675	2M; 1F	In this study
		Rockall Through Seam.	2006	7	*D. calcea*	3COI; 4COI+CR	650–850	5M; 2F	In this study
		Ireland	2006	1	*D. calcea*	COI	?	?	Veríssimo et al., 2014
	MAR-middle	Azores bank	2007	1	*D. calcea/D. hystricosa*	COI+CR	975	F	In this study
				4	*D. profundorum*	CR	775–975	2M; 2F	In this study
		Princess Alice bank	2003	1	*D. profundorum*	COI	751–800	M	In this study
		Faial/Pico Is.	2007	5	*D. calcea/D. hystricosa*	1CR; 4COI+CR	975	3M; 2F	In this study
				8	*D. profundorum*	7CR; 1COI+CR	725–775	8F	In this study
		southern Pico Is.	2009	1	*D. hystricosa*	COI+CR	1,120	F	In this study
		Flores/Corvo Is.	2007	6	*D. calcea/D. hystricosa*	1CR; 5COI+CR	575–1,175	5M; 1F	In this study
				1	*D. profundorum*	CR	725	1F	In this study
		Flores Is.	2003	2	*D. profundorum*	COI+2CR	775	1M; 1F	In this study
		Terceira Is.	2007	1	*D. profundorum*	CR	625	F	In this study
		S. Miguel Is.	2007	12	*D. profundorum*	1COI; 9CR; 2COI+CR	675	6M; 2F; 4?	In this study
		S. Maria Is.	2007	7	*D. profundorum*	CR	625–775	2M; 5F	In this study
		Sedlo Seam.	2003	1	*D. calcea*	COI+CR	901–950	M	In this study
		Mid-Atlantic Ridge	?	3	*D. hystricosa*	COI	?	?	EU148140-1[a]; MAECO250-06[b]
	MAR-southern	Atlantis Seam.	2007	1	*D. calcea*	COI	975	M	In this study
				5	*D. calcea/D. hystricosa*	2CR; 3COI+CR	825–975	2M; 3F	In this study
				2	*D. profundorum*	COI	625–775	2F	In this study
		Great Meteor Seam.	2007	1	*D. calcea*	COI+CR	825	F	In this study
				1	*D. calcea/D. hystricosa*	COI+CR	1,275	M	In this study
				5	*D. profundorum*	1COI; 4COI+CR	825–975	1M; 4F	In this study
Atlantic	MAR-southern	Irving Seam.	2007	9	*D. profundorum*	4CR; 5COI+CR	725–825	3M; 5F; 1?	In this study
		Plato Seam.	2007	3	*D. calcea/D. hystricosa*	CR	925	3M	In this study
	Madeira Is.	Seine Seam.	2004	4	*D. calcea*	2COI; 2COI+CR	850–1,250	3M; 1F	In this study
				2	*D. profundorum*	COI	700–850	2F	In this study
				2	*D. hystricosa*	COI+CR	1,000	2M	In this study
		Bay of Funchal	2004	13	*D. hystricosa*	2COI; 11COI+CR	1,000	7M; 6F	In this study
		Porto Santo	2005	1	*D. hystricosa*	COI+CR	1,500	F	In this study
		Desertas Is.	2005	1	*D. hystricosa*	COI+CR	1,000	F	In this study
		Cabo Girão	2011	1	*D. hystricosa*	COI	1,200	F	In this study
	Iberian Peninsula	Portugal	?	3	*D. calcea*	COI	?	?	KJ083233-5[a]
				2	*D. profundorum*	COI	?	?	KJ083236-7°
			2006	4	*D. profundorum*	COI	735	?	Costa et al., 2012
		Spain	?	2	*D. calcea*	COI	?	?	JN161152-3[a]
				1	*D. profundorum*	COI	?	?	JN161154[a]
	USA	Gulf of Mexico	2009	2	*D. calcea*	COI	?	2F	GMSHK078-9[b,c]
Pacific	Australia	Tasman Sea	2010	9	*D. calcea*	CR	?	4M; 5F	Genetics in this study; Samples from Rochowski et al. (2015)
		Tasman Sea	1998	4	*D. calcea*	COI	950–1,121	?	Ward et al., 2005
		New S. Wales	?	1	*D. quadrispinosa*	COI	?	M	IRREK406-08[b]

	Chile	?	2007	8	*D. calcea*	COI	?	?	KU737827-34[a]
		Huinay	2007	1	*D. calcea*	COI	?	?	Straube et al., 2010
	Taiwan	?	2005	1	*D. quadrispinosa*	COI	?	F	FOAG104-07[b]
		?	2014	6	*D. quadrispinosa*	COI	?	?	Chuang et al., 2016
		Taitung County	2001/3	1	*Deania* sp.	COI	?	?	Liu et al., 2013
Indian	India	?	?	5	*D. profundorum*	COI	?	?	KF899378-82[a]
	south Indian O.	?	?	1	*D. profundorum*	COI	?	?	AB639850[a]

M = male; F = female; ? = missing information; a GenBank; b BOLD; c Sequences wrongly assigned to *Deania*, therefore not used in our analysis.

We used jmodeltest (Guindon and Gascuel, 2003; Darriba et al., 2012) for the nucleotide substitution model selection under AICc (Akaike, 1974), and MrBayes v. 3.2.6 (Ronquist et al., 2012) and PhyML v 3.0 (Guindon and Gascuel, 2003) for phylogeny reconstruction (Bayesian inference, BI, and Maximum likelihood, ML, respectively). We have reconstructed phylogenies for both markers and for the concatenated data set. We ran PhyML online on the ATCG bioinformatics platform (http://www.atgc-montpellier.fr/) using the proposed model and assessed node supports with 1,000 bootstrap replicates. We have run MrBayes on the CIPRES Science Gateway portal v. 3.3 (Miller et al., 2010) using the BEAGLE library (Ayres et al., 2012) in two independent runs of 10 million generations sampled every 1,000 generations for each of the data sets. After each run we verified adequate sampling (ESS >> 200) and convergence with Tracer (Rambaut et al., 2014) and applied a 25% burn-in.

To resolve the phylogenetic relationships between the main *Deania* clades we compared the marginal likelihoods of different topological hypothesis. We estimated those using the Bayes factors (BF) and the stepping-stone (SS) approaches as proposed by Xie et al. (2011). For the marginal likelihood calculations, we selected a subset of COI sequences composed of two sequences from each clade and sequences belonging to the outgroups. We used pairwise distances estimated with Maximum Composite Likelihood in MEGA X v. 10.1 (Stecher et al., 2020) to select the two most distant sequences from each clade. We tested the topological hypothesis in MrBayes by placing a hard constrain to force the sister relationships between all the combinations of the three *Deania* clades and compared their marginal likelihoods. For the BF approach we estimated marginal likelihoods using harmonic means of the likelihood values of the MCMC sample by running two independent runs of 10 million generations sampled every 1,000 generations for each of the three tested hypotheses. Finally, we plotted the distribution of pairwise genetic distances using uncorrected pdistances and applied two species delimitation models for testing the presence of a barcoding gap and partitioning the data into candidate species. We applied the sequence-based ABGD (Automatic Barcode Gap Discovery; Puillandre et al., 2012) and the phylogeny-based mPTP (Multi-rate Poisson tree processes; Kapli et al., 2017) models to both mtDNA markers. ABGD analysis was performed using the default setting with both pairwise uncorrected p-distances and by applying the K2P nucleotide substitution model; while them PTP analyses were fed with the BI tree performing four independent MCMC chains each lasting 10 million iterations with samples saved every 50,000 generations.

The relationships between the COI and CR haplotypes were also estimated and visualized as haplotype networks constructed using the Integer neighbor-joining (IntNJ) technique approach available in the PopART software v. 1.7 (Leigh and Bryant, 2015).

Dermal Denticle Analysis

A portion of skin was collected from the area just below the first dorsal fin from specimens caught in the Azores and Madeira archipelagos. A total of 149 *Deania* species skin were sampled from individuals of different sizes and sexes, collected between 575 and 1500 m depth. Skins were then inspected under a Leica MZ 16FA stereomicroscope, using a 13.5x zoom, and measurements of the denticles were taken using tpsDig 2.31 software (Rohlf, 2017). *D. profundorum* were checked for comparison purposes only, as emphasis was addressed on those specimens visually identified as either *D. calcea*, *D. hystricosa* or of uncertain taxonomic status (*D. calcea*/*D. hystricosa*).

Images were taken from the top and the side to reveal details on shapes and sizes of the denticles, and the crown lengths were used to perform a multiple regression analysis using linear models. The mean of the measurement of three dermal denticles belonging to each specimen was used to investigate any correlation between biological variables (total length, sex, and capture depth) and denticle size and the interaction effect between variables. The best model fit was chosen according to the lowest AIC value, and in case the difference in AIC between two models were <2 units, the model with less estimated parameters was selected for statistical inference (Burnham and Anderson, 2002). Statistical analyses were performed in R v. 3.6.3 (R Core Team, 2020).

Results

Genetic Diversity Among *Deania* Species

The concatenated sequence alignment was 1,663 bp long (1,629 bp without outgroups): 619 bp (for COI) and 1,012 bp (1,044 bp without outgroups; for CR), respectively. All sequences were deposited in GenBank (Supplementary Table S2, S3).

All samples visually identified as *D. profundorum* and *D. quadrispinosa* grouped according to their predicted taxonomy, except for two *D. calcea* sequences downloaded from BOLD that were wrongly identified as *D. quadrispinosa* (FOAN841-11.COI- 5P, FOAN842-11.COI-5P). On the other hand, the specimens initially identified as *D. calcea* or *D. hystricosa* grouped together in a single clade except for four specimens that clustered in a separate well-defined subclade. The large clade was named *D. calcea* while the subclade (housing haplotypes form the UK, Azores Is., Madeira Is., and Seine seamount) was named *D. calcea*2 (Figure 2).

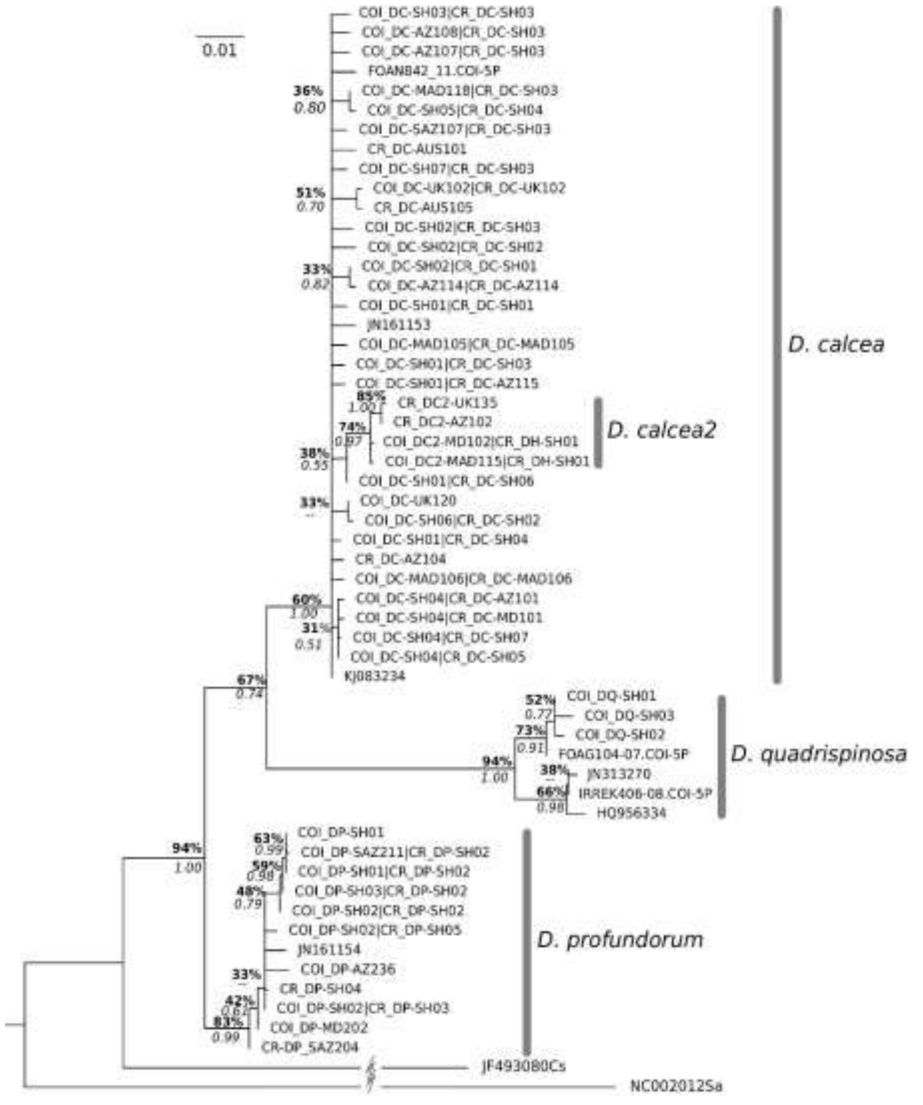

Figure 2 - Bayesian phylogenetic tree of *Deania* species obtained using concatenated sequences (COI and CR). The scale bar indicates the number of substitutions per site and values at branches represent Bayesian posterior probabilities and bootstrap values obtained for the Maximum Likelihood tree. Nodes where Bayesian posterior probability was under 0.50 are not reported.

While for two of the four *D. calcea*2 specimens both markers were sequenced (shared haplotype for CR "CR_DH-SH01," and unique haplotypes for COI "COI_DHMD102" and "COI_DH-MAD115") for the other two only the CR (haplotypes "CR_DH-UK135" and "CR_DH-AZ102") was sequenced (Figure 2).

Overall, the analysis of COI sequences of 144 and CR sequences of 111 *Deania* individuals, identified 30 COI and 26 CR distinct sequences, respectively. Most of these sequences belonged to the *D. calcea* clade: 83 COI (19 haplotypes) and 60 CR (20 haplotypes). The *D. profundorum* clade had a smaller number of sequences: 55 COI (eight haplotypes) and 48 CR (six haplotypes). The *D. quadrispinosa* clade had the lowest number of sequences: 12 COI (seven haplotypes). The *D. calcea* clade hosted the highest levels of haplotype diversity in CR (Hd = 0.889), while *D. quadrispinosa* showed the highest in COI (Hd = 0.872), and *D. profundorum* had the lowest values for both mtDNA genes (Hd = 0.654 and 0.671, in CR and COI respectively) (Table 2). *D. quadrispinosa* hosted by far the highest levels of nucleotide diversity in COI (= 0.0086), while values for *D. profundorum* were among the lowest for both genes (π= 0.0020 and 0.0025), in CR and COI, respectively) (Table 2).

Table 2 - Summary statistics for COI and CR.

	N	H_n	H_u	S	M	*ti/tv*	H_d	π
COI								
Deania	150	36	22	60	69	5.65	0.882	0.0253
D. calcea	83	19	15	19	21	3.83	0.760	0.0025
D. calcea (no *D. calcea2*)	81	17	10	15	16	5.19	0.748	0.0017
D. calcea2	2	2	2	1	1	–	0.500	0.0016
D. profundorum	55	8	4	8	8	7.01	0.654	0.0020
D. quadrispinosa	12	7	4	16	16	10.10	0.872	0.0086
CR								
Deania	111	26	13	49	49	2.64	0.904	0.0186
D. calcea	63	20	12	17	17	2.87	0.889	0.0023
D. calcea (no *D. calcea2*)	59	17	10	13	13	2.62	0.874	0.0020
D. calcea2	4	3	2	3	3	2.00	0.833	0.0018
D. profundorum	48	6	1	9	9	3.51	0.671	0.0025

N = number of individuals; Hn = number of haplotypes; Hu = number of unique haplotypes; S = number of polymorphic (segregating) sites; M = total number of mutations; ti/tv = transition to transversion ratio; Hd = haplotype diversity; π = nucleotide diversity.

The best nucleotide substitution model for COI and CR was HKY+G+I (Hasegawa et al., 1985; Yang, 1993). The phylogenetic inference based on the concatenated, as well as separated mitochondrial DNA markers (Supplementary Figures 1, 2), retrieved four distinct clades with *D. quadrispinosa* being the sister taxon to the clade *D. calcea* and *D. profundorum* represented the basal split within *Deania* (Figure 2). Both tree topologies placed *D. calcea*2 subclade nested within the *D. calcea* grouping (Figure 2). Bootstrap support and posterior probability values of the *D. calcea*2 subclade nested within the *D. calcea* grouping are not very high (0.74 and 0.97, respectively; Figure 2), but there is consistency in recovering the same topology also from phylogenetic inference using individual genes. Marginal likelihood of this tree topology has been compared with the other two alternatives by placing a hard constrain to force different sister relationships within the *Deania* clade (Table 3). Both approaches support as the most probable phylogenetic inference, the topology where *D. profundorum* is basal in the *Deania* genus and *D. calcea*2 is nested within *D. calcea* clade (SS = −1616.43 and BF = −1591.40, respectively) (Table 3).

Table 3 - Marginal likelihood calculations for the three tree topologies using subset of COI sequences (see text for details) by placing a hard constrain to force different sister relationships within the *Deania* clade.

Topology	Marginal likelihood (SS)	Marginal likelihood (BF)
(DC,DP)DQ	−1617.94	−1592.90
	(−1617.93 to −1617.96)	(−1591.88 to −1593.39)
(DC,DQ)DP	−1616.43	−1591.40
	(−1616.40 to −1616.40)	(−1589.13 to −1591.96)
(DP,DQ)DC	−1618.63	−1593.47
	(−1618.59 to −1618.69)	(−1591.08 to −1594.11)

BF = Bayes factors approach; SS = stepping-stone approach; DC = *D. calcea*; DP = *D. profundorum*; DQ = *D. quadrispinosa*. Selected topologies according to SS and BF are in bold.

The ABGD analysis does not provide any support for *D.calcea*2 subclade to be considered as a distinct species, either using K2P or uncorrected p-distances, for COI and CR. Nevertheless, applying the test on the COI matrix of distances calculated with K2P model, ABGD detects recursive partitioning within the *D. quadrispinosa* clade (Figure 3).

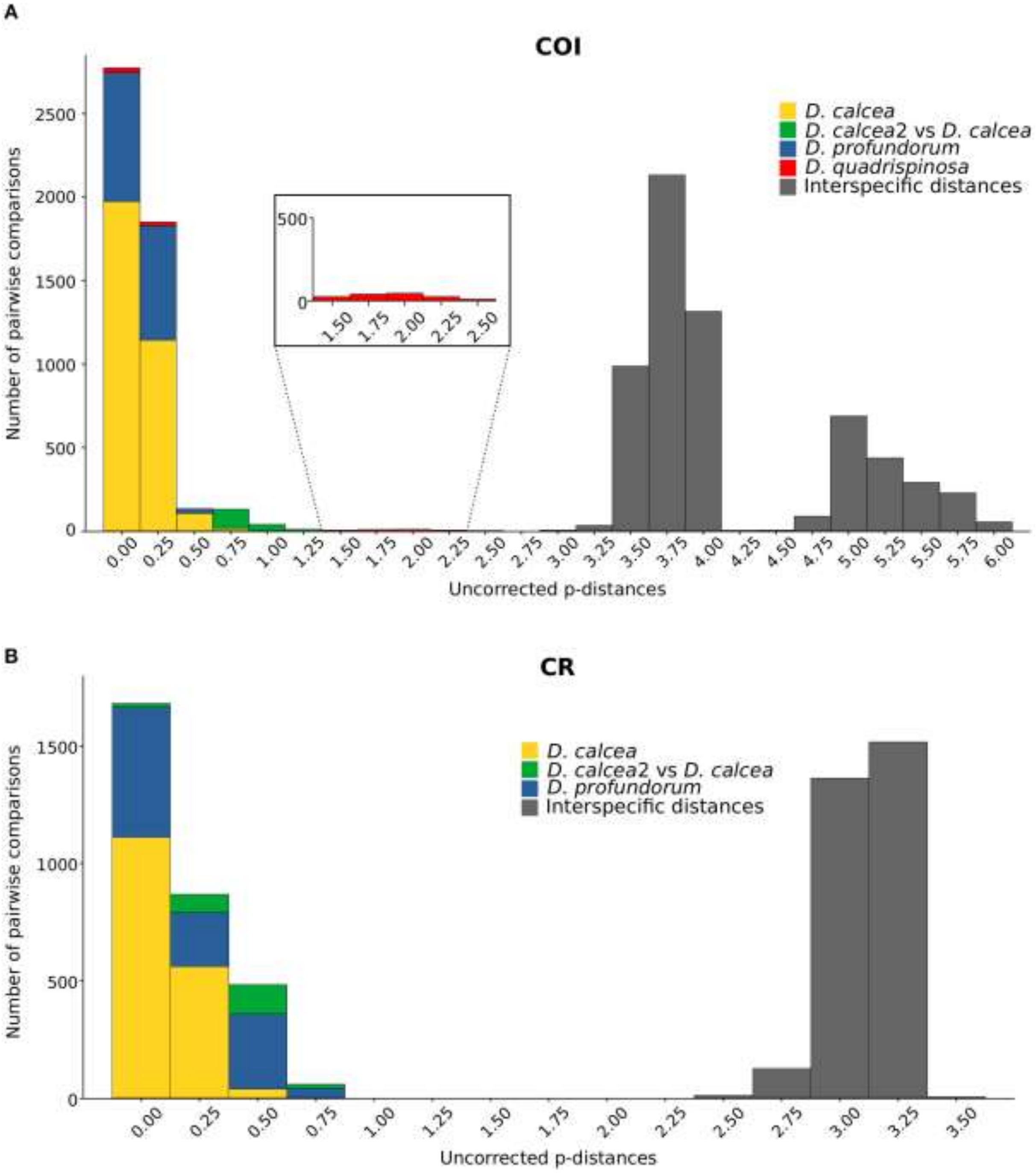

Figure 3 - Histograms with genetic uncorrected p-distances for COI (A) and CR (B). Square in (A) is a magnification.

The tree topologies estimated for the mPTP analyses reflected the ABGD output providing no support for *D. calcea*2 as distinct species for both mtDNA markers, but indicating the two putative species within *D. quadrispinosa* clade (Supplementary Figure 3).

The intraspecific relationship between *D. calcea* and *D. calcea*2 was further explored using a haplotype gene genealogy reconstruction analysis. The IntNJ network positions the *D. calcea*2 in a peripheral position of *D. calcea* haplotypes, for both mtDNA markers (Figure 4). There is a minimum of 3 (in CR) or 4 (in COI) nucleotide substitutions from the nearest *D. calcea* haplotype, one (in CR) or two (in COI) mutations more than among the *D. calcea* haplotypes (Figure 4A). The nucleotide substitutions that unambiguously distinguish *D. calcea* from *D. calcea*2 are: two transitions (C–T at position 721 and G–A at position 738) in CR, and two transversions (T–A at position 49, A–T at position 235) and two transitions (T–C at position 379 and 475) in COI (Figure 4B).

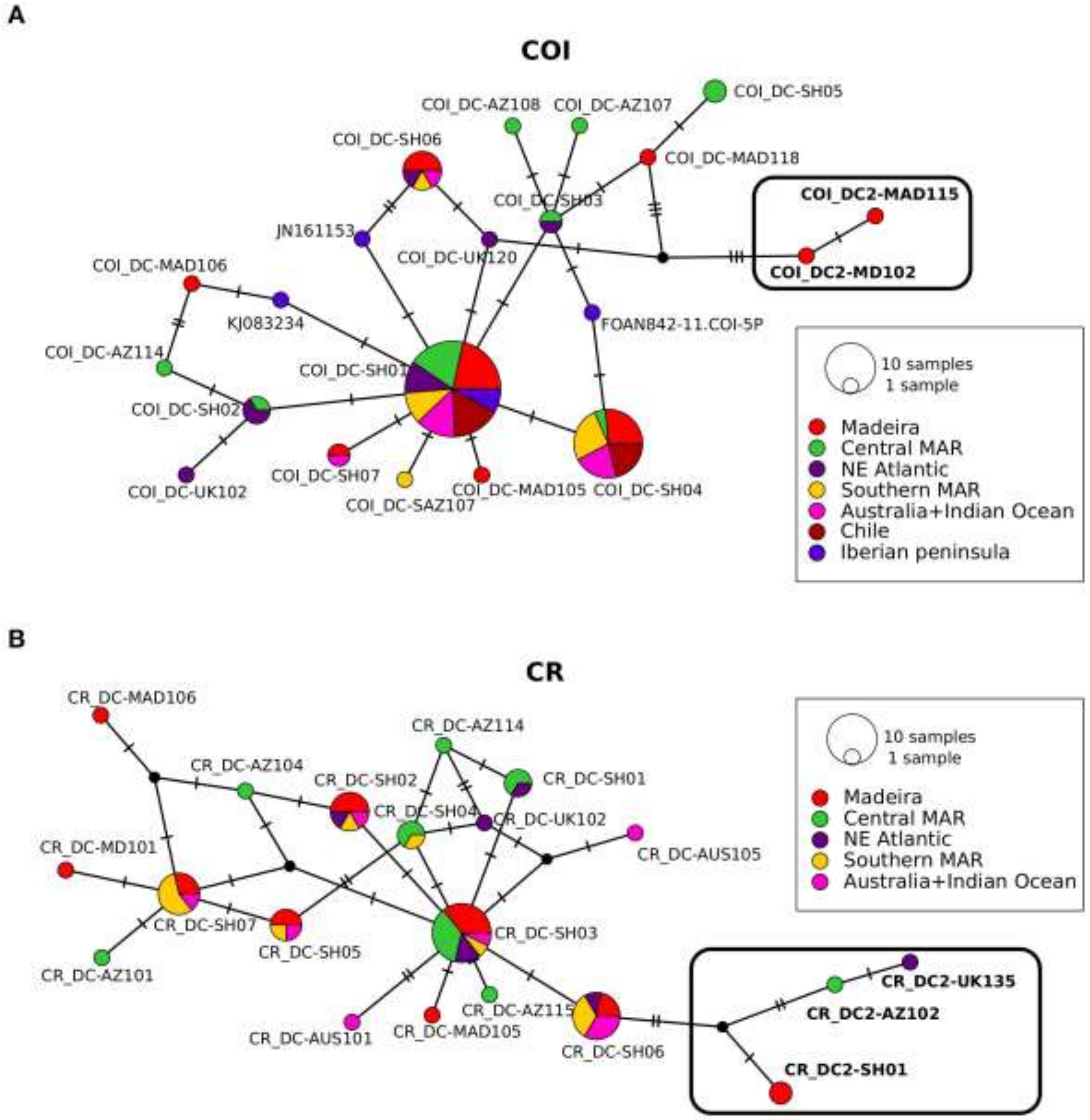

Figure 4 - Integer neighbour-joining haplotype networks for COI (A) and CR (B). Circles represent haplotypes and size is proportional to the relative frequencies.

Colours are associated to sampling localities and the numbers of substitutions are indicated with bars when more than one. Haplotype coding is given in Supplementary Table S1.

Denticle Shape and Size Among *Deania* Species of the NE Atlantic

From the 149 *D. calcea*/*D. hystricosa* skin samples analyzed, 52 belonged to females measuring between 80 and 111 cm TL (mean =96.2 cm TL), while 92 belonged to males measuring between 75 and 90 cm TL (mean = 84.3 cm TL). Skin denticle height varied between 1.080–2.102 and 0.753–1.908mm (for females and males, respectively); while crown length varied between 0.544– 1.200 and 0.380–1.013mm (for females and males, respectively).

Dermal denticles in *Deania* are pitchfork-shaped (Figure 5), formed by a medial cusp and two lateral cusps, one on each side. From the visual inspection, differences among individuals are noticeable in the shape (e.g., slender or wide) and relative size (elongated or short) of the three cusps. Some denticles also showed extra spines along the cusps or at the anterior edge of the crown (e.g., Figure 5D). Among the 4 specimens whose sequences clustered as *D. calcea*2, dermal denticles were only available for specimen MAD115 (Figure 5B) and they presented short and wide cusps.

In *D. calcea* specimens, the majority had elongated and slender denticles (Figure 5C), however a few individuals (e.g., MAD111; Figure 5F) had shorter denticles with wide cusps.

The analyses of denticle data indicated that crown length increases proportionally with specimen body size and it is also related to sex. The best supported model was the one where denticle size is explained by both TL and sex (linear model: = 0.20, SE = 0.18: $p < 0.0001$, adjusted $R^2 = 0.48$; AIC: −220.86, df = 4), but still, size alone is a good predictor of denticle crown length ($p < 0.001$). On the other hand, depth did not show any statistical correlation in predicting denticle size, although large females were captured at shallower depths than males (Supplementary Figure 4).

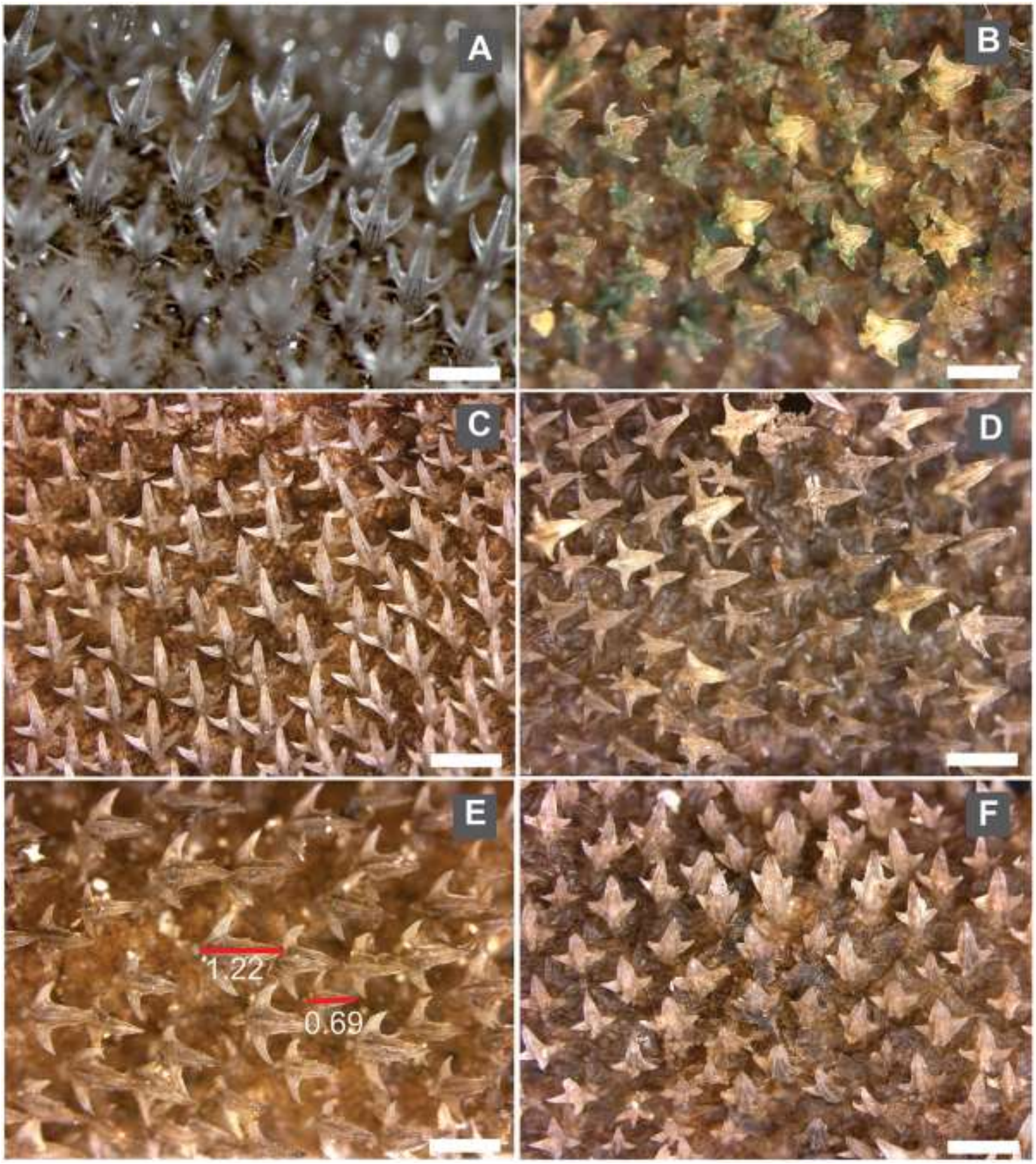

Figure 5 - Images of dermal denticles belonging to different *Deania* species from the NE Atlantic (A) Dermal denticles from *D. profundorum*; (B) *D. calcea*2 MAD115 (see Figure 2), a female with TL = 93.5 cm; (C) *D. calcea* MAD117, a male with TL = 83.7 cm; (D) *D. calcea* MAD110, a female with TL = 83.6. The white mark in each image corresponds to 1mm.

Discussion

According to the literature accompanied by dichotomous keys for the identification of three *Deania* species for the North Atlantic (e.g., Cadenat and Banche, 1981; Compagno, 1984; Castro, 2011; Ebert and Stehmann, 2013), the character that uniquely identifies *D.*

profundorum is the presence of a subcaudal keel, which is absent in the other species. Our molecular findings based on the two mtDNA genes (COI and CR) supported the visual identification for *D. profundorum*, but leave uncertainty for the separation between *D. calcea* and *D. hystricosa*. Morphological identification relying on the skin roughness assessment was not supported by the genetic analysis, since all sequences of the specimens classified as *D. hystricosa* or as *D. calcea*/*D. hystricosa* clustered together as *D. calcea*. Such findings are also supported by the recent study by Rodríguez-Cabello et al. (2020) indicating the difficulties of visually inspecting of *Deania* specimens from northern Spain.

Phylogenetic inferences suggest *D. profundorum* to be the basal split in *Deania* and *D. quadrispinosa* as the sister taxon of the clade *D. calcea* (Figure 2). Although, four of our individuals showed distinct haplotypes that formed the only well-defined subclade *D. calcea*2 nested within the *D. calcea* clade (Figure 2), more focused analyses shows that the supports on the *D. calcea*2 node are not very high, regardless of the inference approach used. In both ABGD and mPTP analyses the subclade *D. calcea*2 was never delimited as a distinct species, but always tightly clustered within the *D. calcea* clade. The only situation in which the two analyses reveal any further clustering on putative species is in *D. quadrispinosa*. *D. quadrispinosa* is the clade with the lowest number of COI sequences but hosted by far the highest levels of nucleotide diversity. However, *D. quadrispinosa* was not actively sampled in our research and all sequences derived from publicly accessible databases (GenBank and BOLD). Therefore, interpretation of this results should be taken with caution as nucleotide diversity may be overestimated.

*D. calcea*2 uniquely differs genetically from *D. calcea* sequences for two transitions in CR and two transversions + two transitions in COI. This level of genetic differentiation is comparable to the one reported for the intraspecific variability between *Centroscymnus coelolepis*, another deep water shark, from the Atlantic and the Mediterranean Sea (Catarino et al., 2015). Here the Strait of Gibraltar may have acted as geographical barrier and the authors invoked cryptic speciation by genetic drift (Catarino et al., 2015), but for *D. calcea*, the distribution of the main clade and the subclade overlaps as they live in sympatry (Weigmann, 2016; Froese and Pauly, 2019). For this reason, we might consider two plausible hypotheses to explain the relationship between these two units: incipient speciation or introgression. Nevertheless, the fact that *D.calcea*2 sub-clade is not supported by morphology nor phylogeography, coalescent stochasticity could also be accounted for the formation of a separate sub-clade as coalescence is a random process (Knowles and Maddison, 2002; Hudson and Turelli, 2003).

No inference can be made on the basis of the molecular makers used in this study and validations of the most plausible hypothesis, either biological or merely a result of stochastic forces, can only be made exploring genomic data. Only fine resolution analysis of nuclear markers might provide further insights on the speciation processes associated to these two species. A recent comparative study applying ddRAD sequencing to identify inter-gene pool SNPs in *Deania calcea* from the Atlantic and the Pacific, reported effective panmixia across sampling sites (Keggin, 2017). However, this work does not seem to have included specimens whose COI sequences match with any those reported for *D. calcea2* specimens, that for us remains an open question. The lack of hybrids between *D. calcea* and *D. calcea*2 would support the hypothesis of incipient speciation, while evidence of hybridization between the two would favor the hypothesis of an historical vicariance event. An example of vicariance or lineage sorting in a large panmictic population of deep-sea sharks is reported for *Centroscymnus crepidater* (Cunha et al., 2012). This species presents a marked divergence between the two clades (24 mutational steps in CR), and the trigger for the separation was attributed to the oceanic cooling observed during the Miocene (Cunha et al., 2012).

The original description of *D. hystricosa*, refers to the type specimen that was a female captured off Japan (Garman, 1906). Half a century later, with the revision of several species belonging to the suborder Squaloidea, Bigelow and Schroeder (1957) revised the classification of *Deania* species based on the shape of their teeth. The *D. hystricosa* type specimen was lost, but from the detailed original description the authors did not find any support to maintain the status of distinct species for *D. hystricosa*, considering it a synonym of *D. calcea*. A few decades later, Compagno (1984) resurrected the species name after revising the description of *D. mauli* (Cadenat and Banche, 1981) from Madeira Island. This newly reported species presented large denticles compared to those of *D. calcea*, but very similar to the ones reported for *D. hystricosa* (Garman, 1906). Therefore, *D. mauli* was synonymised with *D. hystricosa*, and no further revision on this genus has been made since, adopting as discriminant character between *D. calcea* and *D. hystricosa* the size of their dermal denticles (e.g., Ebert and Stehmann, 2013).

In our study the specimens genetically identified as *D. calcea* exhibited skin denticles with a large variety of patterns (e.g., slender/wide, extra spines, etc), including similar to the ones reported in Cadenat and Banche (1981) described as *D. calcea* and *D. mauli*. We did not find distinctive patterns or size ranges to be attributed to either *D. calcea* or *D. hystricosa*. Moreover, the only denticles available for *D. calcea*2 (MAD115, Figure 5B) were among the smallest compared to those measured in *D. calcea* specimens of similar total length (Figure 6). According to our findings, denticle crown length increased accordingly to the size of the specimen (Figure 6) strengthening the doubt on the validity of considering *D. hystricosa* as a nominal species. In this respect, our findings are in agreement with Rodríguez- Cabello et al. (2020) although they scrutinized a limited number of specimens. Our results also suggested that crown length was marginally correlated with sex, contrarily to the findings of Rodríguez-Cabello et al. (2020). Although in *D. calcea,* as in many squaloid sharks, females attain bigger sizes than males (Irvine et al., 2012; Rochowski et al., 2015), the results shown by the regression lines, mean that for specimens of the same size, in general females had slightly bigger crown lengths compared to males, suggesting some degree of sexual dimorphism in denticle crown length. While positive correlation between denticle and body size in sharks is commonly reported (e.g., in deep-sea sharks: Weigmann et al., 2015), evidence of sexual dimorphism in denticle morphology is rarely described (e.g., in *Scyliorhinus canicula*: Crooks et al., 2013). Sexual dimorphism associated with larger denticles in females has been suggested to be an adaptation to male biting during mating (Crooks et al., 2013) that in extreme situations may cause severe wounds on the female partner (Ritter and Amin, 2019).

According to the crown length diagnosis, most of the females were identified as *D. hystricosa*, while most males were identified as *D. calcea*. In our dataset (n = 149) we found that those specimens with an average crown length ≥0.85 mm (as a proximity to the definition of "very large—around 1 mm" and therefore attributable to the classification as *D. hystricosa*), resulted to be mainly females with only few males (58 vs. 4%, respectively). We found that crown length could not be used as a diagnostic character (either 0.5 or 1.0 mm), since it was impossible to draw a boundary to distinguish either one or the other species. Moreover, denticle size varies within individuals according to region of the body (Rodríguez-Cabello et al., 2020), leading to the conclusion that this is not a good identification character for discriminating between *D. calcea* and *D.*

hystricosa. Although shape and size of dermal denticles are useful to distinguish between families or genera (e.g., *Centrophorus* vs. *Deania*), there are cases in which dermal denticles go through marked ontogenic changes from juveniles to adults that could resemble denticles belonging to distinct taxa (e.g., White et al., 2013; Veríssimo et al., 2014; *Centrophorus* spp.).

Targeted fishing of deep-water sharks is prohibited in European waters, although by-catch is still allowed in certain circumstances and limits (quota; Reg. UE 2018/2025) and is likely to be a threat for this long-lived species. Biological and catch information are fundamental to assess species vulnerability and for a sustainable fisheries management, and at the base of this information is an accurate species identification. A better knowledge of the species diagnostic features and molecular taxonomy, will reduce the level of taxonomic uncertainties and misidentification, improving fisheries management and promoting species conservation. In European waters, the long snouted deepwater dogfish is captured as a by-catch of deep- water fisheries that started to be exploited during the early 1960’s (Gordon, 2001), when the traditional fisheries on the continental shelf declined (Koslow et al., 2000).

Current conservation assessments and fisheries management consider *D. calcea* and *D. hystricosa* as separate species, at least in the NE Atlantic. According to our analyses, past datasets reporting them separately, should now be merged and any time series or stock assessments adjusted accordingly. The landings of *D. calcea* in Portugal were around 120 tons/year in the last decade (DGPA, 2010). Similarly, the IUCN red list reports *D. calcea* as a species of least concerned (LC) and *D. hystricosa* as data deficient (DD) species. The IUCN red list assessment should likewise be revised to reflect the fact that these are the same species in the NE Atlantic. Lumping of species is likely to result in a more favorable assessment of conservation or stock status, but it should be born in mind that this species, like most deep-water sharks, is still highly vulnerable to exploitation. Despite protection in the form of landings prohibition and an EU wide trawling ban at depths >800 m, bycatch by longline and trawler vessels remains a threat.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Ethics statement

All specimens were caught during scientific surveys authorized by: the local Government of the Azores and the local Government of Madeira following the protocols accepted by the Institute for Marine Research (IMAR) and the University of the Azores, Department of Oceanography and Fisheries (UAz-DOP) in accordance with the Portuguese law and the Scottish Fishery Research annual surveys.

Author contributions

SS, GM, and FN conceived and designed the study. SS, DC, PR, GM, FN, and MF carried out the sampling. SS, DC, PR, and DS performed all the analysis. SS, DC, and DS drafted the manuscript. All authors contributed to reach the final version, gave final approval for publication, and agree to be held accountable for the work performed therein.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars. 2020.588192/full#supplementary-material

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Chapter 6

Taxonomic status of the rough long nose dogfish *Deania hystricosa* (Centrophoridae)

CHAPTER 6 - Taxonomic status of the rough long nose dogfish *Deania hystricosa* (Centrophoridae)

Abstract

The taxonomic status and identification of the deep-sea sharks of the *Deania* genus have been controversial mainly due to the morphological similarity between some of its species. This work studies the taxonomic status of one of the species, *Deania hystricosa*, and its validity as a true taxon. Traditionally, individuals of the *Deania* genus, including *D. hystricosa*, *D. calcea* and *D. profundorum*, were classified according to the length of the denticle crown. This character was found to be significantly dependent on the sexual maturity stage or length of the individual and the area of the body where the denticles were taken. Here, 23 individuals of these species were caught during campaigns carried out in the Atlantic Ocean (East-Central and Southeast) and in the North Atlantic (Cantabrian Sea), in order to be analysed for the mitochondrial genes 16S ribosomal RNA (16S rRNA) and cytochrome oxidase subunit I (COI). Phylogenetic analysis of concatenated sequences showed two clearly differentiated groups: one consisting of the species *D. profundorum*, and the other one consisting of the species belonging to *D. calcea* and *D. hystricosa*. The genetic differences measured between the *D. profundorum* group and the *calcea-hystricosa* group (3.9%) were within the range of congeneric species, whereas those differences obtained between *D. calcea* and D. *hystricosa* (0.2%) were within the range of intraspecific variation of any of the 3 species analyzed. The results found suggest that *D. calcea* and *D. hystricosa* are the same species.

Keywords

Deania, taxonomy, dermal denticles, COI, 16S rRNA.

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Introduction

The family Centrophoridae Bleeker, 1859 (Chondrichthyes: Squaliformes) consists of two genera, *Centrophorus* (Müller & Henle, 1837) and *Deania* (Jordan and Snyder, 1902), both of which have a complex taxonomic history. *Deania* genus is a group of deepwater sharks with worldwide distribution in continental slope regions (Compagno, 1984).

Up to now, *Deania* genus was composed by four species: *Deania calcea* (Lowe, 1839), *Deania hystricosa* (Garman, 1906), *Deania profundorum* (Smith & Radcliffe, 1912) and *Deania quadrispinosa* (Ebert & Stehmann 2013). The rough longnose dogfish (*Deania hystricosa*) is a deepwater shark little known. This species is characterized by large denticles, a crown length of around 1 mm, and the miss of a subcaudal keel on the lower part of the caudal peduncle. The first dorsal fin is long and low, originating from the bases of the pectoral fins. The distance from the origin of the first dorsal fin spine to the rear tip is much greater than the distance from the free rear tip to the second dorsal fin spine. Adults are between 84 to about 109 cm (Compagno, 1984). The colour varies from blackish brown to canescent brown and the fins are a little darker than the body. However, lightly coloured individuals with large denticles and sizes up to 111 cm have been identified as *D. hystricosa* by Brito *et al.* (1998) near the Canary Islands.

D. hystricosa is irregularly distributed throughout the oceans. Occasional specimens have been informed in Canary Islands, Azores, Madeira Islands, the British Isles, Bay of Biscay, Namibia and South Africa. It has also been reported in the Western North Pacific: Japan and New Zealand (Ebert and Stehmann, 2013). This species is caught incidentally in Madeira in the black scabbardfish fishery (*Aphanopus* spp.), at depths ranging from 800 to 1,200 m. and has been used for human consumption and for the use of liver oil (Biscoito et al., 2018). In the Canary Islands, there was a very profitable industrial exploitation of this species for the use of oil from their livers and meat between the 1940s and 1950s (Brito *et al.* 1998; Brito *et al.* 2002). Little information about *D. hystricosa* is available from the Azores, North Atlantic Ocean or West Africa where the fisheries are on seamounts, banks and coastal areas.

D. hystricosa has been synonymized with *D. calcea* by Bigelow and Schroeder (1957) and the latter has been synonymized with *Deania eglantina* (Jordan and Snyder, 1902). Cadenat and Blache (1981) named a new species *Deania mauli*, from the large specimens that landed in Camara de Lobos (Madeira), later recognized as *D. hystricosa* because there was no difference with Garman's description (Garman 1906). Finally, Compagno (1984) differentiated *D. calcea* and *D. hystricosa* as two distinct species. The characteristics to differentiate *D. hystricosa* from *D. calcea* have been controversial and should be reviewed (Ebert & Stehmann 2013). Morphologically, *D. hystricosa* has similar characteristics to *D. calcea.* Both species are characterized by a flattened head with a long face, low dorsal fins and very long fin base with hard and grooved spines. The only feature distinguishing *D. hystricosa* from *D. calcea* is the lateral trunk denticle size (Compagno, 1984). The dermal denticles on the outer surface, in the oral cavity, fins and in the pterigopodia of the elasmobranchs have been widely studied in different species of shark (Atkinson and Collin, 2012; Rodrigues, 2009; Valenzuela *et al.*, 2008). They are a basal plate embedded in the dermis from which a peduncle grows from the base to the crown (Rodrigues, 2009). Dermal denticles have hydrodynamic functions, being able to reduce friction, although they can also protect against predators and ectoparasites (Bone, 1975, Raschi and Tabit, 1992, Reif, 1985). *D. calcea* has rough skin with denticles like small tridents, which have a maximum crown length about 0.5 mm long in adults (Ebert & Stehmann 2013). This measure is the taxonomic criteria to differentiate it from its congener *D. hystricosa*, which has denticles with a crown length of about 1 mm (Ebert & Stehmann 2013) as mentioned above. Both *D. calcea* and *D. hystricosa* don't have a subcaudal keel on the lower surface of the caudal peduncle, the main difference with *D. profundorum* (Guisande *et al.*, 2011; Ebert & Stehmann 2013).

Molecular markers have become a very useful tool to delimitate species. Mitochondrial genes such as 16S ribosomal RNA (16S rRNA) and cytochrome oxidase I (COI) are common in phylogenetic studies. Its usefulness has been demonstrated in studies of sharks (Straube *et al.*, 2010) and fishes (Ward *et al.*, 2005), and considered in general as barcodes in the identification of animal species (www.barcodeoflife.org). Thus, COI and 16S rRNA genes sequences in conjunction with morphometric data for example, have been used to re-evaluate the diversity of *Centrophorus* genus in Atlantic waters and the Mediterranean Sea (Veríssimo *et al.*, 2014).

Likewise, Sanjuán et al. (2012), based on sequences of COI, confirmed differentiation between *D. calcea* and *D. profundorum* species, but not between *D. calcea* and *D. hystricosa*. They suggested that analysis of a larger number of specimens of *D. hystricosa* would be necessary to clarify its taxonomic status with respect to the other two species.

The aim of this study was to clarify the validity of the taxonomic status and the identification of *D. hystricosa*, studying specimens from the Atlantic (East-Central and Southeast) and the North Atlantic (Cantabrian Sea), through the analysis of sequences of the genes COI and 16S rRNA, and comparative analysis of meristic characters of the skin on different parts of the body of these deep sharks to support the genetic conclusion. Since there is no morphometric or meristic character of its own for this species, molecular techniques can be useful to assist in the unequivocal taxonomic identification of this species.

Materials and Methods

24 deep elasmobranchs were caught throughout Morocco, Mauritania and Namibia research cruises on the African coast and from the Canary Islands, Madeira and the North Atlantic Ocean (Galician waters and Cachucho bank) by commercial vessel fishing with drifting longlines (Figure 1). At each station, elasmobranchs were separated and identified to species level according to Compagno (1984) and Ebert & Stehmann (2013), then counted, measured and weighed. Maturity stage by sex was recorded according to Stehmann (2002) and the specimens were stored frozen for further studies.

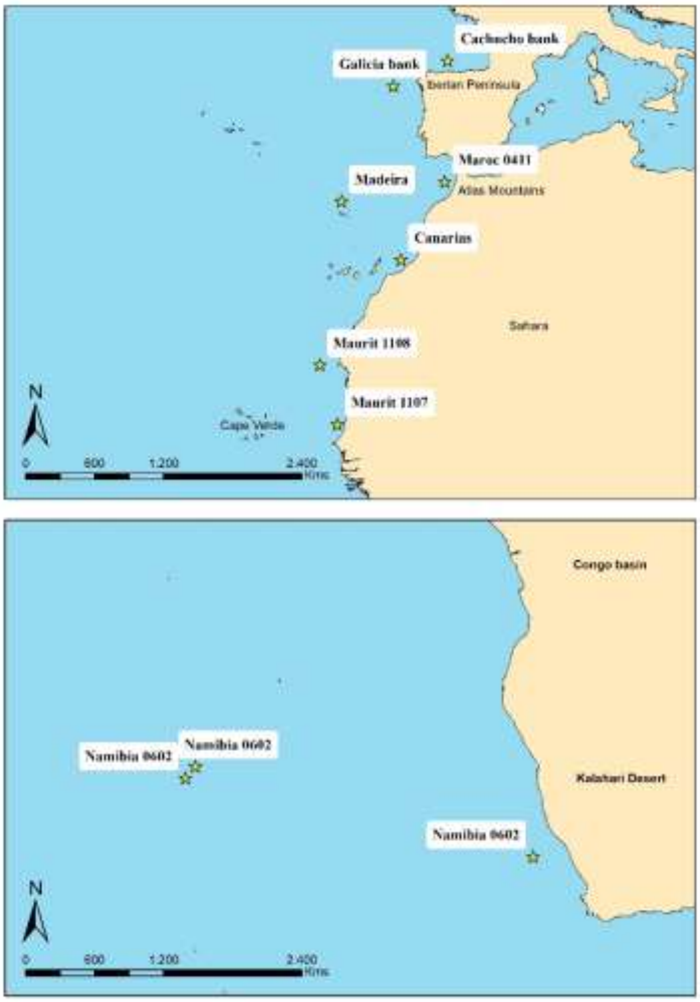

Figure 1. *Locations where the Deania samples were captured.*

2.1 Morphology of dermal denticles

Skin samples were taken from 13 *Deania* specimens, 6 adults and 7 juveniles. Samples were taken from four areas of the body: head (h), dorsal back (d), ventral (v) and tail (t) (Figure 2).

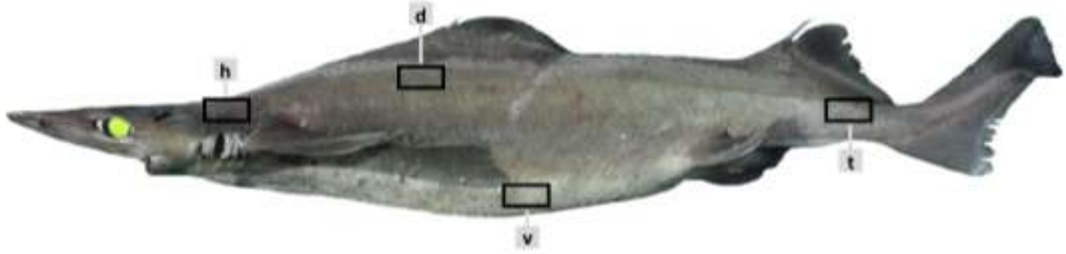

Figure 2. Location of the regions on body with samples in the present study: head (h), dorsal back (d), ventral (v) and tail (t).

From each area of the body, the crown length measurements of at least 10 randomly selected denticles were taken. A total of 295 and 422 crown length measurements were taken in adults and juveniles, respectively (Figure 3). Skin samples preserved in 70% alcohol were prepared fresh for observation in a magnifying glass (Nikon AZ100, 20X, Tokyo) connected to a camera (Nikon DS-SM) linked to the computer. For image capture, the NIS-elements f 3.2 software was used. Later, the images were analysed with Image-Pro 6.3 software (Franco-Santos *et al.*, 2016) and Image J software (Rasband, 2016).

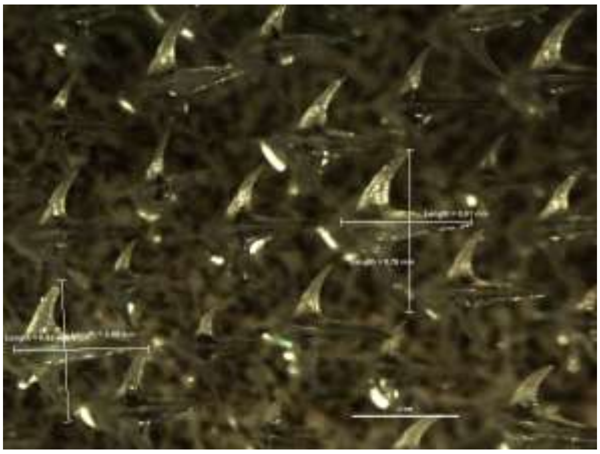

Figure 3. Crown width and length measurements on skin (length of crown used).

The measurements of the dermal denticles were statistically analysed using the IBM SPSS Statistics 25 software. We used the Kolmogorov-Smirnoff Normality Test to determine the goodness of fit of the numerical data to a normal distribution and the

Levene test to test the homogeneity of the variances. A descriptive statistic and a two-way ANOVA were carried out to check if there was an effect of stage of sexual maturity (adult and juvenile) and body area factor on the crown length of the dermal denticles, as well as a possible effect of the interaction of both factors following interaction model: *aov (variable_respuesta~factor1 x factor2, data)* in R-studio (Amat J., 2016). In all cases, a p-value less than 0.05 was considered statistically significant.

2.2 Genetic analysis

Total genomic DNA was extracted from samples of muscle of 24 sharks (23 *Deania* specimens and one outgroup (*Centroscymnus crepidater*). For extractions, we used a standard phenol/chloroform procedure (Sambrook *et al.*, 1989) after an overnight proteinase K digestion (20 mg/ml) at 56 °C. Two fragments of mitochondrial genes, COI and 16S rRNA, were amplified by polymerase chain reaction (PCR) using the primer pairs FishF2/ FishR1 (Ward *et al.*, 2005) and 16SarL/16SbrH (Palumbi *et al.*, 1991), respectively.

PCR amplifications were carried out in a BioRad T100 thermocycler (BioRad, Hercules, California, USA), using VWR Taq DNA polymerase (VWR International) following the manufacturer's instructions. PCR cycle conditions consisted of an initial step at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 15 s, annealing at 50 °C for 16S rRNA, 52 °C for COI, for 20 s, extension at 72 °C for 30 s and a final extension step at 72 °C for 5 min. Aliquots of amplified products were electrophoresed on 1.7% agarose gel to verify DNA amplification. Subsequently, PCR products were enzymatically purified with ExoSAP-IT kit (Thermo Fisher Scientific) and finally sequenced in Macrogen Europe (Amsterdam, Netherlands).

Nucleotide sequences were aligned using CLUSTAL W (Thompson *et al.*, 1994) as implemented in the software MEGA X v. 10.1 (Stecher *et al.*, 2020) and the resulting sequences were deposited in GenBank. Accession numbers for COI: OQ605455-OQ605465. Accession numbers for 16S rRNA: OQ605527-OQ605534.

Maximum likelihood (ML) and Bayesian Inference (BI) trees were constructed from both individual mitochondrial COI and 16S rRNA, as well as from concatenated sequences. The best-fit nucleotide substitution model for the two fragments (COI and 16S rRNA) was determined using the software JModelTest v2.1.5 (Darriba *et al.*, 2012), according to the Bayesian information criterion (BIC) (Schwarz, 1978). HKY (Hasegawa, Kishino and Yano, 1985) was the chosen model for both fragments.

All phylogenetic analyses were performed through the Mobyle SNAP Workbench (Monacell and Carbone, 2014). ML analyses were conducted with RAxML 7.2.8 software (Stamatakis, 2006), using 1000 bootstrap replicates (BT). When concatenated sequences were analyzed, a partitioned analysis was used to accommodate the variation among data sets. For BI analyses we used MrBayes v.3.2.1 software (Ronquist *et al.*, 2012). Two independent runs were performed with default prior values, running 10^7 generations with sampling frequency every 100 generations. All parameters were unlinked across partitions when concatenated sequences were used. Of the resulting trees, the first 25,000 trees were discarded as burn-in and the following 75,000 trees were used to estimate the topology of a consensus tree. The percentage of times a node occurred within those 75,000 trees was interpreted as the Bayesian posterior probability (BPP) of the node. The visualization and edition of all the trees was made with Fig Tree v1.4.0 software (Rambaut, 2009).

Finally, we used the sequence-based ABGD (Automatic Barcode Gap Discovery) (Puillandre et al., 2012) model, for the concatenated sequences of both DNA markers, to delimitate hypothetical species. The analysis was performed online (https://bioinfo.mnhn.fr/abi/public/abgd/) under Kimura 2-Parameter (K2P) model (Kimura 1980), and uncorrected distance (p-distance) with relative gap width X = 1.5, intraspecific divergence (P) values ranging from 0.001 to 0.100 and default settings for the rest of the parameters.

Results

Biological data of 24 shark specimens are presented, belonging to two families and four species from Namibia, Mauritania, Morocco, North Spain, Madeira and Canary Islands (Table 1). The scientific name used in "species" refers to the taxonomic identification according to Compagno (2001). Samples from a very wide range of latitudes, from 43º North to -22º South and longitude, from 12º East to 18º West are presented (Figure 1 and Table 1).

Table 1. List of specimens analysed.

ID	Specie	Family	Country	Coordinates	Centre	Survey
1	*Centroscymnus crepidater*	*Somniosidae*	Namibia	*-22.15633º S and 12.3252º E*	IEO Tenerife	Namibia 0602
2	*Deania calcea*	*Centrophoridae*	Mauritania	*20.5967º N and -18.0813º E*	IEO Tenerife	Maurit 1108
3	*Deania calcea*	*Centrophoridae*	Mauritania	*20.5967º N and -18.0813º E*	IEO Tenerife	Maurit 1107
4	*Deania calcea*	*Centrophoridae*	Namibia	*-22.156333ºS and 12.3252º E*	IEO Tenerife	Namibia 0602
5	*Deania calcea*	*Centrophoridae*	Namibia	*-23.72733º S and 13.0176º E*	IEO Tenerife	Namibia 0602
6	*Deania calcea*	*Centrophoridae*	Namibia	*-22.15633º S and 12.3252º E*	IEO Tenerife	Namibia 0602
7	*Deania calcea*	*Centrophoridae*	Spain	*44.2º N and 5.2666667º W*	IEO Santander	Cachucho Bank
8	*Deania calcea*	*Centrophoridae*	Spain	*44.2º N and 5.2666667º W*	IEO Santander	Cachucho Bank
9	*Deania calcea*	*Centrophoridae*	Spain	*42.25º N and 11.15º W*	IEO Santander	Galicia Bank
10	*Deania hystricosa*	*Centrophoridae*	Spain	*28.0166º N 12.6833º W*	IEO Tenerife	Canarias
11	*Deania hystricosa*	*Centrophoridae*	Namibia	*-29.382333º S and 14.2291º E*	IEO Tenerife	Namibia 0602
12	*Deania hystricosa*	*Centrophoridae*	Morocco	*35.4550º N and 6.84866º W*	IEO Tenerife	Maroc 0411
13	*Deania hystricosa*	*Centrophoridae*	Morocco	*35.4550º N and 6.84866º W*	IEO Tenerife	Maroc 0411
14	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
15	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
16	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
17	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
18	*Deania calcea*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
19	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
20	*Deania hystricosa*	*Centrophoridae*	*Portugal*	*33.5321º N and 17.6908º W*	Funchal Station	Madeira
21	*Deania profundorum*	*Centrophoridae*	Mauritania	*16.9708º N and -16.8976º E*	IEO Tenerife	Maurit 1107
22	*Deania profundorum*	*Centrophoridae*	Mauritania	*16.9708º N and -16.8976º E*	IEO Tenerife	Maurit 1107
23	*Deania profundorum*	*Centrophoridae*	Spain	*42.25º N and 11.15º W*	IEO Santander	Galicia Bank
24	*Deania profundorum*	*Centrophoridae*	Spain	*42.25º N and 11.15º W*	IEO Santander	Galicia Bank

3.1 Morphometric denticles analysis

A statistical summary of the horizontal length measurements of the dermal denticle crown is presented for the 13 specimens according to maturity state and the regions of the body selected for this study. The size range in the adult specimens ranged from 79 to 112 cm. In adults, the mean crown length was 0.869 mm, with a minimum of 0.361 mm and a maximum of 1.347 mm. The maximum lengths were observed in the ventral zone (v) with a maximum of 1.237 mm and a mean of 0.916 mm. The minimum sizes were observed in the caudal zone (t) with a maximum length of 0.776 mm and a mean of 0.572 mm. The size range in juvenile specimens ranged between 54.3 and 96 cm, the mean crown length was 0.525 mm, with a minimum of 0.249 mm and a maximum of 1 mm. The maximum lengths were observed in the dorsal area (d) with a maximum of 1 mm and a mean of 0.582 mm. The minimum sizes were observed, in the caudal zone (t) with a maximum length of 0.647 mm and a mean of 0.396 mm (Table 2).

Table 2. Summary statistic description of the crown length denticle. Regions body: d=dorsal zone, h=head zone, t= tail zone, v=ventral zone. (TL, Total Length)

Denticles	N	Size range TL (cm)	Body zone	Nº measures of crown length	Mean crown length (mm)	Desvest crown length (mm)	Min crown length (mm)	Max crown length (mm)
Adult	6	79-112	d	95	0.885	0.190	0.361	1.257
			h	105	0.878	0.194	0.471	1.223
			t	20	0.572	0.133	0.397	0.776
			v	75	0.916	0.207	0.450	1.347
			all	295	0.869	0.208	0.361	1.347
Juvenile	7	54,3-96	d	135	0.582	0.166	0.249	1.000
			h	111	0.517	0.081	0.332	0.702
			t	86	0.396	0.068	0.300	0.647
			v	90	0.574	0.119	0.369	0.902
			all	422	0.525	0.139	0.249	1.000
Total				717	0.667	0.241	0.249	1.347

Denticle length showed significant differences between body regions; therefore, the area of the body where the measurements are taken is critical for the comparative analysis between species. Graphical representation and statistical calculation of the means clearly show that the difference between the size of the dermal denticle crown depends on the state of maturity (size body) and the region of the body (Figure 3a). The length of the crown of the dermal denticle seems to increase as size increases or according to the body region. In addition, it is clearly observed that the tail area has the smallest denticles in both adults and juveniles (Figure 3b).

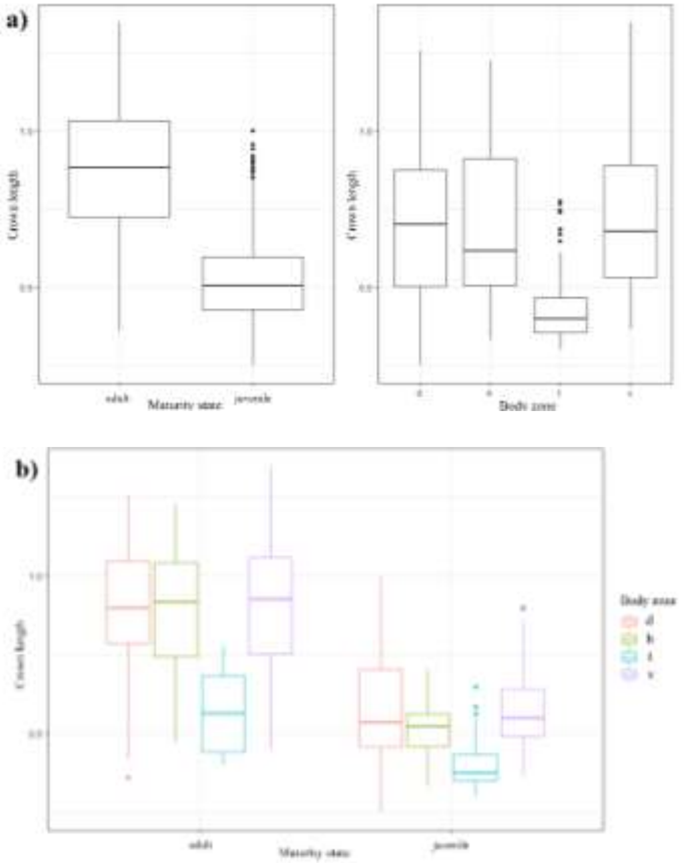

Figure 3. Crown length, visualize summary statistics with box plot by maturity state and Body zone in general (a). Crown length by Body zone; visualize summary statistics with box plot for each Maturity state (b).

Table 3 shows the results for the two-way ANOVA, significant results are observed on the dependent variable, "crown length" as a function of the factors "maturity state" and "body zone", as well as in the joint effect of both ($p < 0.005$).

Table 3. Two-way ANOVA by maturity state, body zone and the interaction.

2-way ANOVA	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Maturity state	1	20.55	20.55	864.67	< 2e-16***
Body zone	3	3.59	1.20	50.40	< 2e-16***
Mat.State:BodyZone	3	0.47	0.16	6.56	0.00022***
Residuals	709	16.85	0.02		

Signif. codes: *** p<0.001

In the interaction graphs, significant differences are observed in the size of the denticle crown as a function of the state of maturity (Figure 4a) and between the regions of the body (Figure 4b). A proportional reduction in the size of the crown is observed, for all the regions of the body analysed, between adults and juveniles (Figure 4a). It is clearly observed how the size of the crown of the dermal denticle is always greater in adult specimens in the four regions of the body studied (Figure 4b).

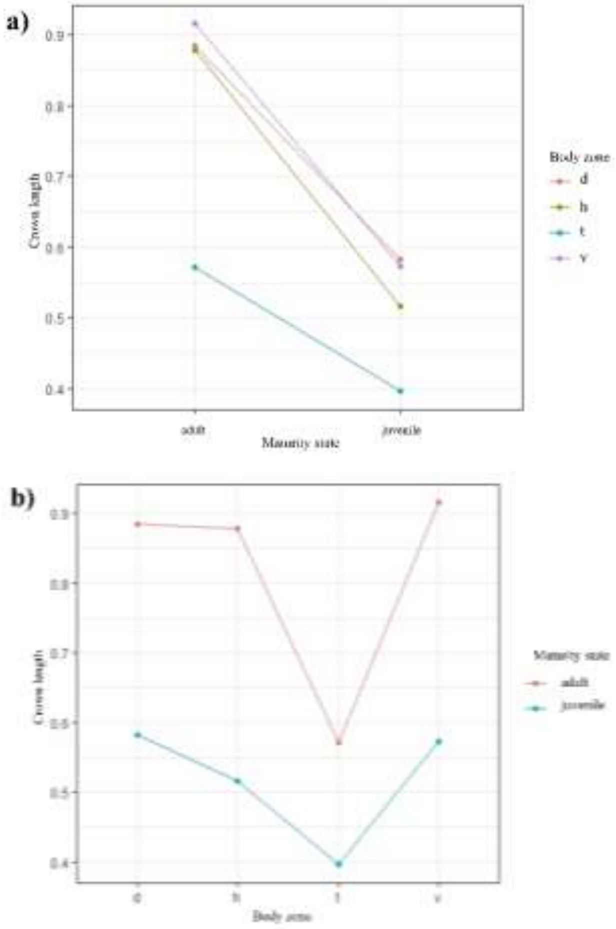

Figure 4. Interaction graphs in two-way ANOVA analysis by body zone (a) and by maturity state (b).

3.2 Genetic Results

The 5’ end of COI gene (589 bp) was amplified and sequenced for 24 specimen representatives of *D. calcea* (9), *D. hystricosa* (10), *D. profundorum* (4) species and one specimen of the *C. crepidater* as outgroup. Overall, 25 positions were variable, defining 3 haplotypes in *D. calcea*, 5 in *D. hystricosa* and 2 in *D. profundorum*. Interestingly, 3 haplotypes were shared between *D. calcea* and *D. hystricosa*. All substitutions occurred at the third codon position and none of them involved amino acid change.

On the other hand, a fragment of the 16S rRNA was sequenced for the same specimens. To obtain the best possible alignment, it was necessary to include gaps (insertion/deletion, “indel”) in sequence alignments, generating a 565 bp matrix. Of the 565 sites, 7 showed variation (one indel and 6 nucleotide substitutions), generating 3 haplotypes in *D. calcea*, 2 in *D. hystricosa* and 2 in *D. profundorum.* Again, 2 haplotypes for this fragment were shared between *D. calcea and D. hystricosa.*

ML and BI phylogenetic trees obtained for the concatenated sequences of COI and 16S rRNA, were identical to those obtained for each marker independently (data not shown). Therefore, only the BI tree, for the concatenated data set is shown, with the Bayesian posterior probabilities and bootstrap values of the BI and ML analysis, respectively (Figure 5).

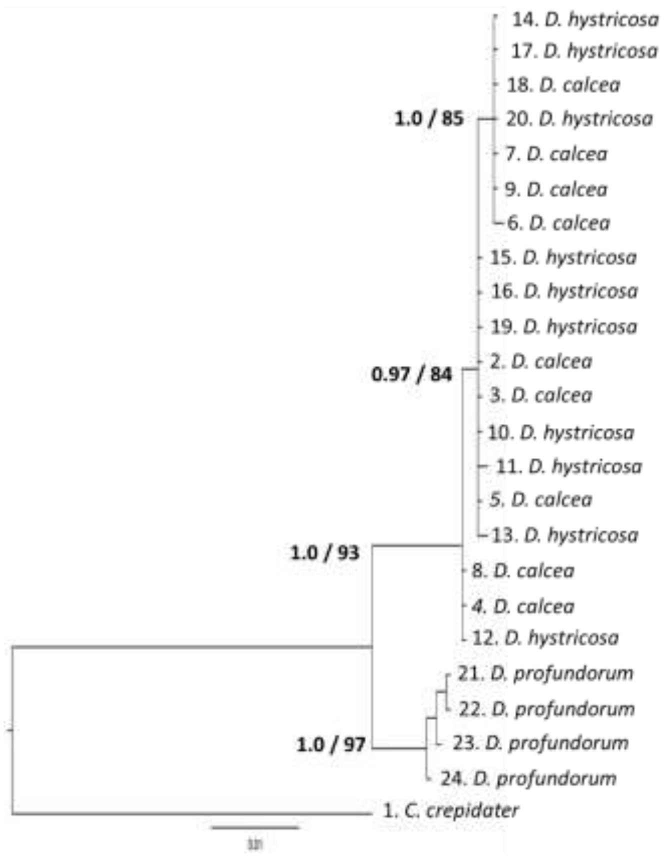

Figure 5. Bayesian tree based on COI and 16S rRNA sequences from the current study. The PPB/BT value are shown above the branch.

The trees revealed two clades statistically well supported. The one constituted by the individuals of *D. profundorum* (1 PPB; 97% BT) and a second clade grouping the specimens of *D. calcea* and *D. hystricosa* (1 PPB; 93% BT). It is noteworthy that specimens of these species (*D. calcea* and *D. hystricosa*) even share combined haplotypes for both markers (samples 12, 4 and 8; 15, 16, 19, 2, 3, 10 and 5; 14, 17, 18, 20, 7 and 9).

The uncorrected p-distances within and between species for the COI gene (Barcode), are shown in Table 4. The intraspecific variation was 0.10 in *D. profundorum*, and 0.20 % in *D. calcea* and *D. hystricosa*. Regarding the interspecific distance, the values were 3.9 % between *D. profundorum* and the other two species. It is worth mentioning the low genetic distance obtained between *D. calcea* and *D. hystricosa* (0.20%), the same as the intraspecific variation obtained in both species (Table 4).

Table 4. Uncorrected p-distances (%) obtained for the COI sequences.

	D.calcea	***D.hystricosa***	***D.profundorum***
D.calcea	0.18		
D.hystricosa	0.16	0.15	
D.profundorum	2.36	2.38	0.10

On the other hand, ABGD analysis did not provide any support to consider *D. calcea* and *D. hystricosa* as two distinct species either using uncorrected p-distances or Kimura 2-Parameter model (Figure 6).

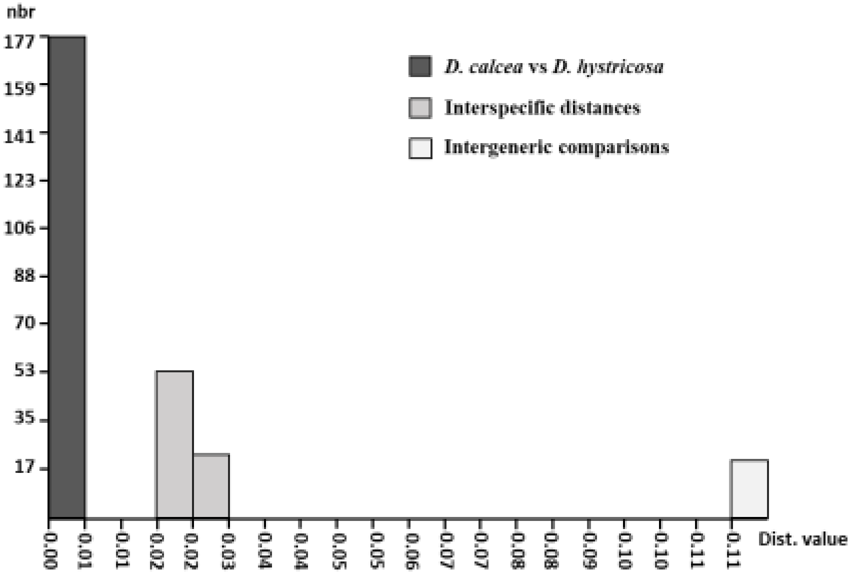

Figure 6. ABGD (Automatic barcode gap discovery) partition analysis of COI+16S rRNA sequences of *Deania* genus (23) and *C. crepidater* (1) with Kimura 2 Parameter model, generated via (https://bioinfo.mnhn.fr/abi/public/abgd/). Nbr, number of runs.

Discussion

There exist controversies in the taxonomy of some species in the Centrophoridae family due to morphological similarity, the few specimens collected, and the limited taxonomic analyses carried out in different genera (Bañón *et al.*, 2008). Species-specific morphological characteristics have been applied especially as tools for taxonomic (family-level) studies. In the genus *Deania*, the taxonomic status of *Deania hystricosa* has been enigmatic. Different authors have remarked on the need to review the characters that differentiate *D. calcea* from *D. hystricosa* (Sanjuán *et al.*, 2012; Ebert and Stehmann, 2013; Rodríguez-Cabello *et al.*, 2020; Stefanni *et* *al.*, 2021). The scarce information on the species and its reduced geographical distribution has conditioned and prevented further studies and due to this, it is considered under the category “data deficient” in the IUCN red list (Ebert *et al.* 2009).

According to the initial descriptions of the holotype carried out by Garman in 1906, the most important characters to distinguish *D. hystricosa* from *D. calcea* were the length of the dermal denticles, colour of the body and the location of the first dorsal fin. All morphological, meristic and colour characteristics were found in both species with overlapping data ranges, not significant enough to distinguish between the two species. Thus, the only taxonomic criterion recognized and used in the taxonomic keys to finally differentiate between both species has been the horizontal length of the denticles crown (Compagno, 1984; Ebert and Stehmann, 2013).

However, the length of the dermal denticles can vary depending on various factors. Denticles around the gill openings are morphologically similar but smaller in size than those on the body, which is a common feature on sharks’ squamation depending on body area (Reif, 1985). Species living near the bottom on hard substrates have scales resistant to abrasion and there is a high diversity shapes in the small regions such as mouth or fins subjected to abrasive stress (Reif, 1985). In addition, for *Rhizoprionodon lalandii* or *Heptranchias perlo* species, it has been cited how the size and shape of the denticles can vary within individuals depending on the body location, and the stage of sexual maturity (Laranjeira *et al.*, 2015; Rangel *et al.*, 2019). Between 8 and 20 distinct areas data on the body and fins from leopard, Atlantic sharp nose, shortfin mako, spiny dogfish, gulper, angel, and white sharks were studied by Ankhelyi *et al.* (2018). These measurements confirmed that denticles on different body areas of these shark species varied widely in size, shape, and spacing (Ankhelyi *et al.*, 2018). Our results confirm that the length of the dermal denticles varies greatly depending on body area and therefore, it is not suitable as a taxonomic key to distinguish these species.

Other morphological traits such as the size of the specimens were originally used to differentiate these species. In the Bulletin of the Museum of Comparative Zoology at Harvard College. Vol. XLVI. No. 1 (1906), three new species of the genus *Deania* were presented with a preliminary description and were published in more detail and with illustrations by Samuel Garman (Garman, 1906). The descriptions show the size of the type specimens as: "*Acanthidium rostratum,* sp. Nov. Total length, 34 inches or 86.3 cm; *Acanthidium aciculatum,* sp. Nov. Total length, 34.05 inches or 87.6 cm; and *Acanthidium hystricosum,* sp. Nov. Total length, 36.4 inches or 92.4 cm". Currently, the first two species, which are smaller, have been synonymized as *D. calcea* and the latter, the largest one (~ 93 cm), is still maintained as *D. hystricosa*. Also, Bigelow and Schoroeder (1957) reviewed *Deania* specimens from Japan classified as *D. eglantina* (a 30 cm female)*, D. rostrata* (87.3 cm female) and *D. aciculata* (89 cm male), concluding that the differences between these species were due to growth stage and consistent with the variation reported by Regan (1908) for *D. calcea* in the Atlantic. Based on this, all *Deania* specimens recorded in Japan up to that date were classified as a single species (Bigelow and Schoroeder, 1957). Later, a new species was described as *D. mauli* from Madeira Islands (Cadenat and Bache, 1981). The type specimens of this new species measured 83.8 cm and 96.5 cm for male and female adults respectively, being these the largest of all specimens studied. Currently, this species is also synonymized as *D. hystricosa*. All these misidentifications suggest that the size of the specimen does not constitute a good taxonomic key to identify these species. Our comparative morphological analysis of the horizontal length of the dermal denticles with specimens from very distant areas and with very different sizes, has shown that there is a strong correlation between the area of the body, the horizontal size of the denticle and the length of the specimen, which indicates that the size of the specimen is the most determining and influencing factor in the final horizontal length of the denticles of this species. This variable size of the dermal denticles in this species could be one of the reasons for the different discrepancies and many "new species" identified by different authors throughout history.

At molecular level, our results confirm that *D. profundorum* and *D. calcea* are different species agreeing with Sanjuán *et al.* (2012). They found that the genetic distance based on COI gene between *D. profundorum* and *D. calcea* was 3.6%, similar to the values obtained in our analyses (3.9%) between D. *profundorum-D. calcea* or *D. profundorum-D. hystricosa* (Table 4) and which are within the range of congeneric species (Ward *et al.*, 2005). In addition, the genetic distance among *D. calcea* and *D. hystricosa* specimens (0.20 %) was similar to the intraspecific variation of the three species (Table 4), suggesting that both are the same species.

Furthermore, ABGD analysis for delimitation of species did not provide support for *D. hystricosa* and *D. calcea* to be considered as different species (Figure 6). Our results again show that the use of morphological characters for species identification can lead to errors, especially if they depend on factors such as size and maturity stage of the specimens analysed.

On the other hand, it is noteworthy that specimens of the *calcea-hystricosa* group from very distant localities as Cantabrian Sea, Morocco, Madeira and Namibia, share haplotypes (Figure 5). At least two explanations could account for this low differentiation: a reduced rate of nucleotide substitution in these species or a high genetic flow between populations.

Martin *et al.* (1992), analysing the genetic variation of the COI gene among populations of sharks of the species *Sphyrna tiburo* from both sides of the Isthmus of Panama, found little differentiation between them despite the time they have been separated, suggesting a very low rate of nucleotide substitution (7-8 times lower than detected in primates or ungulates) in this shark species. However, studies on migration patterns with radio tracking, electronic marks and other analyses on deep-shark species, have shown that these species do not show patterns of "home-range". By contrast, they are active wandering migrants. (Yano and Tanaka, 1986; Bagley *et al.*, 1994; Veríssimo *et al.*, 2011; Moura *et al.*, 2014; Rodríguez-Cabello and Sánchez, 2014). Perhaps, the homogeneity of deep environments could explain the large displacements (Merrett and Haedrich, 1997).

Analyses of polymorphic nuclear markers such as microsatellites or single nucleotide polymorphism, could shed light on one or the other explanation.

In conclusion, our results show that *D. calcea* and *D. hystricosa* are the same species. Therefore, it is proposed that *Deania hystricosa* be considered as a synonym for *Deania calcea*.

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PART III

DEEP SEA CHONDRICHTHYES FROM SEAMOUNTS

Chapter 7

Records of some rare deep-sea fishes caught in the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira (East-Central Atlantic)

CHAPTER 7 - Records of some rare deep-sea fishes caught in the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira (East-Central Atlantic)

Abstract

Fish communities off the seamounts inside the Madeira exclusive economic zone are scarcely known, hence the need to improve this knowledge. A bottom trawl fishing survey targeting orange roughy, *Hoplostethus atlanticus* Collett, 1889, was carried out on the Lion, Susan, and Unicorn seamounts in the autumn of 2001. The aim of this paper is to give an account of the catches of that survey, during which 9 tows were conducted and 21 deep-sea fish species caught, including species rarely caught. The following fish species were collected: *Chlamydoselachus anguineus* Garman, 1884; *Scymnodon ringens* Barbosa du Bocage et de Brito Capello, 1864; *Dalatias licha* (Bonnaterre, 1788); *Centrophorus squamosus* (Bonnaterre, 1788); *Deania profundorum* (Smith et Radcliffe, 1912); *Deania hystricosa* (Garman, 1906); *Serrivomer beanii* Gill et Ryder, 1883; *Rouleina maderensis* Maul, 1948; *Argyropelecus gigas* Norman, 1930; *Chauliodus sloani* Bloch et Schneider, 1801; *Macroparalepis nigra* (Maul, 1965); *Neoscopelus microchir* Matsubara, 1943; *Gadomus arcuatus* (Goode et Bean, 1886); *Mora moro* (Risso, 1810); *Melanonus zugmayeri* Norman, 1930; *Chaunax suttkusi* Caruso, 1989; *Diretmoides pauciradiatus* (Woods, 1973); *Hoplostethus mediterraneus* Cuvier, 1829; *Beryx splendens* Lowe, 1834; *Epigonus telescopus* (Risso, 1810); *Aphanopus carbo* Lowe, 1839. The presence of *Diretmoides pauciradiatus* was confirmed in the area and *Gadomus arcuatus* was recorded for the first time from Madeira. Aspects of the life history traits of some of the species caught are presented. This includes a first approach to the estimation of the length-weight relations of 11 deep-water, data-deficient species for which prior information, estimated from data collected, did not exist in FishBase and some new insights about the biology of *Hoplostethus mediterraneus*.

Keywords

Deep-water fishes, species composition, relative growth, life history.

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Introduction

A growing interest emerged, in the last decades of the 20th century, in the development of the exploitation of deep-sea species (Merret and Haedrich 1997). During this period, commercial fishing has greatly increased the fishing effort directed to seamount-aggregated species like the orange roughy, *Hoplostethus atlanticus* Collett, 1889, oreos (Oreosomatidae), and alfonsinos (*Beryx* spp.) (see Koslow et al. 2000, Morato and Clark 2007). Although the seamount-related fisheries represent nowadays a high stake of the world deep-water fish catches, seamount research has mostly followed fisheries exploitation. Seamounts are still poorly understood habitats, among other issues concerning the living communities they support (Brewin et al. 2007).

There is also a lack of knowledge about the life history of seamount fishes, with the majority of studies focusing on the main commercial species. Contributions on these issues are particularly important considering that seamount species, and particularly seamount-aggregating species, are more vulnerable to overfishing than other deep-sea species (Morato and Clark 2007).

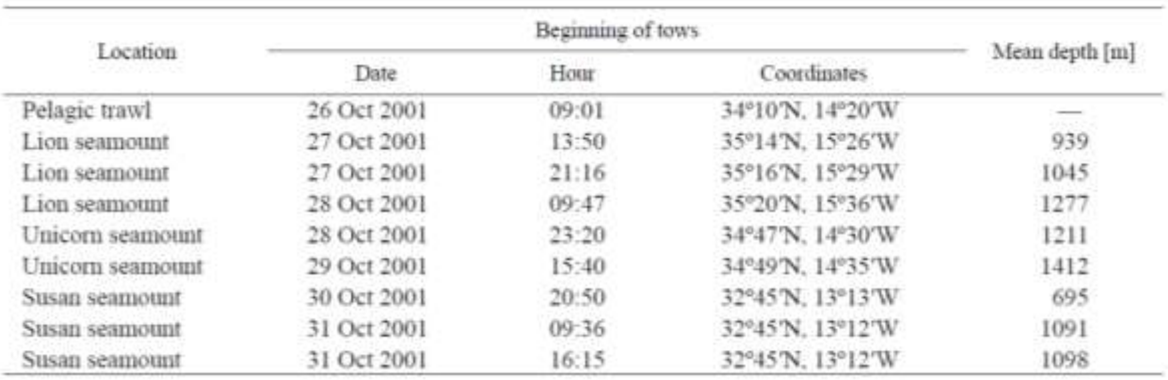
Before the establishment of Exclusive Economic Zones (EEZ) in 1977, some 10 seamounts around the archipelagos of Madeira and Canaries were exploited by fishermen. The fishing gear used were mostly pelagic trawl, less frequently bottom trawl and seine. These fisheries continued intermittently after that date in the seamounts in international waters (Clark et al. 2007). Nowadays, the seamounts inside the Madeira EEZ are subject only to small scale fisheries using bottom or drifting longlines to catch demersal fishes, mostly the bathypelagic - black scabbardfish, *Aphanopus carbo*, and intermediate scabbardfish, *Aphanopus intermedius* Parin, 1983 (see Biscoito et al. 2011, Delgado et al. 2013).

In October 2001, a fishing survey was done using a commercial trawler in order to assess potential fishing opportunities for orange roughy in the seamounts inside the Madeira EEZ. The survey failed in encountering the target species, but allowed to obtain information about some rare or poorly known deep-sea fishes and provided an opportunity to gather biological data of the most caught species.

The main purpose of this paper is to give an account on the species recorded in the catches of the trawling survey, including some species that are seldom caught or the presence of which in the area was doubtful until now. It also provides a contribution to the knowledge about some aspects of the life history traits of the most caught species during the tows, namely its length composition and relative growth.

Fish specimens were collected during a trawl survey at depths of about 1500 m using a commercial trawler (F/V Pakura) within 26 - 31 October 2001. Nine tows taking in average 55 min were made at Unicorn, Lion, and Susan seamounts within the Portuguese EEZ near Madeira (eastern-central Atlantic) (Table I).

Table I - Characteristics of the fisheries survey carried out at the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira. Mean depth obtained from depths recorded at the beginning and end of each set.



Location	Beginning of tows			Mean depth [m]
	Date	Hour	Coordinates	
Pelagic trawl	26 Oct 2001	09:01	34°10'N, 14°20'W	—
Lion seamount	27 Oct 2001	13:50	35°14'N, 15°26'W	939
Lion seamount	27 Oct 2001	21:16	35°16'N, 15°29'W	1045
Lion seamount	28 Oct 2001	09:47	35°20'N, 15°36'W	1277
Unicorn seamount	28 Oct 2001	23:20	34°47'N, 14°30'W	1211
Unicorn seamount	29 Oct 2001	15:40	34°49'N, 14°35'W	1412
Susan seamount	30 Oct 2001	20:50	32°45'N, 13°13'W	695
Susan seamount	31 Oct 2001	09:36	32°45'N, 13°12'W	1091
Susan seamount	31 Oct 2001	16:15	32°45'N, 13°12'W	1098

The species composition of each catch was assessed before processing the specimens and the list of species is arranged taxonomically according to Nelson (2006). Whenever possible, specimens of species that are seldom caught were retained and frozen for further identification. Voucher specimens were deposited in the collection of the Funchal Natural History Museum (MMF).

For each specimen, the total length (TL) was recorded to the nearest centimetre and total weight (W) and gonad weight (GW) to the nearest gram. Whenever possible, sex and gonad development stages were determined macroscopically. Gonad development was classified according to a six-point maturity scale adapted from Holden and Raitt (1974):

0 = immature; I = recovering spent; II = early maturing, development; III = late maturing, ripening; IV = ripe; V = spawned, spent.

Due to insufficient number of specimens collected for the majority of species, length–weight relation (LWR) was estimated following a method suggested in Froese (2006), setting the slope to 3 (b=3)

$$a = W\ x\ (L^3)^{-1}$$

and taking the geometric mean of "a" for species where several specimens were available. For *Hoplostethus mediterraneus*, the sole species with a sufficient number of collected specimens, length–weight relation was estimated by least-square linear regression analysis of log transformed length and weight data (Bagenal and Tesch 1978)

$$\log W = \log a + b\ x \log L$$

In this species the gonadosomatic index was obtained following the formula (King 2007)

$$\mathrm{GSI} = 100\ x\ \ GW\ x\ W^{-1}$$

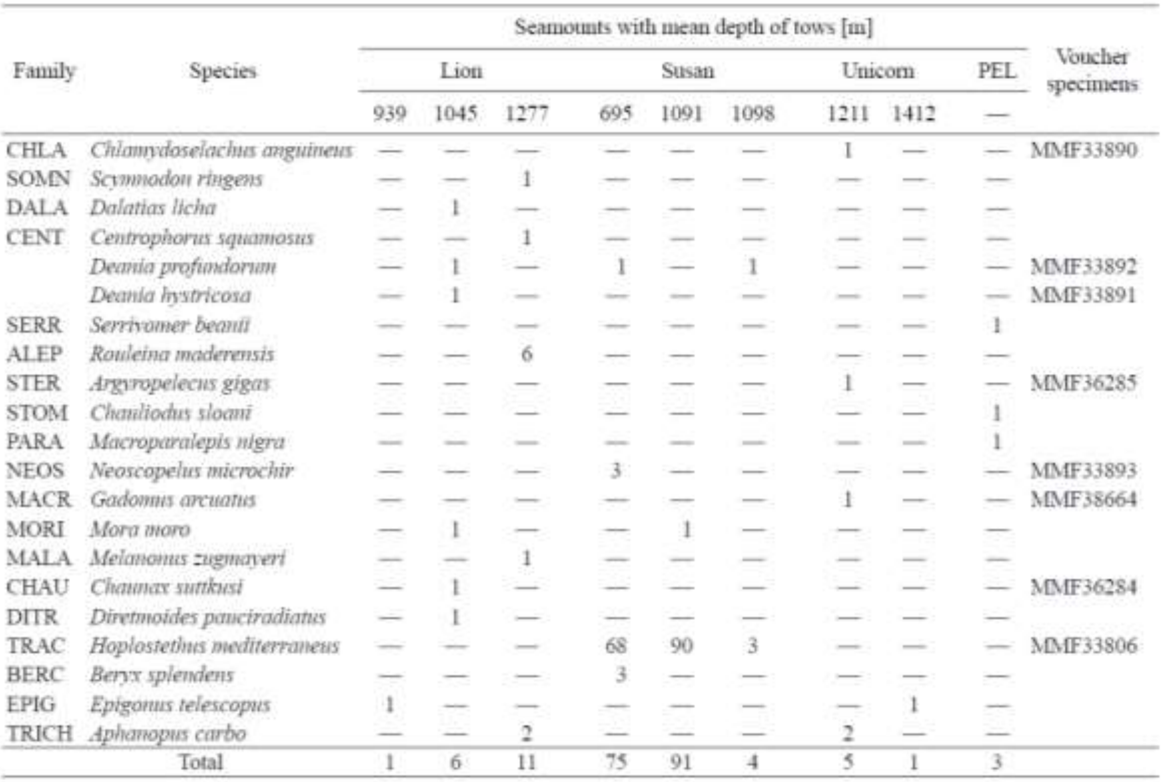
Whenever parametric tests were used to compare means, the samples were tested for normality and homogeneity of variances (respectively Kolmogorov-Smirnov and Levene's tests; $\alpha = 0.05$).

A total of 197 specimens of 21 fish species, belonging to 19 families, were caught during the survey tows (Table 2). The following fish species were collected: *Chlamydoselachus anguineus* Garman, 1884; *Scymnodon ringens* Barbosa du Bocage et de Brito Capello, 1864; *Dalatias licha* (Bonnaterre, 1788); *Centrophorus squamosus* (Bonnaterre, 1788); *Deania profundorum* (Smith et Radcliffe, 1912); *Deania hystricosa* (Garman, 1906); *Serrivomer beanii* Gill et Ryder, 1883; *Rouleina maderensis* Maul, 1948; *Argyropelecus gigas* Norman, 1930; *Chauliodus sloani* Bloch et Schneider, 1801; *Macroparalepis nigra* (Maul, 1965); *Neoscopelus microchir* Matsubara, 1943; *Gadomus arcuatus* (Goode et Bean, 1886); *Mora moro* (Risso, 1810); *Melanonus zugmayeri* Norman, 1930; *Chaunax suttkusi* Caruso, 1989; *Diretmoides pauciradiatus* (Woods, 1973); *Hoplostethus mediterraneus* Cuvier, 1829; *Beryx splendens* Lowe, 1834; *Epigonus telescopus* (Risso, 1810); *Aphanopus carbo* Lowe, 1839. The highest number of fishes caught (86%) occurred in the Susan seamount, but the catch mainly (82%) constituted of specimens of the Mediterranean slimehead, *H. mediterraneus*.

Three of the species recorded (*Serrivomer beanii, Chauliodus sloani,* and *Macroparalepis nigra*) are bathypelagic fish caught during a trial pelagic trawl.

Descriptive statistics of the size of the specimens are indicated for all the species caught and provided the values obtained for the parameter a of the LWR of 20 species (Table III).

Table II - List and abundance of species caught in the fisheries survey carried out at the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira.



Family	Species	Seamounts with mean depth of tows [m]									Voucher specimens
		Lion			Susan			Unicorn		PEL	
		939	1045	1277	695	1091	1098	1211	1412	—	
CHLA	*Chlamydoselachus anguineus*	—	—	—	—	—	—	1	—	—	MMF33890
SOMN	*Scymnodon ringens*	—	—	1	—	—	—	—	—	—	
DALA	*Dalatias licha*	—	1	—	—	—	—	—	—	—	
CENT	*Centrophorus squamosus*	—	—	1	—	—	—	—	—	—	
	Deania profundorum	—	1	—	1	—	1	—	—	—	MMF33892
	Deania hystricosa	—	1	—	—	—	—	—	—	—	MMF33891
SERR	*Serrivomer beanii*	—	—	—	—	—	—	—	—	1	
ALEP	*Rouleina maderensis*	—	—	6	—	—	—	—	—	—	
STER	*Argyropelecus gigas*	—	—	—	—	—	—	1	—	—	MMF36285
STOM	*Chauliodus sloani*	—	—	—	—	—	—	—	—	1	
PARA	*Macroparalepis nigra*	—	—	—	—	—	—	—	—	1	
NEOS	*Neoscopelus microchir*	—	—	—	3	—	—	—	—	—	MMF33893
MACR	*Gadomus arcuatus*	—	—	—	—	—	—	1	—	—	MMF38664
MORI	*Mora moro*	—	1	—	—	1	—	—	—	—	
MALA	*Melanonus zugmayeri*	—	—	1	—	—	—	—	—	—	
CHAU	*Chaunax suttkusi*	—	1	—	—	—	—	—	—	—	MMF36284
DITR	*Diretmoides pauciradiatus*	—	1	—	—	—	—	—	—	—	
TRAC	*Hoplostethus mediterraneus*	—	—	—	68	90	3	—	—	—	MMF33806
BERC	*Beryx splendens*	—	—	—	3	—	—	—	—	—	
EPIG	*Epigonus telescopus*	1	—	—	—	—	—	—	1	—	
TRICH	*Aphanopus carbo*	—	—	2	—	—	—	2	—	—	
	Total	1	6	11	75	91	4	5	1	3	

PEL = pelagic trawl; CHLA = Chlamydoselachidae, SOMN = Somniosidae, DALA = Dalatiidae, CENT = Centrophoridae, SERR = Serrivomeridae, ALEP = Alepocephalidae, STER = Sternoptychidae, STOM = Stomiidae, PARA = Paralepididae, NEOS= Neoscopelidae, MACR = Macrouridae, MORI = Moridae, MALA = Melanonidae, CHAU = Chaunacidae, DITR = Diretmidae, TRAC = Trachichthyidae, BERC = Berycidae, EPIG = Epigonidae, TRICH = Trichiuridae.

The samples of the Mediterranean slimehead, the most abundant species, were taken from the catches obtained on the bathyal bottom in the Susan seamount, in 3 bottom trawling tows. The mean tow depths were 695, 1091, and 1098 m. The length composition of all the individuals of *H. mediterraneus* caught is showed in Fig. 1. The size of the specimens ranged from 16 to 29 cm TL. The mean size (TL) of males (24.36 cm) and females (24.14 cm) caught was equal (t-test, $P > 0.05$), however, fish caught at deeper tows (1091 m and 1098 m: 24.60 cm) had a higher mean size than fish caught at a lower depth (695 m: 23.53 cm) (t-test, $P < 0.05$).

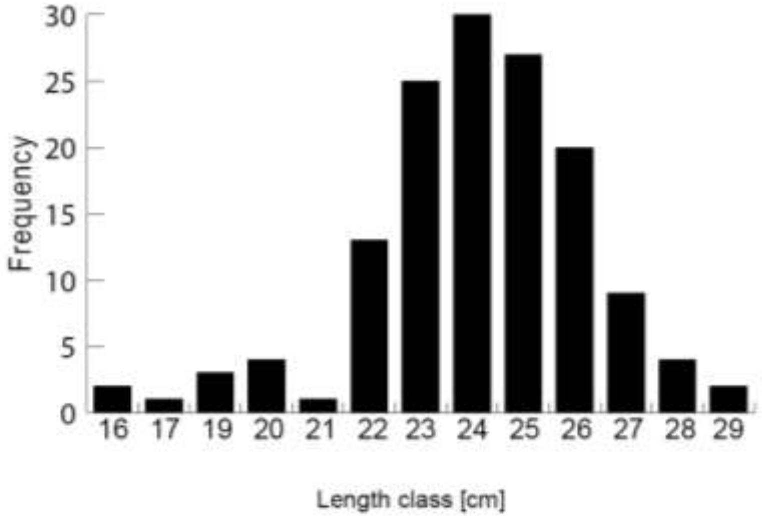


Fig. 1. Length composition of *Hoplostethus mediterraneus* (n = 141; mean TL = 24.09 cm) caught at Susan seamount, off the archipelago of Madeira

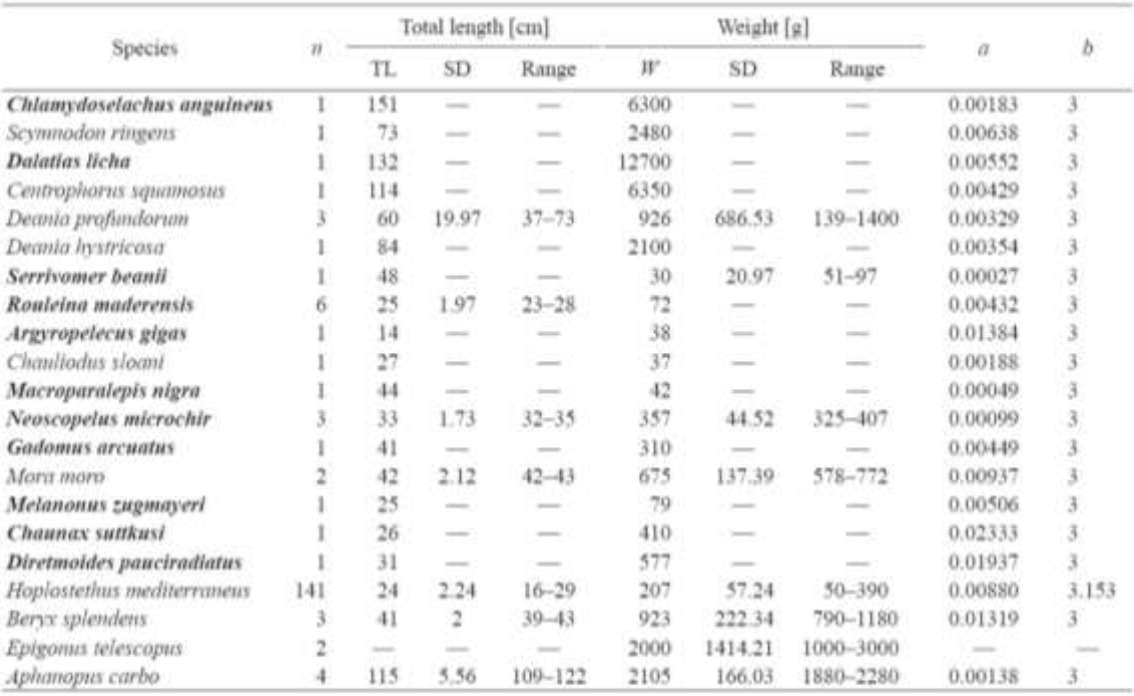
A relation between FL and TL (both in cm), was obtained from 75 specimens: $TL = 1.0518\ FL + 3.4014$; $r^2 = 0.8785$; n = 75; the relation between TL [cm] and W [g] in the pooled specimens was: W = 0.0088 TL3.1533; $r^2 = 0.9258$; n = 141; both relations were significant (ANOVA; $P < 0.05$).

The analysed gonads (n = 28) showed a 1 ÷ 1 sex ratio in an early stage of maturation (II). The respective mean GW and GSI were: 3.01 ± 0.97 (females), 0.76 ± 0.25 (males) and 1.43 ± 0.29 (females), 0.37 ± 0.11 (males).

Among the catches the presence of one specimen of *Diretmoides pauciradiatus* is a rare occurrence and confirms the presence of this species in the FNAM area (Whitehead et al.

1986), which was considered as doubtful by Post (1986). In the case of *Gadomus arcuatus*, although its occurrence was known from off the Canaries, Morocco, Azores, and Portugal (Geistdoerfer 1986, 1990, Froese and Pauly 2016) this is, to our knowledge, the first record of this species from the Madeiran waters.

Table III - Length and weight descriptive statistics of the species caught in the fisheries survey carried out at the Lion, Susan, and Unicorn seamounts, off the archipelago of Madeira.



Species	*n*	Total length [cm]			Weight [g]			*a*	*b*
		TL	SD	Range	*W*	SD	Range		
Chlamydoselachus anguineus	1	151	—	—	6300	—	—	0.00183	3
Scymnodon ringens	1	73	—	—	2480	—	—	0.00638	3
Dalatias licha	1	132	—	—	12700	—	—	0.00552	3
Centrophorus squamosus	1	114	—	—	6350	—	—	0.00429	3
Deania profundorum	3	60	19.97	37–73	926	686.53	139–1400	0.00329	3
Deania hystricosa	1	84	—	—	2100	—	—	0.00354	3
Serrivomer beanii	1	48	—	—	30	20.97	51–97	0.00027	3
Rouleina maderensis	6	25	1.97	23–28	72	—	—	0.00432	3
Argyropelecus gigas	1	14	—	—	38	—	—	0.01384	3
Chauliodus sloani	1	27	—	—	37	—	—	0.00188	3
Macroparalepis nigra	1	44	—	—	42	—	—	0.00049	3
Neoscopelus microchir	3	33	1.73	32–35	357	44.52	325–407	0.00099	3
Gadomus arcuatus	1	41	—	—	310	—	—	0.00449	3
Mora moro	2	42	2.12	42–43	675	137.39	578–772	0.00937	3
Melanonus zugmayeri	1	25	—	—	79	—	—	0.00506	3
Chaunax suttkusi	1	26	—	—	410	—	—	0.02333	3
Diretmoides pauciradiatus	1	31	—	—	577	—	—	0.01937	3
Hoplostethus mediterraneus	141	24	2.24	16–29	207	57.24	50–390	0.00880	3.153
Beryx splendens	3	41	2	39–43	923	222.34	790–1180	0.01319	3
Epigonus telescopus	2	—	—	—	2000	1414.21	1000–3000	—	—
Aphanopus carbo	4	115	5.56	109–122	2105	166.03	1880–2280	0.00138	3

TL and W represent mean values when n > 1, SD = standard deviation; the parameter a from the WLR was estimated setting b = 3; Bold font denotes the fish species with no prior LWR parameters in FishBase.

This study added information to the knowledge on the relative growth of deep water fishes considering that for 11 of the species caught (in bold in Table 3) no prior information estimated from data collection existed for LWR parameters in FishBase (Froese and Pauly 2016). In three species (*S. beanii*, *M. nigra*, and *N. microchir*) the value of *a* obtained in this study is outside the range indicated by the Bayesian estimates available in FishBase following the model developed by Froese at al. (2013).

This study provides an addition to the growth data studied in demersal fish species from this area of the Atlantic Ocean (Ferreira et al. 2007) representing a useful contribution to improve further species-specific parameter estimates in data deficient deep-sea fishes.

Concerning the Mediterranean slimehead, this species was only present in the catches made along the Susan seamount and, according to the growth performance of this species reported by D’Onghia (1998), the size composition of catches suggests all specimens caught were adult. Although young specimens were reported in catches of an experimental survey off the Greek and Italian Ionian Sea (Mytilineou et al. 2001) and from commercial trawling off South Portugal (Pais 2001), they were totally absent in this survey. The results obtained also showed an increase of the mean size of fish with depth, reflecting probable vertical segregation (the youngest up, the oldest down). This pattern was also reported by several other authors who have studied this species (D’Onghia et al. 1995, 1998, Figueiredo et al. 1995, Pais 2001, Vitale et al. 2006) and probably the cause for the absence of small sized individuals in this study, was the survey covering only depths deeper than 600 m.

The maturity stages found (late autumn) by this study suggest a later spawning season than found by Figueiredo et al. (1995) (winter), for this species off Portugal mainland. Based on the occurrence of spent fish from autumn to spring at the same latitudes, Pais (2001) suggested a more extended spawning season, which is more in line with the data obtained in this study.

Overall, this survey, with a few fishing hauls performed, resulted in new knowledge about the fish communities on seamounts, only confirming the need for further investigation about these ecosystems and strict conservation and management approaches to deal with activities, such as fisheries, in these peculiar and vulnerable sites that, appropriately, Pitcher et al. (2007) called: “the depths of ignorance”.

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Chapter 8

Biodiversity in seamounts: The Madeira-Tore and Great Meteor.

BIOMETORE 5 cruise report

CHAPTER 8 - Biodiversity in seamounts: The Madeira-Tore and Great Meteor. BIOMETORE 5 cruise report

Abstract

In the present paper a research cruise done in March 2017, at the Seine and Unicorn Seamounts in the NE Atlantic Ocean, is described. Collecting methods, vessel and area surveyed are described and illustrated. The list of stations is presented, as well as a preliminary list of the species collected.

Keywords

Deep-sea, seamounts, biodiversity, fish, crustaceans, Seine, Unicorn, NE Atlantic.

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Introduction

The interest in the conservation and sustainable exploration of seamounts and associated biological communities boosted the need for a better understanding of these ecosystems and the threats to which they are subject. In this context, in the framework of the BIOMETORE project (Santos et al., 2016), two seamount complexes located in Portuguese waters, the Madeira – Tore and the Great Meteor, were studied in some detail. These seamount complexes are especially interesting, since Portugal plans to classify them as Marine Protected Areas in the coming years under the framework of the European Marine Strategy Framework Directive (EU-MSFD).

Among the research cruises done in the framework of this project, the BIOMEORE 5 cruise was part of the Task 2.4 – Benthopelagic species characterization, Work package 2 – Benthic habitats characterization – whose main objectives were, among others, to collect and process abiotic and biotic data suitable for: addressing knowledge gaps regarding MSFD biodiversity descriptors; obtaining/improving knowledge on Vulnerable Marine Ecosystems (VME) indicator and taxa distribution to develop habitat suitability models; characterising benthopelagic fish species composition and assemblage structure; addressing trophic interactions; testing the proof of concept of seamounts endemicity and their role as “stepping stones” and providing voucher specimens for museum collections.

It is expected that the results of the project will contribute to providing baseline information for sustainable use and management measures of the Portuguese marine environment and to the development of the strategies for the continuous assessment of the environmental status of Portuguese marine waters towards the achievement and maintenance of their good environmental status (GES).

Methodology

Study area

The area surveyed during BIOMETORE 5 cruise covers the Seine and Unicorn seamounts (Fig. 1). Sampling took place between the top of the seamounts and 1500 m of depth. The cruise took place between 8 and 23 March, 2017.

Research vessel

For this cruise the F/V Ponta Calhau (Fig. 2) was chartered. This vessel is one of the units of the tuna fishing fleet from Madeira, operating since 2015. She is 26 m long and 6,41 m beam. It is equipped with a 600 HP diesel engine, and a power generator, attaining 10 knots. It possesses two hydraulic winches, the largest operating at starboard. It has a storage capacity of 20 tons of fish at 0°C and sea water tanks for keeping live bait. It is also equipped with standard navigation, communications and echo sounding equipment (down to 1700 m). Two additional GPS navigation and logging systems were installed for the cruise. All operations and ship positions were recorded in real time.

For the purpose of this research, the vessel was equipped with specific collecting gear and a minimum crew of 9, including the master, was used. The remaining berth capacity (8) was used by the scientific team.

Collecting gear

Four different collecting gear – bottom long-line, mid-water drifting long-line, benthic baited traps and semifloating baited traps – were used in this cruise.

The bottom long-line used, locally called “aparelho pedra-boia” (Figs. 3 and 4) was built at Horta, Azores and has been thoroughly used by the Department of Oceanography and Fisheries of the University of Azores in their demersal fish surveys (Menezes et al., 2006, 2009). A set of 3600 hooks (LLA) was used for shallower depths (less than 300 m) with a soaking time of 3.5 hours. For deeper depths (more than 500 m), a set of 1200 hooks (LLB) was used with a soaking time of 8 hours.

The mid-water drifting long-line, locally called “aparelho de espada” (Figs. 5 and 6), is identical to the ones used by the Madeiran black scabbard fish commercial fishery (Gordo, 2009). Sets of 480 squid baited hooks were used, with a mean soaking time of 7 hours.

Baited trap sets were made of 10 benthic (Biscoito, 1993) and 10 semi-floating traps (González et al., 1992), placed alternately (Figs. 7 and 8), all baited with salted sardines. Soaking times averaged 24 hours. Whenever possible, a TDR (temperature and depth recorder) was attached to the collecting gear to validate depth of collection and obtaining temperature data.

Biological sampling

All specimens caught were identified to the lowest taxonomic rank (usually species). Invertebrates were labelled and deep-frozen on board for later study in the laboratory (Fig. 9). Some crabs caught in large numbers were measured and weighed on board, before being discarded (Fig. 10). Fishes were all counted, measured and weighed. From the more common teleost species, at least four voucher specimens were preserved frozen on board for museum collections.

Specimens from all other species were all frozen to be further studied in detail at the laboratory. All specimens collected were photographed before being preserved (Fig. 11). Due to rough weather conditions and lack of appropriate laboratory space on board, tissue samples were not taken from the specimens caught. This was later done on the laboratory on shore.

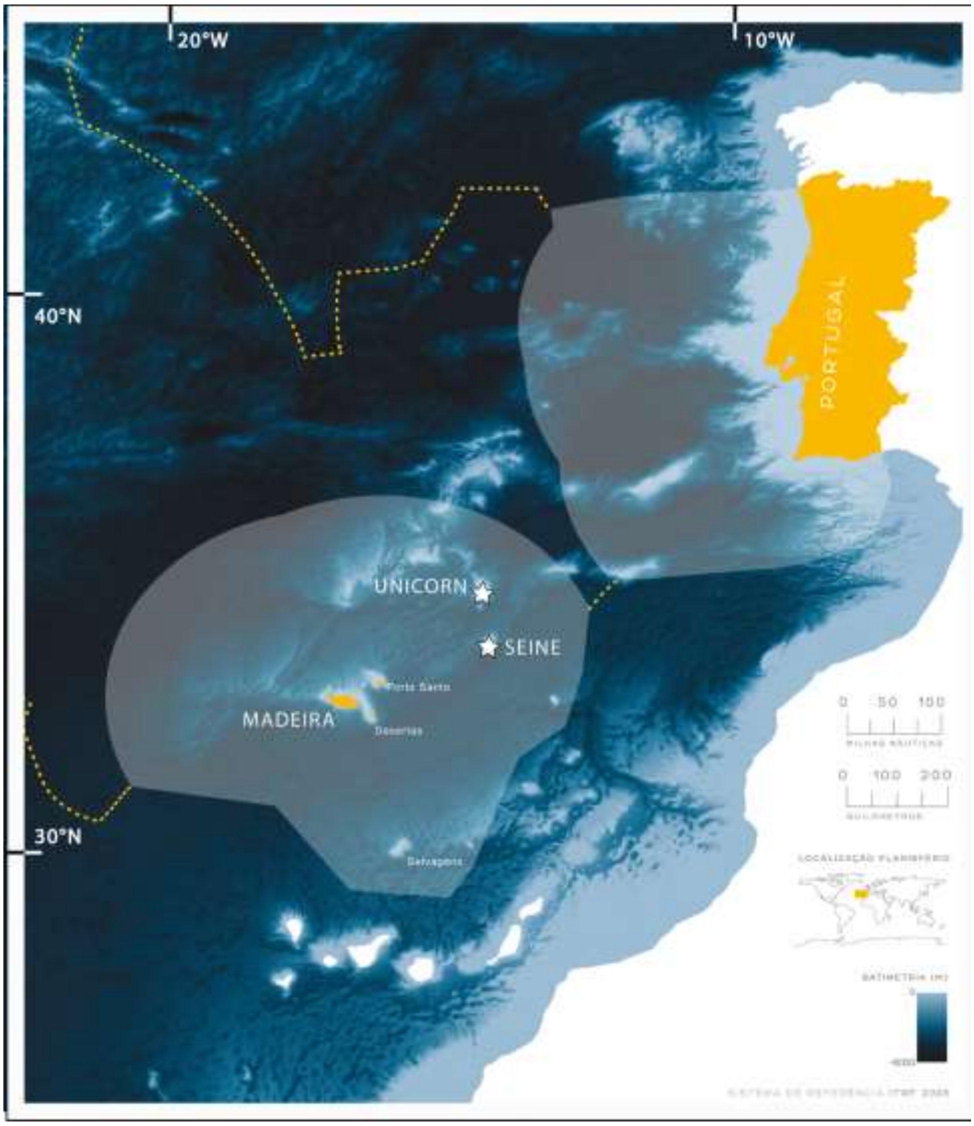


Fig. 1 – Location of the Seine and Unicorn Seamounts, surveyed during the BIOMETORE 5 cruise. (Shaded areas show the EEZ and dotted yellow lines the limits of the extended platform). (Base map from EMEPC).

Fig. 2 – The F/V Ponta Calhau at Caniçal harbour.

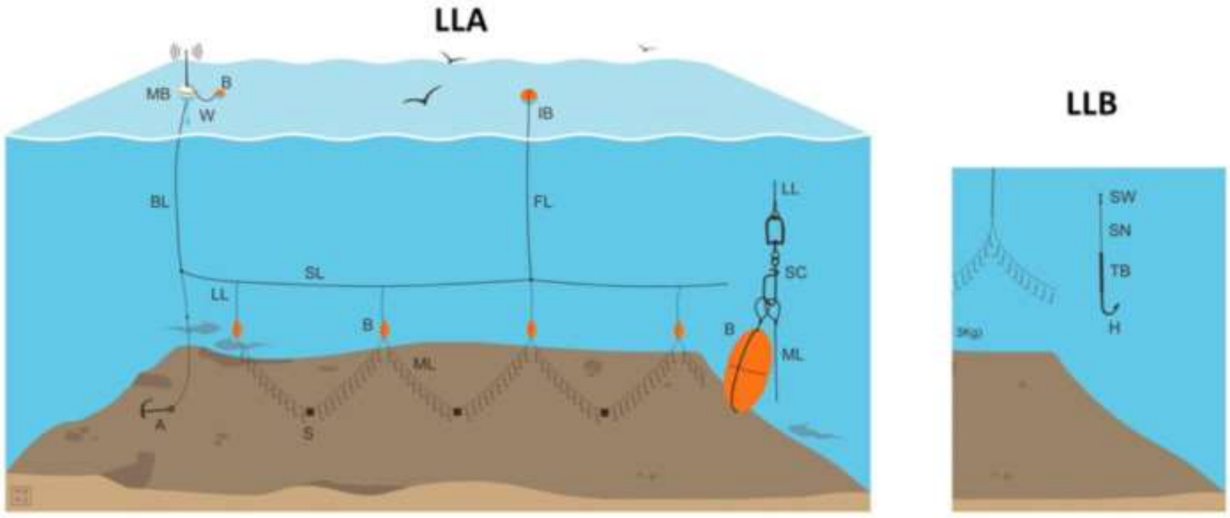


Fig. 3 – Schematic drawing of the bottom long-line ("aparelho pedra-boia") (LLA) with "safety-line" ("retenida") with alternate floats and sinkers and a branch line or snood detail of the longline (LLB) used in the deeper sets. Common labelling: marker buoy (MB); buoy (B); weight (W); mainline (ML); sinker (S); anchor (A); safety line or "retenida" (SL); buoy line (BL); free line (FL); snood (SN); hook (H); intermediate buoy (IB); Link line (LL); Snap swivel or clip (SC); swivel (SW); Twisted brass (TB). (Drawings: Nuno Brito©ImagDOP).

Fig. 4 – Deployment of the long-line at stern of the ship. A metallic table was built in order to allow a safe operation of the long-line.

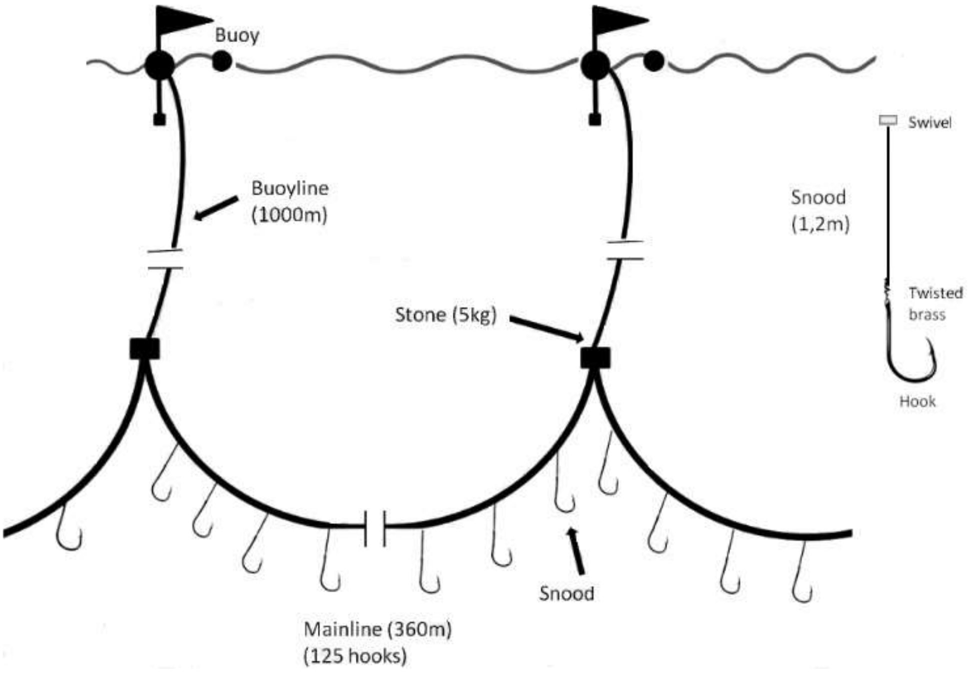


Fig. 5 – Schematic drawing of the mid-water drifting long-line (“aparelho de espada”).

Fig. 6 – Deployment of the mid-water drifting long-line (“aparelho de espada”). Each plastic container carries 120 squid-baited hooks.

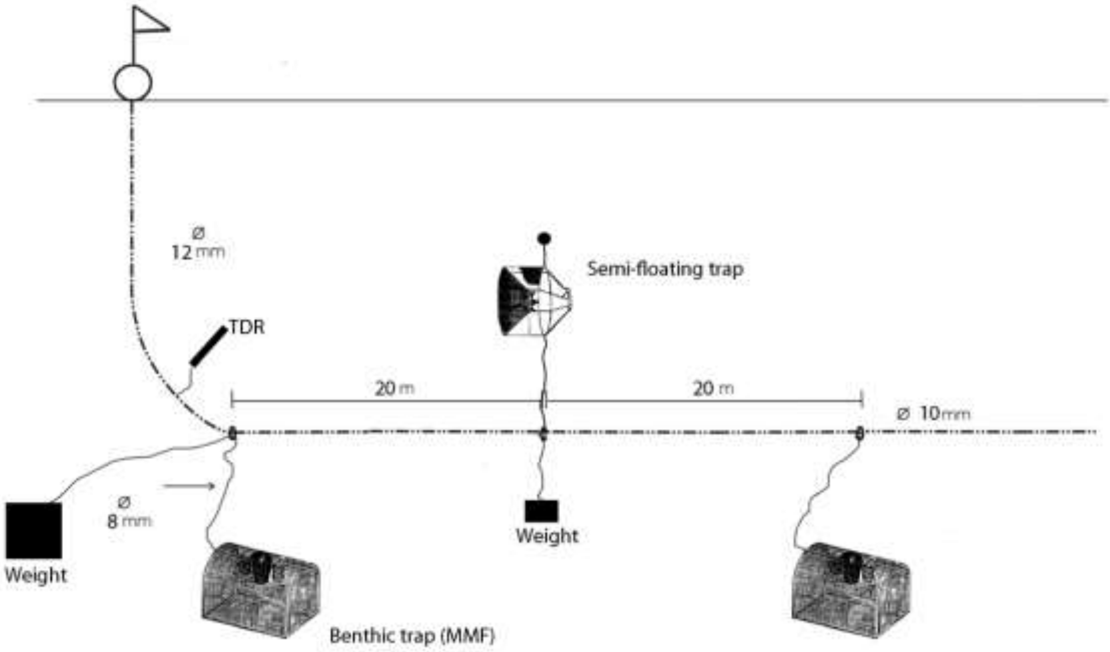


Fig. 7 – Schematic drawing of the baited fish trap set used. Each set had 10 traps of each kind attached alternately. Salted sardines were the bait used and soaking time was 24 hours on average.

Fig. 8 – The two trap models used. A - benthic fish trap MMF model; B - Semi-floating shrimp trap.

Fig. 9 – Packaging of specimens on board prior to freezing.

Fig. 10 – Measuring a specimen of *Chaceon affinis* on board.

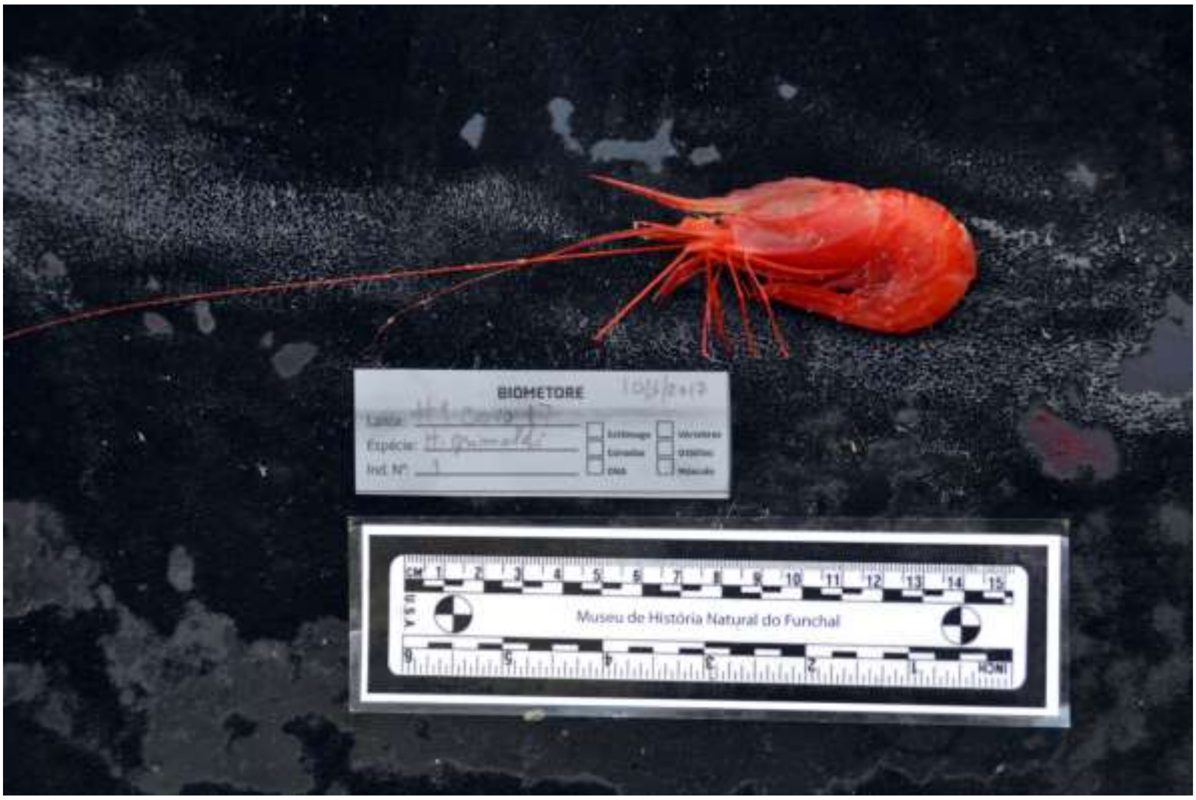


Fig. 11 – Photography setting on board. *Heterocarpus grimaldii* caught on a fish trap.

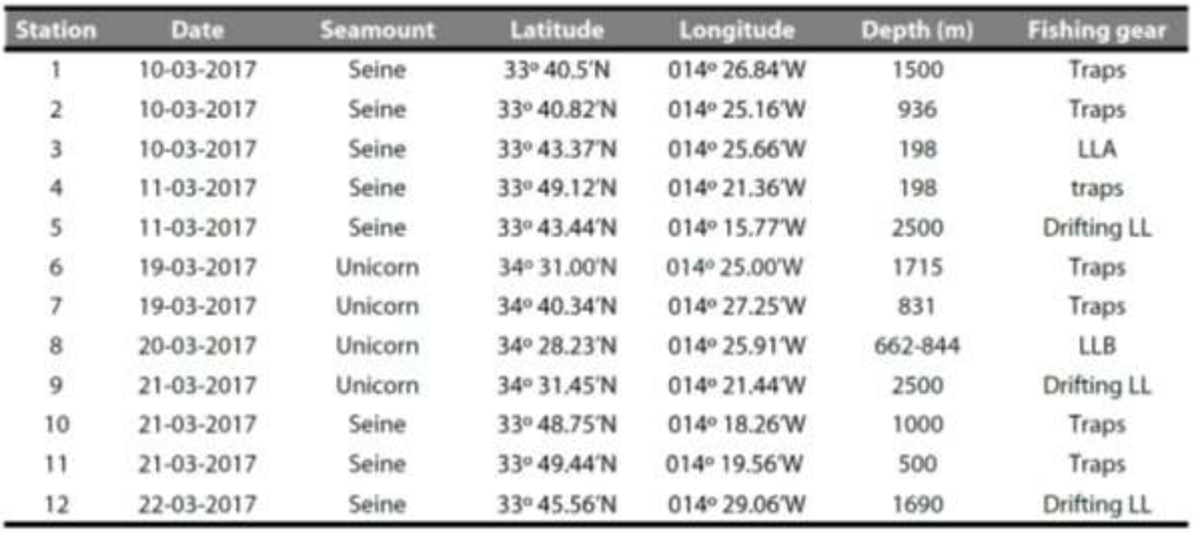
Results

A total of 12 stations were done during the BIOMETORE 5 cruise (Table 1). Of these 8 were at the Seine seamount and 4 at the Unicorn seamount. Seven stations were done with fish traps, 3 with the mid-water drifting long-line and 2 with the bottom long-line. Due to rough weather the cruise had to be interrupted two times and the ship had to call Madeira for shelter. This has prevented the use of the bottom long-line more often.

In the two surveyed seamounts, 42 species were collected (Table 2): 8 decapod crustaceans, 1 anthipatharian, 1 mollusc, 1 echinoderm, 10 chondrichthyan fish and 21 teleost fish species. Thirty-two species were collected at the Seine seamount and 15 at the Unicorn seamount.

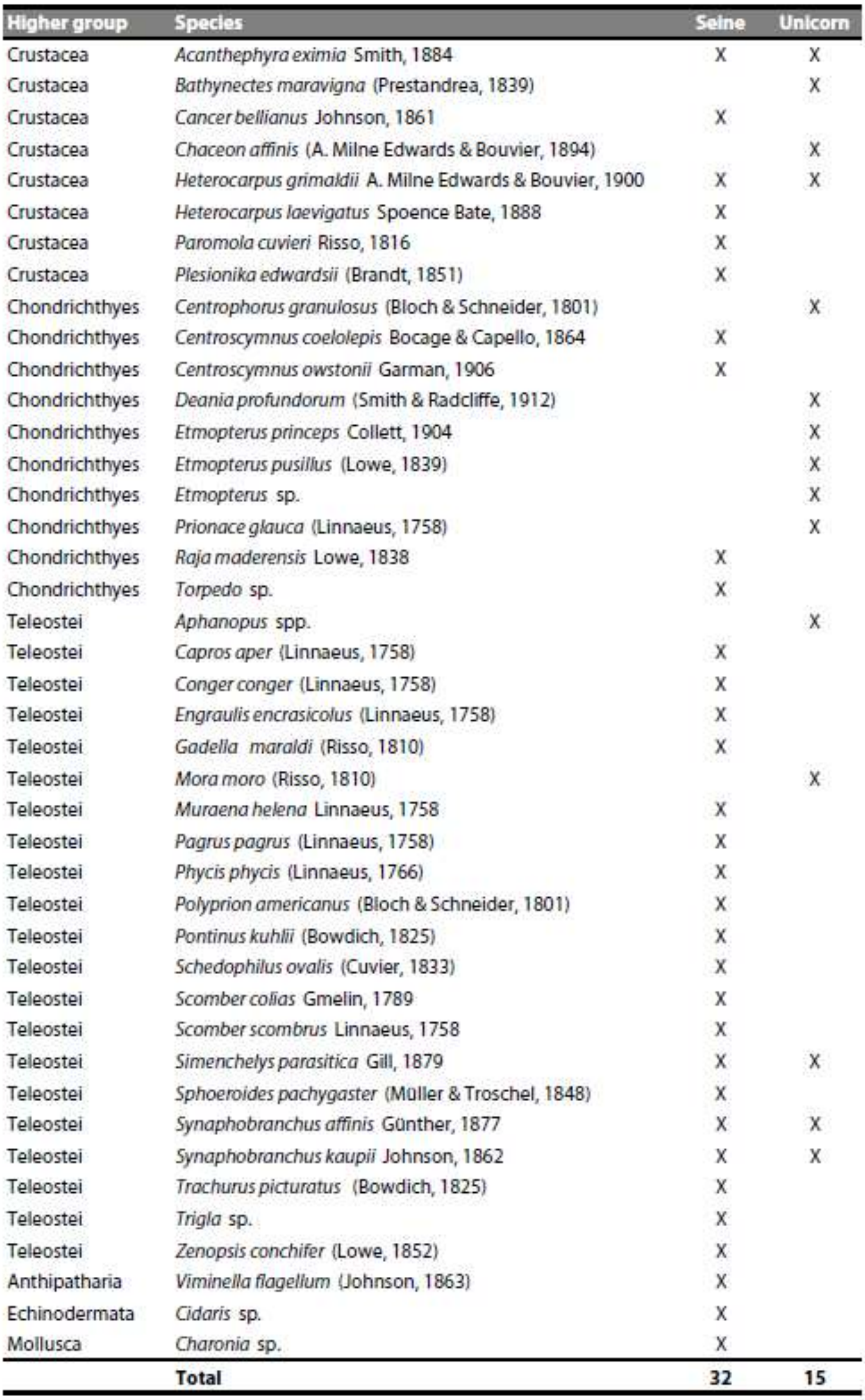
A total of 1042 specimens were collected, 649 of which were preserved for museum collections and/or further biological research.

Table 1 – List of stations of BIOMETORE 5 cruise.



Station	Date	Seamount	Latitude	Longitude	Depth (m)	Fishing gear
1	10-03-2017	Seine	33° 40.5′N	014° 26.84′W	1500	Traps
2	10-03-2017	Seine	33° 40.82′N	014° 25.16′W	936	Traps
3	10-03-2017	Seine	33° 43.37′N	014° 25.66′W	198	LLA
4	11-03-2017	Seine	33° 49.12′N	014° 21.36′W	198	traps
5	11-03-2017	Seine	33° 43.44′N	014° 15.77′W	2500	Drifting LL
6	19-03-2017	Unicorn	34° 31.00′N	014° 25.00′W	1715	Traps
7	19-03-2017	Unicorn	34° 40.34′N	014° 27.25′W	831	Traps
8	20-03-2017	Unicorn	34° 28.23′N	014° 25.91′W	662-844	LLB
9	21-03-2017	Unicorn	34° 31.45′N	014° 21.44′W	2500	Drifting LL
10	21-03-2017	Seine	33° 48.75′N	014° 18.26′W	1000	Traps
11	21-03-2017	Seine	33° 49.44′N	014° 19.56′W	500	Traps
12	22-03-2017	Seine	33° 45.56′N	014° 29.06′W	1690	Drifting LL

Table 2 – Preliminary list of species collected at the Seine and Unicorn seamounts during BIOMETORE 5 Cruise.



Higher group	Species	Seine	Unicorn
Crustacea	*Acanthephyra eximia* Smith, 1884	X	X
Crustacea	*Bathynectes maravigna* (Prestandrea, 1839)		X
Crustacea	*Cancer bellianus* Johnson, 1861	X	
Crustacea	*Chaceon affinis* (A. Milne Edwards & Bouvier, 1894)		X
Crustacea	*Heterocarpus grimaldii* A. Milne Edwards & Bouvier, 1900	X	X
Crustacea	*Heterocarpus laevigatus* Spoence Bate, 1888	X	
Crustacea	*Paromola cuvieri* Risso, 1816	X	
Crustacea	*Plesionika edwardsii* (Brandt, 1851)	X	
Chondrichthyes	*Centrophorus granulosus* (Bloch & Schneider, 1801)		X
Chondrichthyes	*Centroscymnus coelolepis* Bocage & Capello, 1864	X	
Chondrichthyes	*Centroscymnus owstonii* Garman, 1906	X	
Chondrichthyes	*Deania profundorum* (Smith & Radcliffe, 1912)		X
Chondrichthyes	*Etmopterus princeps* Collett, 1904		X
Chondrichthyes	*Etmopterus pusillus* (Lowe, 1839)		X
Chondrichthyes	*Etmopterus* sp.		X
Chondrichthyes	*Prionace glauca* (Linnaeus, 1758)		X
Chondrichthyes	*Raja maderensis* Lowe, 1838	X	
Chondrichthyes	*Torpedo* sp.	X	
Teleostei	*Aphanopus* spp.		X
Teleostei	*Capros aper* (Linnaeus, 1758)	X	
Teleostei	*Conger conger* (Linnaeus, 1758)	X	
Teleostei	*Engraulis encrasicolus* (Linnaeus, 1758)	X	
Teleostei	*Gadella maraldi* (Risso, 1810)	X	
Teleostei	*Mora moro* (Risso, 1810)		X
Teleostei	*Muraena helena* Linnaeus, 1758	X	
Teleostei	*Pagrus pagrus* (Linnaeus, 1758)	X	
Teleostei	*Phycis phycis* (Linnaeus, 1766)	X	
Teleostei	*Polyprion americanus* (Bloch & Schneider, 1801)	X	
Teleostei	*Pontinus kuhlii* (Bowdich, 1825)	X	
Teleostei	*Schedophilus ovalis* (Cuvier, 1833)	X	
Teleostei	*Scomber colias* Gmelin, 1789	X	
Teleostei	*Scomber scombrus* Linnaeus, 1758	X	
Teleostei	*Simenchelys parasitica* Gill, 1879	X	X
Teleostei	*Sphoeroides pachygaster* (Müller & Troschel, 1848)	X	
Teleostei	*Synaphobranchus affinis* Günther, 1877	X	X
Teleostei	*Synaphobranchus kaupii* Johnson, 1862	X	X
Teleostei	*Trachurus picturatus* (Bowdich, 1825)	X	
Teleostei	*Trigla* sp.	X	
Teleostei	*Zenopsis conchifer* (Lowe, 1852)	X	
Anthipatharia	*Viminella flagellum* (Johnson, 1863)	X	
Echinodermata	*Cidaris* sp.	X	
Mollusca	*Charonia* sp.	X	
	Total	**32**	**15**

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Chapter 9

Sharks, rays and chimaeras of the Seine and Unicorn seamounts (NE Atlantic Ocean)

CHAPTER 9 - Sharks, rays and chimaeras of the Seine and Unicorn seamounts (NE Atlantic Ocean)

Abstract

Background: Seamounts are underwater mountains which typically rise rather steeply at least several hundred meters above the deep-sea floor. These geological features interrupt water flow and hence may induce changes in the circulation of different water masses, in turn causing different physical and biological effects. For this reason, seamounts are biodiversity hotspots, housing a wide number of species, as is with the case of the Seine and Unicorn seamounts, which are a part of the Madeira-Tore seamount chain located between Portugal mainland, southwestern Europe and Madeira archipelago (NE Atlantic).

Methods: Fisheries independent surveys allowed the collection of Chondrichthyes specimens from the Seine and Unicorn seamounts. Individuals were caught over the course of two research cruises, first in 2004 and later in 2017, with species distribution ranging from the summit down to 2500 m of depth.

Results: Fifteen species belonging to 7 different taxonomical families were collected in the two surveyed areas. Two species were recorded for the first time and added to the checklist of the Seine seamount (*Centrophorus granulosus* and *Somniosus rostratus*), and three species for the Unicorn seamount (*C. granulosus*, *Centroscymnus coelolepis* and *Centroselachus crepidater*). Distribution and frequency of occurrence for the collected species were evaluated in relation to depth.

Conclusions: This work is a valuable contribution to the knowledge of seamount-associated fish fauna. Moreover, the checklist of sharks, rays and chimaeras was updated for the Seine and Unicorn seamounts, summing up 20 species.

Keywords

Chondrichthyes, seamounts, fisheries, conservation, NE Atlantic Ocean.

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Background

Seamounts are underwater volcanoes that did not break the sea surface and turn into islands (Kitchingman & Lai, 2004). They host a wide number of species and are physical and biological characteristics. Nonetheless, many seamount species (ca. 26%) have been discovered and described in the last 50 years (Froese & Sampang, 2004). In fact, if scientific surveys at seamounts were further encouraged, many new and undescribed species would likely be found (Froese & Sampang, 2004).

The deep-sea fish fauna of Madeira archipelago (NE Atlantic) has been the object of study of several ichthyologists over the last 150 years. Most species are caught in drifting longlines by local fishermen during the artisanal black-scabbard (*Aphanopus carbo* Lowe, 1839 and *Aphanopus intermedius* Parin, 1983) fishery, which dates back to the early seventeenth century (Merrett and Haedrich, 1997; Silva and Menezes, 1921).

Despite seamount fish fauna having been previously described in several studies, few works have included species captured below 600 m (Tracey et al., 2004). Therefore, many of these deep ocean fish communities remain uncovered and descriptions are restricted to sampling effort, which is primarily associated with fishing activities. Consequently, there is still a knowledge gap regarding seamount associated elasmobranchs (Menezes et al., 2009; Christiansen et al., 2015; Vieira et al., 2018).

The Seine and Unicorn seamounts belong to the Madeira-Tore seamount chain located between Portugal mainland and Madeira archipelago. These seamounts are of special interest and Portugal plans to classify them as Marine Protected Areas (MPAs) in the next years under the European Marine Strategy Framework Directive (EU-MSFD), in light of the fact that these areas often play an important role in species biogeography and connectivity between key stone habitats (Koslow et al., 2016).

This study aims to contribute to the knowledge of fish diversity of the Seine and Unicorn seamounts at different depth strata down to 2500 m. Data on the occurrence of Chondrichthyes species for these ecologically important areas is provided with an update of the existing checklist.

Material and methods

Specimens were collected in 2004 and in 2017, within the scope of RECPROFMAD and BIOMETORE research surveys. Both surveys were conducted for biodiversity assessment of seamount-associated fish fauna. Fishing sets were carried out from the top of the seamounts to around 2500m depth. Drifting and bottom longlines, as well as two types of baited traps were used at Unicorn (34° 35′N, 14° 28′W) and Seine seamounts (33° 45′N, 14° 22′W) (Biscoito et al., 2017).

All specimens were identified to species level, counted and weighed on board. Additionally, they were photographed before being preserved. Once at the laboratory, all individuals were measured (total length TL, in mm), weighed (total weight TW, in g) and sexed. Voucher specimens from the 2004 and 2017 cruises were deposited in museum collections (Funchal Natural History Museum - MMF and The National Museum of Natural History, Lisbon). A new complete annotated checklist for the Seine and Unicorn seamounts was produced. In order to revise the list of Chondrichthyes species previously recorded for these areas, MMF collections and scientific literature were assessed. Species frequency of occurrence was classified into four classes, to which different colours were assigned: red – rare (1 specimen); yellow – occasional (2 to 4 specimens); light green – common (5 to 10 specimens) and dark green – very common (> 10 specimens). Furthermore, the Food and Agriculture Organization (FAO) species catalog for fisheries purposes for the North Atlantic (Ebert and Stehmann, 2013) was consulted for geographic distribution confirmation and previous records for the archipelago of Madeira. For each species depth range and maximum size are listed according to Ebert and Stehmann (2013). In addition, species susceptibility to locally used fishing gear and corresponding IUCN Red List status in Europe (Nieto et al., 2015) is provided. Occurrence data for the collected species was plotted against depth to illustrate the dominant depth strata for each species. This allowed the addition of new information on the vertical distribution of these species at the Seine and Unicorn seamounts.

Results

A total of 134 chondrichthyans (129 sharks, 3 rays and 2 chimaeras species) were captured and correspond to fifteen different species from 7 families: Carcharhinidae, Centrophoridae, Etmopteridae, Somniosidae, Torpedinidae, Rajidae and Chimaeridae.

For the Seine seamount, 66 specimens belonging to 14 different species were identified in the present study (Table 1). Two species (*Centrophorus granulosus* and *Somniosus rostratus*) are recorded for the first time for this seamount, increasing the total number of species to 17.

Regarding the Unicorn seamount, 8 species from a total of 68 specimens were reported in the present study. Three (*Centrophorus granulosus*, *Centroscymnus coelolepis* and *Centroselachus crepidater*) of which were recorded for the first time for this seamount, consequently increasing the total number of species to 11.

Finally, frequency of occurrence of cartilaginous fish species is presented in Table 2. The most frequently observed species were *D. calcea*, *Etmopterus princeps*, *Etmopterus pusillus*, *C. coelolepis* and *Centroscymnus owstonii*, with more than 10 specimens captured each. In turn, the less frequently observed species were *Prionace glauca*, *S. rostratus* and *Tetronarce nobiliana*, with only 1 specimen collected.

Detailed information regarding the species collected during the present study is given below:

ORDER CARCHARHINIFORMES

Family Carcharhinidae

Prionace glauca (Linnaeus, 1758) - Common names: Tintureira; Blue shark.

First published record for Madeira archipelago in Lowe (1838).

This species is a common oceanic shark usually caught with pelagic longlines, hook and lines, pelagic and bottom trawls near the coast (Davidson et al., 2015).

One specimen with 1910 mm TL was caught at 750 m at Unicorn seamount.

Frequency of occurrence: Red (rare).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 0 to 350 m.

Maximum size (Ebert and Stehmann, 2013): 3830 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Near Threatened (NT) [Europe] / Least Concern (LC) [Global]. Remarks: Although this specimen was caught on a bottom longline set at 750 m of depth, it is not possible to confirm if it was hooked at that depth or at midwater, either during the setting or hauling the gear.

Order Squaliformes

Family Centrophoridae

Centrophorus granulosus (Bloch & Schneider, 1801) - Common names: Ramudo; Gulper shark.

First published record for Madeira in Günther (1870).

This species occurs off the outer continental shelves and upper slopes, frequently over or near the bottom.

Nine specimens ranging from 474 to 1540 mm TL were caught at Seine (3) and Unicorn (6) seamounts between 750 and 1000 m depth, using bottom longlines.

Frequency of occurrence: Light green (common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 50 to 1440 m.

Maximum size (Ebert and Stehmann, 2013): 1660 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Critically Endangered (CR) [Europe] / Endangered (E) [Global].

Centrophorus squamosus (Bonnaterre, 1788) – Common names: Xara-branca; Leafscale gulper shark.

First published record for Madeira in Lowe (1852).

This species is a large deep-water gulper shark that occurs on the continental slopes and in the epipelagic or mesopelagic zone.

Five specimens ranging from 1062 to 1275 mm TL were caught at Seine (4) and Unicorn (1) seamounts at 1000 m depth, using bottom longlines.

Frequency of occurrence: Light green (common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

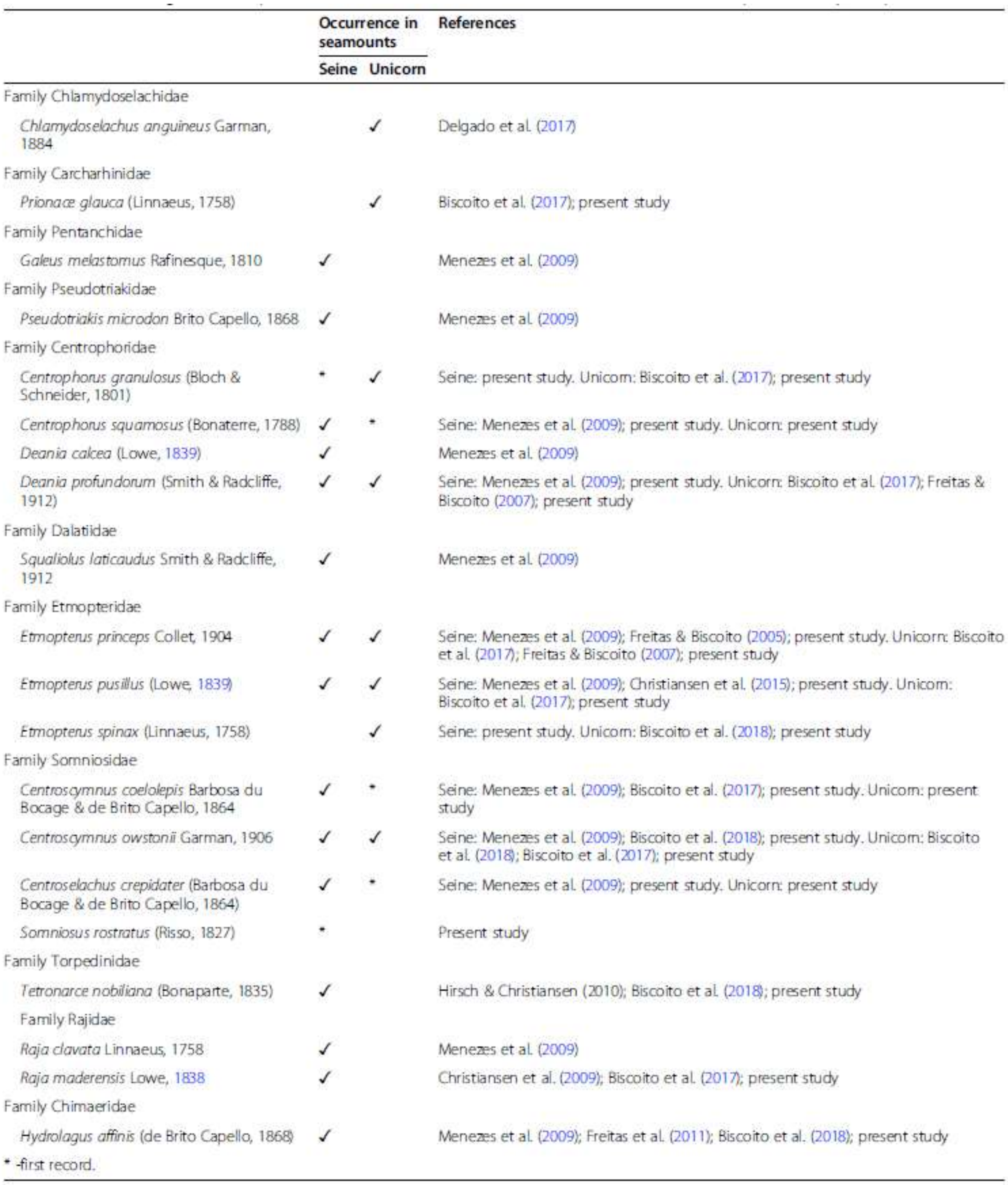
Depth range (Ebert and Stehmann, 2013): 229 to 2359 m.

Maximum size (Ebert and Stehmann, 2013): 1640 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Endangered (EN) [Europe] / Endangered (EN) [Gobal].

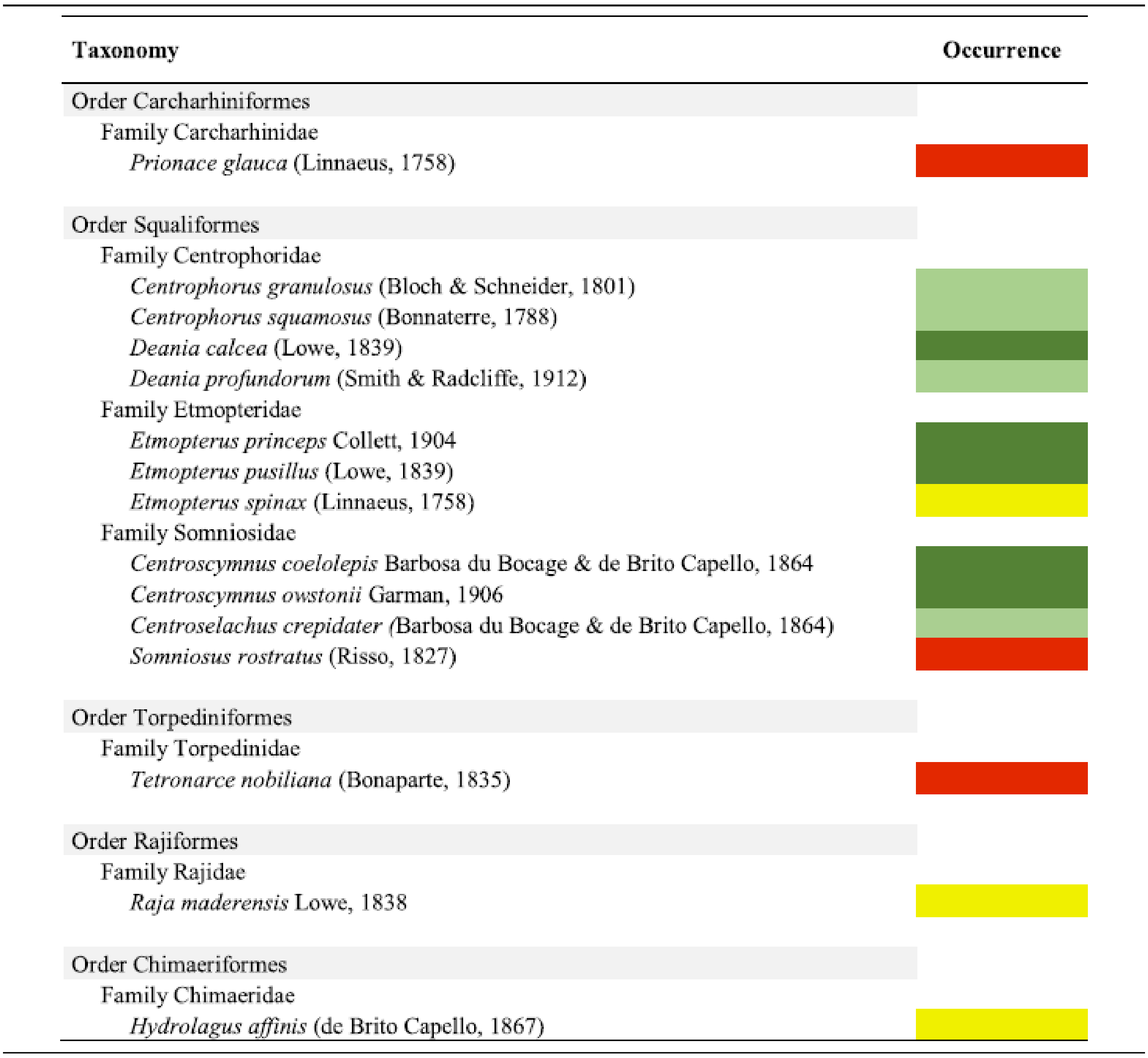
Table 1 - List of cartilaginous fish species recorded for the Seine and Unicorn seamounts from the present study and previous work.



	Occurrence in seamounts		References
	Seine	Unicorn	
Family Chlamydoselachidae			
Chlamydoselachus anguineus Garman, 1884		✓	Delgado et al. (2017)
Family Carcharhinidae			
Prionace glauca (Linnaeus, 1758)		✓	Biscoito et al. (2017); present study
Family Pentanchidae			
Galeus melastomus Rafinesque, 1810	✓		Menezes et al. (2009)
Family Pseudotriakidae			
Pseudotriakis microdon Brito Capello, 1868	✓		Menezes et al. (2009)
Family Centrophoridae			
Centrophorus granulosus (Bloch & Schneider, 1801)	*	✓	Seine: present study. Unicorn: Biscoito et al. (2017); present study
Centrophorus squamosus (Bonaterre, 1788)	✓	*	Seine: Menezes et al. (2009); present study. Unicorn: present study
Deania calcea (Lowe, 1839)	✓		Menezes et al. (2009)
Deania profundorum (Smith & Radcliffe, 1912)	✓	✓	Seine: Menezes et al. (2009); present study. Unicorn: Biscoito et al. (2017); Freitas & Biscoito (2007); present study
Family Dalatiidae			
Squaliolus laticaudus Smith & Radcliffe, 1912	✓		Menezes et al. (2009)
Family Etmopteridae			
Etmopterus princeps Collet, 1904	✓	✓	Seine: Menezes et al. (2009); Freitas & Biscoito (2005); present study. Unicorn: Biscoito et al. (2017); Freitas & Biscoito (2007); present study
Etmopterus pusillus (Lowe, 1839)	✓	✓	Seine: Menezes et al. (2009); Christiansen et al. (2015); present study. Unicorn: Biscoito et al. (2017); present study
Etmopterus spinax (Linnaeus, 1758)		✓	Seine: present study. Unicorn: Biscoito et al. (2018); present study
Family Somniosidae			
Centroscymnus coelolepis Barbosa du Bocage & de Brito Capello, 1864	✓	*	Seine: Menezes et al. (2009); Biscoito et al. (2017); present study. Unicorn: present study
Centroscymnus owstonii Garman, 1906	✓	✓	Seine: Menezes et al. (2009); Biscoito et al. (2018); present study. Unicorn: Biscoito et al. (2018); Biscoito et al. (2017); present study
Centroselachus crepidater (Barbosa du Bocage & de Brito Capello, 1864)	✓	*	Seine: Menezes et al. (2009); present study. Unicorn: present study
Somniosus rostratus (Risso, 1827)	*		Present study
Family Torpedinidae			
Tetronarce nobiliana (Bonaparte, 1835)	✓		Hirsch & Christiansen (2010); Biscoito et al. (2018); present study
Family Rajidae			
Raja clavata Linnaeus, 1758	✓		Menezes et al. (2009)
Raja maderensis Lowe, 1838	✓		Christiansen et al. (2009); Biscoito et al. (2017); present study
Family Chimaeridae			
Hydrolagus affinis (de Brito Capello, 1868)	✓		Menezes et al. (2009); Freitas et al. (2011); Biscoito et al. (2018); present study

* -first record.

Table 2 Frequency of occurrence of cartilaginous fish species caught at the Seine and Unicorn seamounts during the present study. Red - rare (1 specimen); yellow – occasional (2 to 4 specimens); light green - common (5 to 10 specimens); dark green – very common (> 10 specimens)



Taxonomy	Occurrence
Order Carcharhiniformes	
Family Carcharhinidae	
Prionace glauca (Linnaeus, 1758)	🟥
Order Squaliformes	
Family Centrophoridae	
Centrophorus granulosus (Bloch & Schneider, 1801)	🟩
Centrophorus squamosus (Bonnaterre, 1788)	🟩
Deania calcea (Lowe, 1839)	■
Deania profundorum (Smith & Radcliffe, 1912)	🟩
Family Etmopteridae	
Etmopterus princeps Collett, 1904	■
Etmopterus pusillus (Lowe, 1839)	■
Etmopterus spinax (Linnaeus, 1758)	🟨
Family Somniosidae	
Centroscymnus coelolepis Barbosa du Bocage & de Brito Capello, 1864	■
Centroscymnus owstonii Garman, 1906	■
Centroselachus crepidater (Barbosa du Bocage & de Brito Capello, 1864)	🟩
Somniosus rostratus (Risso, 1827)	🟥
Order Torpediniformes	
Family Torpedinidae	
Tetronarce nobiliana (Bonaparte, 1835)	🟥
Order Rajiformes	
Family Rajidae	
Raja maderensis Lowe, 1838	🟨
Order Chimaeriformes	
Family Chimaeridae	
Hydrolagus affinis (de Brito Capello, 1867)	🟨

Deania calcea (Lowe, 1839) - Common names: Gata; Birdbeak dogfish.

First published record from Madeira in Lowe (1839) as *Acanthidium calceus*.

This is the largest and probably the most common of the three *Deania* species occurring in Madeira (see remarks) and is caught as by-catch of the black scabbardfish fishery. The biology of this species is poorly known.

Fifteen specimens ranging from 579 to 1033 mm TL were caught at Seine seamount at 1000 m depth, using bottom longline.

Frequency of occurrence: Dark green (very common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 60 to 1490 m.

Maximum size (Ebert and Stehmann, 2013): 1110 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Data Deficient (DD) [Europe]/ Near Threatened (NT) [Global].

Remarks: This species validity has recently been questioned as phylogenetic analyses did not indicate *D. calcea* to be a distinct lineage from *D. hystricosa* in the NE Atlantic (Steffani et al., 2021). If accepted, there are only two species of *Deania* in Madeiran waters, *D. calcea* and *D. profundorum*, both occurring at the Seine Seamount.

Deania profundorum (Smith & Radcliffe, 1912) – Common names: Sapata; Arrowhead dogfish.

First published record for Madeira and Seine seamount in Freitas & Biscoito (2007).

This is the only *Deania* species with a subcaudal keel beneath the caudal peduncle. It is caught as bycatch in the demersal fishery and its biology is poorly known.

Nine specimens ranging from 551 to 983 mm TL were caught at Seine (4) and Unicorn (5) seamounts between 750 and 1000 m depth, using bottom longlines.

Frequency of occurrence: Light green (common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): No.

Depth range (Ebert and Stehmann, 2013): 275 to 1785 m.

Maximum size (Ebert and Stehmann, 2013): 970 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Data Deficient (DD) [Europe] / Endangered (E) [Global].

Family Etmopteridae

Etmopterus princeps Collett, 1904 - Common names: Lixinha-da-fundura; Great lanternshark.

First published record for Madeira and for the Seine seamount in Freitas & Biscoito (2007).

This is the largest species of *Etmopterus* and can be distinguished from other species of the genus by its lateral trunk denticles with fairly thick and stout cusps, forming inconspicuous, regular longitudinal rows on caudal peduncle and caudal–fin base. It has been recorded for both sides of the North Atlantic.

Twenty-five specimens ranging from 230 to 678 mm TL were caught at Seine (4) and Unicorn (21) seamounts between 750 and 2000 m depth, using bottom longlines and traps.

Frequency of occurrence: Dark green (very common).

Recorded from Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): No.

Depth range (Ebert and Stehmann, 2013): 800 to 1000 m.

Maximum size (Ebert and Stehmann, 2013): 890 mm TL.

Local gear susceptibility: Bottom longlines and traps.

IUCN Red List status: Least Concern (LC) [Europe] / Least Concern (LC) [Global].

Etmopterus pusillus (Lowe, 1839) - Common names: Xarinha-preta; Smooth lanternshark.

Species described by Lowe (1839) as *Acanthidium pusillum*, although previously recorded by the same author (Lowe, 1834) under the preoccupied name *Centrina nigra*.

This species is caught as by-catch of the black scabbardfish fishery and Madeira is the locality type for this species (Syntype BMNH 1855.11.19.27).

Sixteen specimens ranging from 350 to 467 mm TL were caught at Seine (4) and Unicorn (12) seamounts between 750 and 2500 m depth, using bottom longlines and traps.

Frequency of occurrence: Dark green (very common).

Recorded from Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 110 to 1000 m.

Maximum size (Ebert and Stehmann, 2013): 502 mm TL.

Local gear susceptibility: Bottom longlines and traps.

IUCN Red List status in Europe: Data Deficient (DD) [Europe] / Least Concern (LC) [Global].

Etmopterus spinax (Linnaeus, 1758) - Common names: Lixinha-da-fundura; Velvet belly.

First published record for Madeira by Noronha & Sarmento (1934) as *Spinax spinax*.

According to Maul (1948) this species is rare and occurs offshore.

Three specimens ranging from 411 to 461mm TL were caught at Unicorn seamount at 750 m depth, using bottom longlines and traps.

Frequency of occurrence: Yellow (occasional).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): No.

Depth range (Ebert and Stehmann, 2013): 70 to 2000 m.

Maximum size (Ebert and Stehmann, 2013): 410 mm TL.

Local gear susceptibility: Bottom longlines and traps.

IUCN Red List status: Near Threatened (NT) [Europe] / Vulnerable (VU) [Global].

Family somniosidae

Centroscymnus coelolepis Barbosa du Bocage & de Brito Capello, 1864 - Common names: Xara-preta; Portuguese dogfish.

First published record for Madeira in Günther (1870) as *Centrophorus coelolepis*.

This little-known species occurs on or near the bottom on continental slopes and upper and middle rises.

Twenty-nine specimens ranging from 713 to 1115 m TL were caught at Seine (17) and Unicorn (12) seamounts between 1500 and 2500 m depth, using bottom longlines and traps.

Frequency of occurrence: Dark green (very common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 128 to 3675 m.

Maximum size (Ebert and Stehmann, 2013): 1220 mm TL.

Local gear susceptibility: Bottom longlines and traps.

IUCN Red List status: Endangered (EN) [Europe] / Near Threatened (NT) [Global].

Centroscymnus owstonii Garman, 1906 – Common names: Xara-preta-de-natura; Roughskin dogfish.

First published record for Madeira in Günther (1870) as *Centrophorus coelolepis* (see remarks in Biscoito et al. 2018: 474).

This little-known dogfish occurs off the outer continental shelves and upper continental slopes, on or near bottom.

Eleven specimens ranging from 711 to 1096 mm TL were caught at Seine (7) and Unicorn (4) seamounts between 1000 and 1500 m depth using bottom longlines and traps.

Frequency of occurrence: Dark green (very common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 150–1459 m.

Maximum size (Ebert and Stehmann, 2013): 1200 mm TL.

Local gear susceptibility: Bottom longlines and traps.

IUCN Red List status in Europe: Not assessed [Europe] / Vulnerable (VU) [Global] (Finucci & Kyne, 2018).

Centroselachus crepidater (Barbosa du Bocage & de Brito Capello, 1864) - Common names: Sapata-de-natura; Longnose velvet dogfish.

First published record for Madeira in Günther (1870) as *Centrophorus crepidater*. This deep-water shark occurs along the upper continental and insular slopes on or near the bottom.

Five specimens ranging from 558 to 668 mm TL were caught at Seine (2) and Unicorn (3) seamounts at 1500 m depth using bottom longlines.

Frequency of occurrence: Light green (common).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 200–1500 m.

Maximum size (Ebert and Stehmann, 2013): 1050 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Least Concern (LC) [Europe] / Near Threatened (NT) [Global].

Somniosus rostratus (Risso, 1827) - Common names: Trabolha-de-natura; Little sleeper shark.

First published record for the Madeira of two specimens in Maul (1955). This deep-water shark rarely occurs in the region and only a few records exist on the outer continental shelf and upper slope of the northeast Atlantic and western Mediterranean Sea.

One specimen with 1120 mm TL was caught in Seine seamount at 1000 m depth using bottom longline.

Frequency of occurrence: Red (rare).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 180–2200 m.

Maximum size (Ebert and Stehmann, 2013): 1430 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Data Deficient (DD) [Europe] / Least Concern (LC) [Global].

Order Torpediniformes

Family Torpedinidae

Tetronarce nobiliana (Bonaparte, 1835) – Common names: Tremelga; Electric ray.

First published record for the Madeira by Lowe (1938) as *Torpedo hebetans* and confirmed as *T. nobiliana* by Biscoito et al. (2018).

Adults are frequently pelagic or semi-pelagic whereas juveniles are mainly benthic living on soft-substrate and coral reef habitat in shallow water. The biology of this species is poorly known.

One specimen with 972 mm TL and 510 mm DL was caught at Seine seamount at 200 m depth using bottom longline (MMF 47181).

Frequency of occurrence: Red (rare).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): No.

Depth range (Ebert and Stehmann, 2013): 10–927 m.

Maximum size (Ebert and Stehmann, 2013): 1800 mmTL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Least Concern (LC) [Europe] / Least Concern (LC) [Global].

Order Rajiformes

Family Rajidae

Raja maderensis Lowe, 1838 - Common names: Raia-da-Madeira; Madeira ray.

First published record for the Madeira by Lowe (1938). Madeira is the locality type of this endemic species for Madeira and the Azores archipelagos (Portugal) in the northeastern Atlantic. The biology of this species is poorly known.

Two specimens with 680 mm TL (355 mm DL) and 700 mm TL (393 mm DL) were caught at Seine seamount at 200 m depth using bottom longline.

Frequency of occurrence: Yellow (occasional).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): Yes.

Depth range (Ebert and Stehmann, 2013): 0–150 m.

Maximum size (Ebert and Stehmann, 2013): 800 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Vulnerable (VU) [Europe] / Vulnerable (VU) [Global].

Order Chimaeriformes

Family Chimaeridae

Hydrolagus affinis (de Brito Capello, 1867) – Common names: Ratazana-da-fundura; Smalleyed rabbitfish.

First published record for the Madeira in Freitas & Biscoito (2007).

It is a benthopelagic species which occurs on continental slopes and deep-sea plains, feeding on small fishes and invertebrates.

Two specimens with 1075 and 1268 mm TL were caught at Seine seamount at 2500 m depth using bottom longline.

Frequency of occurrence: Yellow (occasional).

Recorded for Madeira in FAO Species Catalogue (Ebert and Stehmann, 2013): No.

Depth range (Ebert and Stehmann, 2013): 300–2410 m.

Maximum size (Ebert and Stehmann, 2013): 1470 mm TL.

Local gear susceptibility: Bottom longlines.

IUCN Red List status: Least Concern (LC) [Europe] / Least Concern (LC) [Global].

Species' frequency of occurrence was plotted against depth (Fig. 1).

On one hand, *Centrophorus granulosus* and *C. squamosus* occurred at 1000 m in both seamounts. On the other hand, *C. coelolepis* mainly occurred between 1500 and 2000 m deep. However, one specimen of this species was captured at 2500 m deep at the Seine seamount. Furthermore, *D. calcea* was collected at 1000 m deep only at the Seine seamount.

E. princeps occurred in both seamounts, though more frequently at 1500 m, within a depth range between 750 and 2000 m of depth. Nonetheless, *E. pusillus* was the species that presented the widest depth range. Despite being more dominant between the 750 to 1000 m of depth, it also occurred at 2500 m. Moreover, *E. spinax* and *P. glauca* were exclusively collected at the Unicorn seamount.

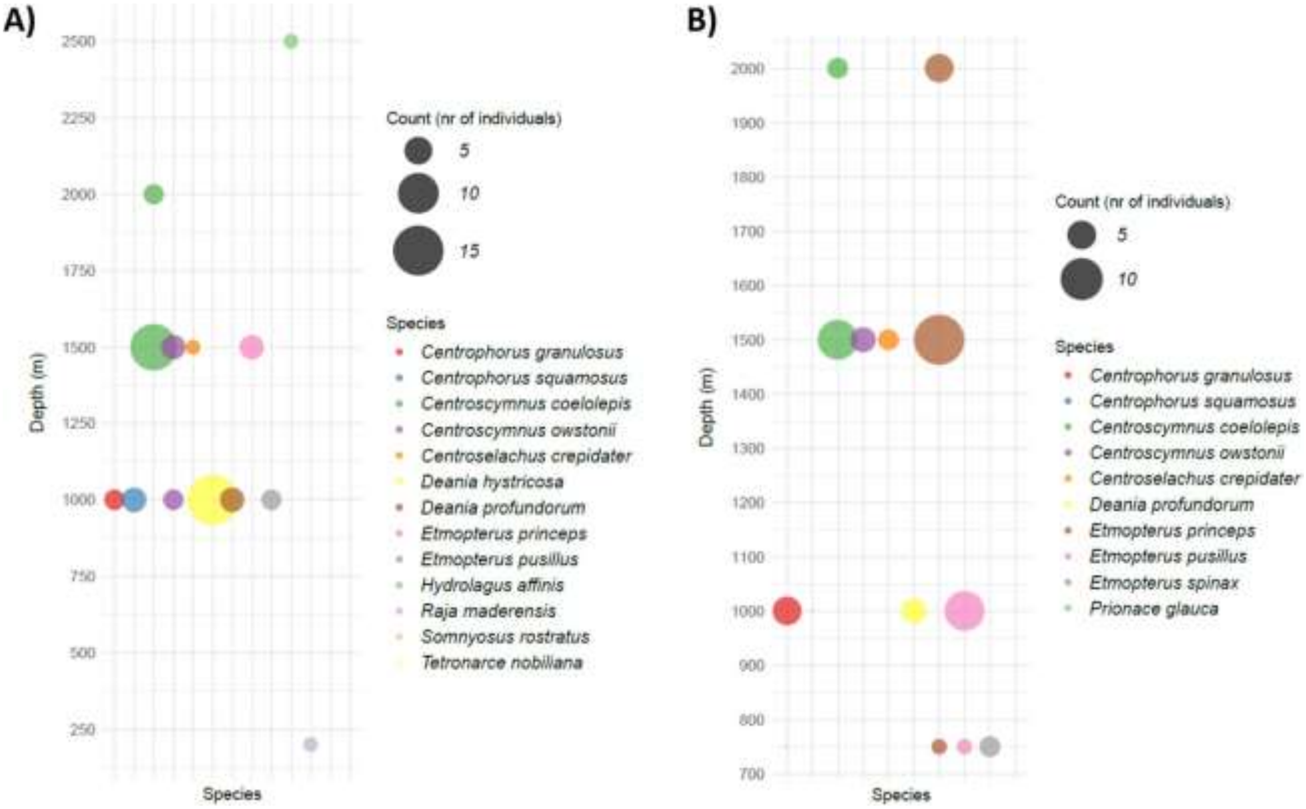


Fig. 1 Frequency of occurrence by depth strata. (A) Seine seamount; (B) Unicorn seamount

Contrarily, *H. affinis*, *R. maderensis*, *S. rostratus* and *T. nobiliana* were only captured at the Seine seamount.

Considering the list of Chondrichthyes (20) for both seamounts (Table 1), and according to IUCN criteria for Europe (Nieto et al., 2015), 1 species (5%) is classified as Critically Endangered (*Centrophorus granulosus*), 3 (14%) as Endangered (*C. squamosus*, *C. coelolepis* and *Deania calcea*) and 2 (10%) as Vulnerable (*Centrocymnus owstonii* and *Raja maderensis*).

Similarly, 3 species (14%) are classified as Near Threatened, 5 (24%) as Data Deficient and 7 (33%) as Least Concern (Fig. 2). Overall, 28.6% of the species recorded for the Seine and Unicorn seamounts are classified as Threatened (CR + VU + EN).

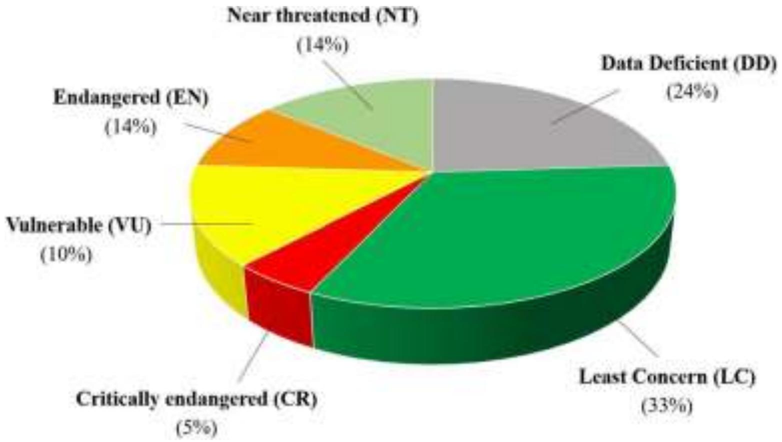


Fig. 2 IUCN European Red List status of Chondrichthyes from the Seine and Unicorn Seamounts

Discussion

Twenty cartilaginous fish species were confirmed in the present checklist for the Seine (17) and Unicorn (11) seamounts, corresponding to approximately 31% of the total valid chondrichthyan species reported for Madeira archipelago (Biscoito et al., 2018), and to 2.3% of the total species worldwide (Weigmann, 2016). Despite having been previously reported for Madeira archipelago, some of the present study's species were reported for the first time for both the Seine (*C. granulosus* and *S. rostratus*) and Unicorn (*C. granulosus*, *C. coelolepis* and *C. crepidater*) seamounts.

Only one specimen of *P. glauca*, *S. rostratus* and *T. nobiliana* was collected over the course of this study, while *C. coelolepis* and *E. princeps* were revealed as the most common species.

Regarding the collected specimens' total length, individuals of *D. profundorum* presented a slightly larger size than the maximum length recorded by Ebert and Stehmann (2013). All other species were within their known size range.

Among the most frequent species *D. calcea* and *C. coelolepis* present a similar depth range when comparing with previous works (Menezes et al., 2009). However, three species (*E. pusillus*, *R. maderensis* and *H. affinis*) were collected at greater depths than those recorded by Ebert and Stehmann (2013). In the case of *E. pusillus,* a wider depth range was observed in the present study in contrast with Menezes et al. (2009). In fact, the widest depth range was recorded for the Etmopteridae family (750–2500 m), while Centrophoridae and Somniosidae species were captured mostly between 1000 and 1500m deep, respectively. The large-scale hydrographic regime characteristic of the Northeast Atlantic might explain the similarity among species composition associated with seamounts located within the same geographical region.

In Europe, 40.4% of Chondrichthyes are listed as Threatened (Nieto et al., 2015). In Madeira archipelago, 35.8% of the total recorded species are labelled under the same category (Biscoito et al., 2018), which is only slightly more than the 28.9% species recorded for the Seine and Unicorn seamounts. Additionally, and when considering that Chondrichthyes are a group particularly sensitive to threats posed by overfishing (Dulvy et al., 2014), this study may be of importance when aiming to improve fisheries regulations currently in place, as shedding light on these species' occurrence at different depths in commercial fishing dominated seamounts might be of help in shark conservation. Finally, this work's relevance is also marked by the updated annotated checklist contribution to the knowledge of seamount-associated fish biodiversity and may serve as a strengthening tool for a future proposal for the creation of an MPA within the Madeira-Tore region.

Acknowledgements

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PART IV

DEEP SEA CHONDRICHTHYES FISHERIES AND BIOLOGY

Chapter 10

Long term overview of elasmobranch fisheries in an oceanic archipelago: the case study of Madeira Archipelago

CHAPTER 10 - Long term overview of elasmobranch fisheries in an oceanic archipelago: the case study of Madeira Archipelago

Abstract

Elasmobranch species represent a worldwide priority at conservation level because of its susceptibility to fishing pressure. In Madeira archipelago, North-eastern Atlantic, most elasmobranch species are caught as bycatch in the artisanal drifting longline fishery for scabbard fishes. All commercial elasmobranch landings carried out in this archipelago over the past three decades (1990-2020) were analyzed, aiming to provide a reliable overview of Madeira's elasmobranch fisheries and its evolution. A total of 2,316 tons of elasmobranchs were landed during the study period, corresponding to approximately €2.1 million in first sale value. The most representative period occurred from 2003 to 2013 with annual landings superior to 70 tons. Overall, a pattern of supply and demand was apparent when looking into annual landed tonnage and mean price values. In general, mean price showed an opposite trend to landings. When looking into species level, *Centrophorus squamosus* appears as the dominant species representing about 89% of the total elasmobranch species landed, followed by *Prionace glauca* with approximately 3%. Management measures currently in place need to be updated and ought to be based on studies on type and size of hook for each fishery, in order to ultimately infer about species-specific survival rates, as well as fishing gears soak time. Moreover, studies on the enhancement of food supply through fisheries discards are still missing, even though it is highly likely that this input may alter the dynamics of marine food webs.

Keywords

Elasmobranchs, fisheries, landings, Madeira archipelago, long-term analysis.

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Introduction

Overfishing is currently the most significant and widespread threat for elasmobranchs (Dulvy et al., 2014; Davidson et al., 2016). Fisheries for elasmobranch species are predominantly incidental throughout the world. Moreover, they differ in target species and in type of gears and vessels used. This diversity makes assessment, and especially management, difficult to achieve. As such, data compilation on a national and regional basis is crucial to enable assessments of the status of elasmobranch stocks worldwide (Bonfil, 1994).

In oceanic archipelagos fisheries are extremely important to coastal populations, namely as a source of food and employment (Gillett, 2010). The oceanic Portuguese island of Madeira is part of a volcanic archipelago in the Northeastern Atlantic Ocean (Alves and Delgado, 2002). The geomorphological features of the island's coastline and ocean floor, such as narrow insular shelves and steep slopes that drop abruptly to more than 1800 m at approximately five nautical miles from the coast, have imposed severe constraints on regional fisheries (Morato et al., 2012). Additionally, the nature of its oligotrophic waters (Caldeira et al., 2012) explains the small biomass of fishing resources mainly concentrated in the neritic zone (Alves and Delgado, 2002). Even so, and due to isolation from the mainland, fishery products have always played a major role in the diet of the inhabitants of the archipelago.

Consequently, fisheries are of importance to the economy of the archipelago of Madeira. This activity has been traditionally undertaken by the coastal population, since the discovery of the archipelago in the fifteen century (Vieira, 1995). In the last three decades, the total production presented an average annual value of approximately 7,000 t, corresponding to an average total first sale value of approximately €12 million per year (Figure 1). However, a continuous decrease in landings from 1995 onwards was observed. In 2020, total landings represented 4,000 t, equivalent to an average of about €11 million in auction value (DRP, 2020).

The Madeiran fisheries are artisanal and small-scale, mostly composed of small vessels. The active commercial fishing fleet has decreased gradually in number of vessels from the nineties onwards. Out of the 86 local fishing vessels that landed in regional ports in 2020, 71% were small vessels with less than 12 m and only 5% were bigger than 24 m length. These small-scale fisheries are dominated by mid-water drifting longlines targeting black and intermediate scabbard fishes (respectively *Aphanopus carbo* Lowe, 1839 and *Aphanopus intermedius* (Parin, 1983) and by the pole and line vessels that target tuna (*Thunnus* spp.), together accounting for approximately 89% of the total of the exploited marine resources landed in the archipelago in 2020. The remaining 11% corresponded to the landings of small pelagic species (6%), shellfish (3%) and demersal species (2%) (DRP, 2020).

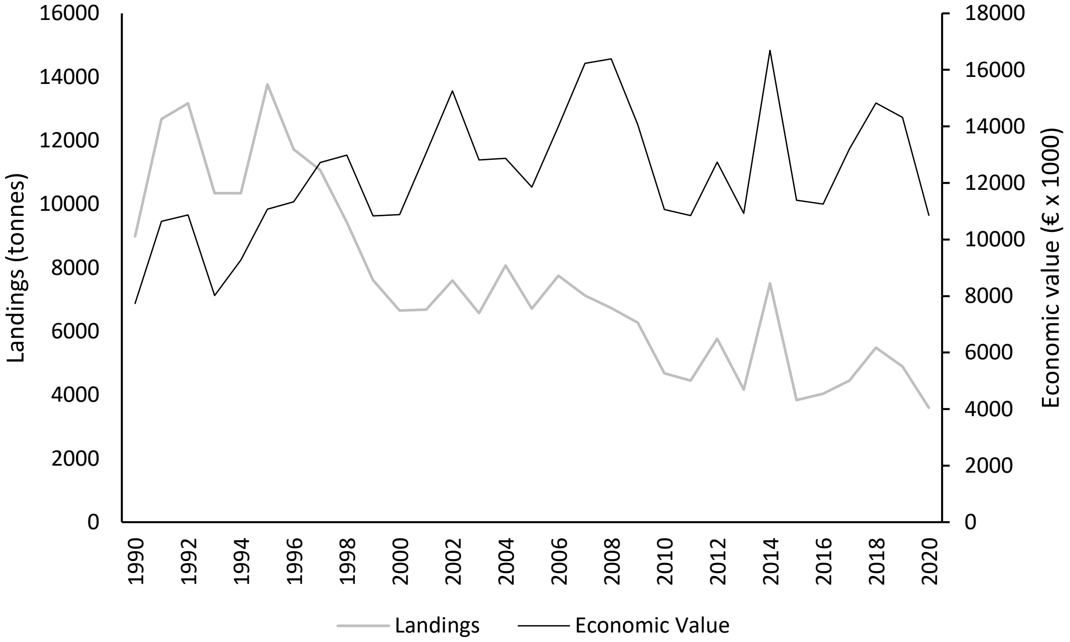

Figure 1 - Landings in tonnes and economic value in thousand euros of total fisheries of the archipelago of Madeira, from 1990 to 2020.

In recent years elasmobranchs have been economically valued, which has led to an increase in catches. However, this group represents a worldwide priority at conservation level because of its susceptibility to fishing pressure (Bonfil, 1994; Fowler et al., 2005; Dulvy et al., 2014). Elasmobranchs' resilience to a fishing pressure will always be subject to its own vulnerability and productivity. In turn, productivity is intimately linked to species life history characteristics, such as slow growth, late maturation, high longevity and low fecundity in the case of elasmobranchs (Stevens et al., 2000; Large et al., 2003). In order to guarantee a sustainable exploitation of these resources, management plans should be based on robust scientific knowledge.

The elasmobranch fishery in the archipelagos of Azores, Madeira and Canaries is regulated by the European amendments of Western Waters Regulation (EC 1954/ 2003) which comprehends the reduction of the 200 nm of the Exclusive Economic Zone to 50 or 100 nm. However, this regulation is restrictive only for vessels registered in the ports of the islands and does not apply to EU Community vessels that traditionally fish in those waters as far as these do not exceed the fishing effort traditionally exerted.

In Madeira archipelago most elasmobranch species are caught as bycatch by the artisanal drifting longline fishery for black and intermediate scabbard fishes, particularly between the 800 and 1300 m of depth (Delgado et al., 2018). Nonetheless, a residual portion of elasmobranch species are also bycaught by the bottom and pelagic longline and handline fisheries targeting demersal and pelagic fish. Contrarily to the pelagic longline, which is set to drift in the ocean’s epipelagic layer, the drifting longline operates strictly within the depth layer of the water column without being anchored and always well above the seafloor (ICES, 2021). In contrast, the bottom longline is a stone-buoy-slim horizonal longline operating near the sea floor, between the 50 and 250 m of depth.

Elasmobranch species, in particular deep-water sharks, are part of the gastronomic cultural heritage of the region. These fish, and more specifically, in Madeira, the leafscale gulper shark (*Centrophorus squamosus*), are appreciated by both the local population and tourists, and have a high social and economic importance (Freitas *et al.*, 2021). They are commercially exploited for both human consumption and for squalene extraction from their livers. However, since 2021, landings of deep-water sharks are prohibited by the Council Regulation (EU) 2021/91 of 28 January 2021, and only demersal and pelagic elasmobranch species are landed in the region’s ports presently.

Apart from bycatch data, information on elasmobranch species occurring around the island is scarcely available (Severino et al., 2009; Freitas et. al., 2017; Biscoito et al., 2018). However, in recent years, there is an increment in the interest regarding the study of these species, including its characterization in terms of biology and population dynamics. Among the 67 cartilaginous fish species reported to Madeira archipelago (Biscoito et al., 2018), 8 species are classified as Vulnerable, 9 as Endangered and 7 as Critically Endangered according to the IUCN European Red List of marine fishes (Nieto et al., 2015). The lack of information about elasmobranch fisheries in the archipelago of Madeira has led to this study, which was developed as a first approach to characterize the long-term exploitation of these resources.

This work intents to provide an overview of Madeira's elasmobranch fisheries in the NE Atlantic Ocean area and its evolution over the past three decades (1990 to 2020). The main scope of this study was to obtain reliable information on the status of the exploited species, in order to provide a basis for their conservation management. These objectives will be achieved by: i) estimating the annual landings and auction values; ii) identifying the main elasmobranch fish species landed; iii) characterizing the elasmobranch fishing fleet and iv) determining temporal trends from the elasmobranch landings.

Material and methods

All commercial elasmobranch landings carried out in the ports of the archipelago of Madeira between 1990 and 2020 were considered for this study. The data were obtained from the local authorities (Direção Regional de Pescas – DRP/ Direção Regional do Mar - DRM) in the auction houses. Landed weights and first sale value were gathered and analysed.

Species landings and mean yearly price per kilogram (PPK) were analysed by fishing gear considering two main categories: landings performed by mid-water drifting longlines (DLL) and by the whole of bottom and pelagic longlines and handlines (BLL/PLL/HL).

Annual and monthly species landings trends were further investigated and mean yearly PPK per species was estimated to verify changes in demand. Additionally, landings by vessel size according to species and year were also evaluated considering four categories: i) VL0012 – vessel length inferior to 12 m; ii) VL1218 – vessel length between 12 and 17.99 m; iii) VL1824 – vessel length between 18 and 23.99 m and iv) VL2440 – vessel length between 24 and 39.99 m.

Data's normal distribution was verified through the Anderson-Darling normality test for sample sizes bigger than 5 thousand observations, and homogeneity of variance was determined using Levene's statistics. Kruskal-Wallis nonparametric test was performed to compare mean weight and selling price between years, months, and vessel size. Dunns's test with the Bonferoni correction was conducted as a post-hoc test when significant differences were observed (Zar, 2010). Differences at p value < 0.05 level were accepted as significant. All statistical analysis was performed using R Core Team

(2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org.

Results

The total annual landings of elasmobranch species were inferior to 55.111 tons between 1990 and 2002. In general, there was an increase in the landed tonnage from 2003 to 2008, when a peak of 283 tons was registered. Since 2010, landings have been decreasing and remained below 12 t in 2020, reflecting UE restrictions for the exploitation of deep-water sharks (Figure 2). In general, mean price showed an opposite trend to landings

A total of 2,316 tons of elasmobranchs species were landed in the archipelago of Madeira, between 1990 and 2020, corresponding approximately to €2.1 million in first sale value. Of the complete tonnage landed, 67% (1,556 t) of elasmobranchs were landed in Funchal, the main fishing port of the region.

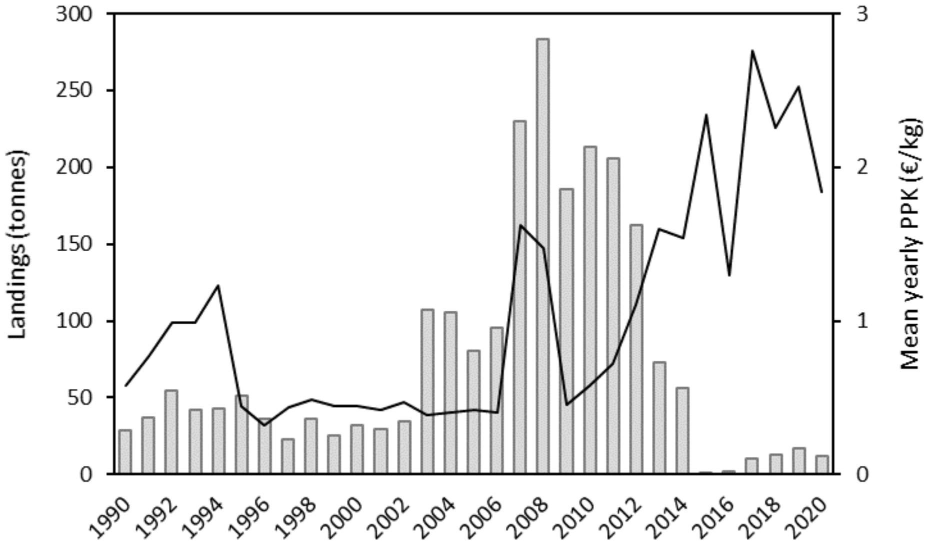

Figure 2. Total elasmobranch landings in tonnes and mean annual price per kilogram in euros, between 1990 and 2020, for all fisheries.

Most elasmobranch's species were caught using mid-water drifting longlines (97.02 %) and only 2.98 % were caught by bottom longlines/pelagic longlines/handlines.

The analysis of landings by fishing gear (Figure 3) showed that *Centrophorus squamosus* (Bonnaterre, 1788) was the dominant species corresponding to about 91% of the total species caught with mid-water drifting longlines (Figure 3A). The remaining 9%

corresponds to *Prionace glauca* (Linnaeus, 1758), *Dalatias licha* (Bonnaterre, 1788), *Isurus oxyrinchus* Rafinesque, 1810, *Centrophorus granulosus* (Bloch & Schneider, 1801), *Centroscymnus* spp. and *Deania* spp.

Regarding the elasmobranch species caught by bottom longlines, pelagic longlinesand handlines, it was observed that *Galeorhinus galeus* (Linnaeus, 1758) was the most representative species (68%), followed by *Raja* spp. with 12% and by *Sphyrna zygaena* (Linnaeus, 1758) and *Mustelus mustelus* (Linnaeus, 1758) with 10% (Figure 3B).

The annual analysis showed statistically significant differences between the catches performed by mid-water drifting longlines (DLL) and by bottom longlines, pelagic longlines and handlines BLL/PLL/HL), (Kruskal-Wallis test followed by Dunn's, p<0.05). Similarly, the annual mean price also presented significant differences for DLL and BLL/PLL/HL (Kruskal-Wallis test followed by Dunn's, p<0,05).

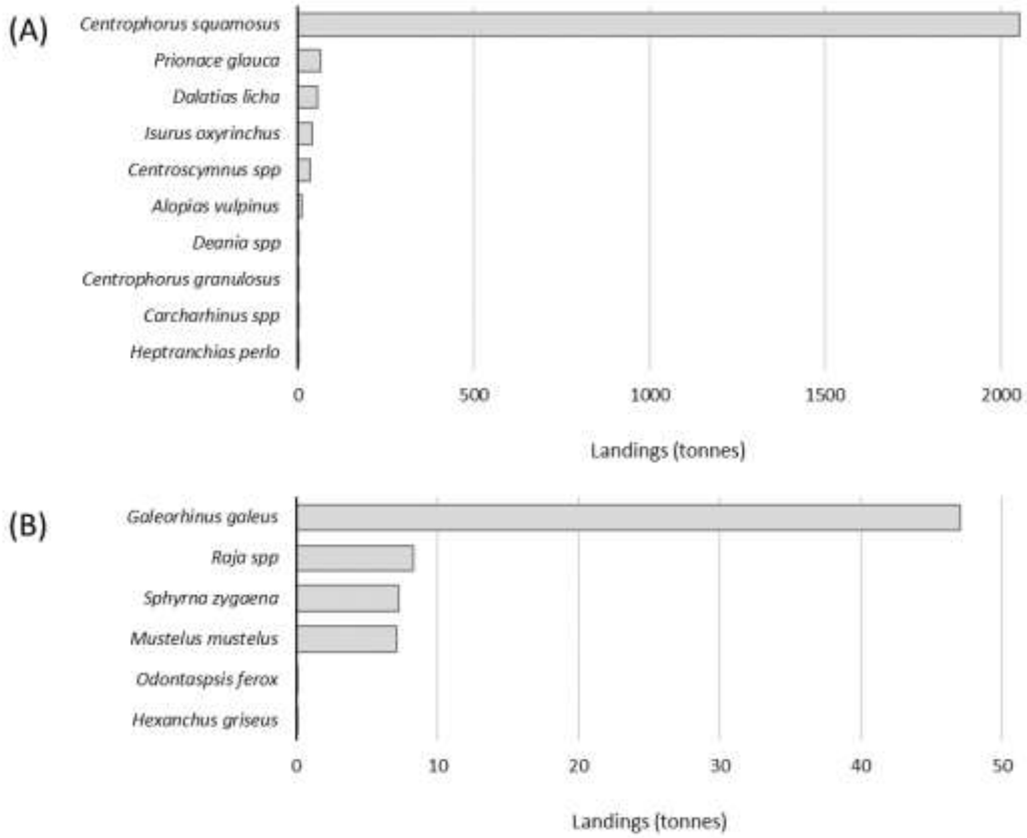

Figure 3. Elasmobranch commercial landings (in tonnes) by fishing gear and species, between 1990 and 2020, in Madeira archipelago. A) Mid-water drifting longlines, B) Bottom longlines/pelagic longlines/handlines.

Annual analysis

Total elasmobranch annual landings performed by mid-water drifting longlines remained below 50 t from 1990 to 2002. In the following years, an increase was observed with a peak of 282 t in 2008. From 2010 to 2014 landings decreased from 213 to 56 t. From 2015 onwards, catches were in line with the Total Allowable Catch (TAC) imposed by the European Union (EU) for deep-water sharks' species, which led to a sharp reduction in global annual landings. As expected, a decrease in landings led to an increase in the price per kilogram (PPK). This pattern was more pronounced between 2008 and 2019. Mean yearly PPK increased from €0.37 in 1996 to €2.96 in 2019, possibly due to an increasing demand during those years (Figure 4A). The observed differences were statistically significant concerning the landed quantity (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Concerning the total elasmobranch annual landings made by bottom longliners, pelagic longliners and handliners, an increase from approximately 4 t in 1990 to 7 t in 1998 was observed. The main peak occurred in 1998 with 7 t. From 2000 onwards, total annual landings decreased to less than 4 t. Additionally, a similar trend was observed for bottom and pelagic longliners and handliners, marked by a decrease in landings accompanied by an increase in the mean yearly price. The mean yearly PPK varied from €0.38 in 1990 to €1.84 in 2017 (Figure 4B). The observed differences were statistically significant for the landed quantity (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

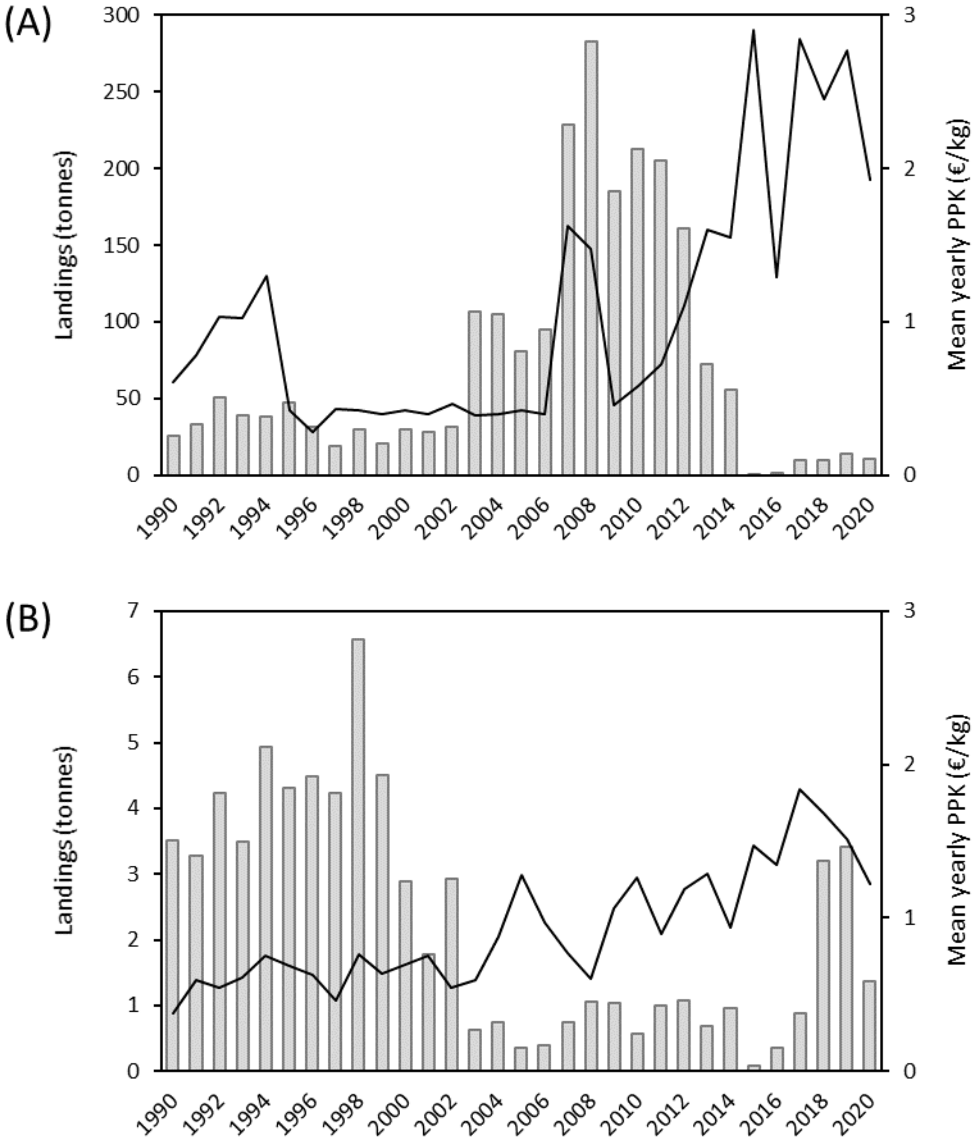

Figure 4. Annual elasmobranch landings in tonnes and mean annual price per kilogram in euros between 1990 and 2020. A) Mid-water drifting longlines, B) Bottom longlines/pelagic longlines/ handlines.

In the first half of the nineties, elasmobranch species' landings performed by mid-water drifting longlines were dominated by *C. squamosus*, *D. licha*, *Centroscymnus* spp., *P. glauca* and *I. oxyrinchus*. In the period between 1997 and 2020 it was possible to verify an increase in the bycatch of *C. squamosus* and its dominance over other species landings during those years. The absence of deep-water sharks' landings in 2015 and 2016 was explained by the EU' restrictive TAC of 0 t (Figure 5A).

A total of 2,055 t of *C. squamosus* was landed in 181 the archipelago of Madeira, between 1990 and 2020, corresponding to approximately €2M (Figure 5A). The annual landings remained below 50 t from 1990 to 2002. An increase was observed for the following years, with a peak of 281 t in 2008. From 2010 to 2014 landings decreased from 212 to 55 t. On the other hand, mean yearly PPK increased from €0.60 in 1990 to €1.41 in 1994. Between 1995 and 2006 it stabilized at around €0.40 and in 2009 a decrease was observed, possibly due to the peak of landings detected in 2008. The highest mean PPK occurred in 2019 at €2.99. The observed differences were statistically significant for the quantity of *C. squamosus* landed from 1990 to 2020 (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and for the mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$). Concerning *D. licha*, 54 t were landed in the period between 1990 and 2020 corresponding to €51,000 (Figure 5B). Landings for this species occurred mainly between 1990 and 1997 (53 t). However, the annual mean price showed an opposite trend to landings. Annual analysis revealed statistical differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) as well as in mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

A total of 33 t of *Centroscymnus* spp. was landed, corresponding to €37,000 (mean annual price of €1.78) (Figure 5C), predominantly between 1993 and 1994 (30 t). Annual analysis showed statistically significant differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Landings of *C. granulosus* yielded a total of 0.5 t, which corresponded to € 1,000 at a mean price of €1.93 kg^{-1} (Figure 5D). This species landings occurred from 2018 onwards. Annual analysis showed statistically significant differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and in mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

A total of 64 t of *P. glauca* were landed from 1990 to 2020 corresponding to €12,000. 90% of this species' total landings occurred in only three years (1995, 1996 and 2003) (Figure 5E). In contrast, an opposite trend was observed in the mean price in relation to landings, with lower annual mean prices during the years marked by higher landings. However, no landings were observed for this species for several years. Annual analysis showed statistical differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) as well as in mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Regarding *I. oxyrinchus,* landings increased from 1990 (*ca.* 1 t) to 1994 (*ca.* 4 t) (Figure 4F). Overall, for more than half of the study period, annual landings were less than 1 t. However, a catch peak was observed in 1994 and 2003 with approximately 4 t. From 2018 to present an increase in landings was observed. Contrarily, the mean price PPK showed an opposite pattern. The mean annual price for this species was €2.25 kg^{-1}. Annual analysis showed statistically significant differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and in mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

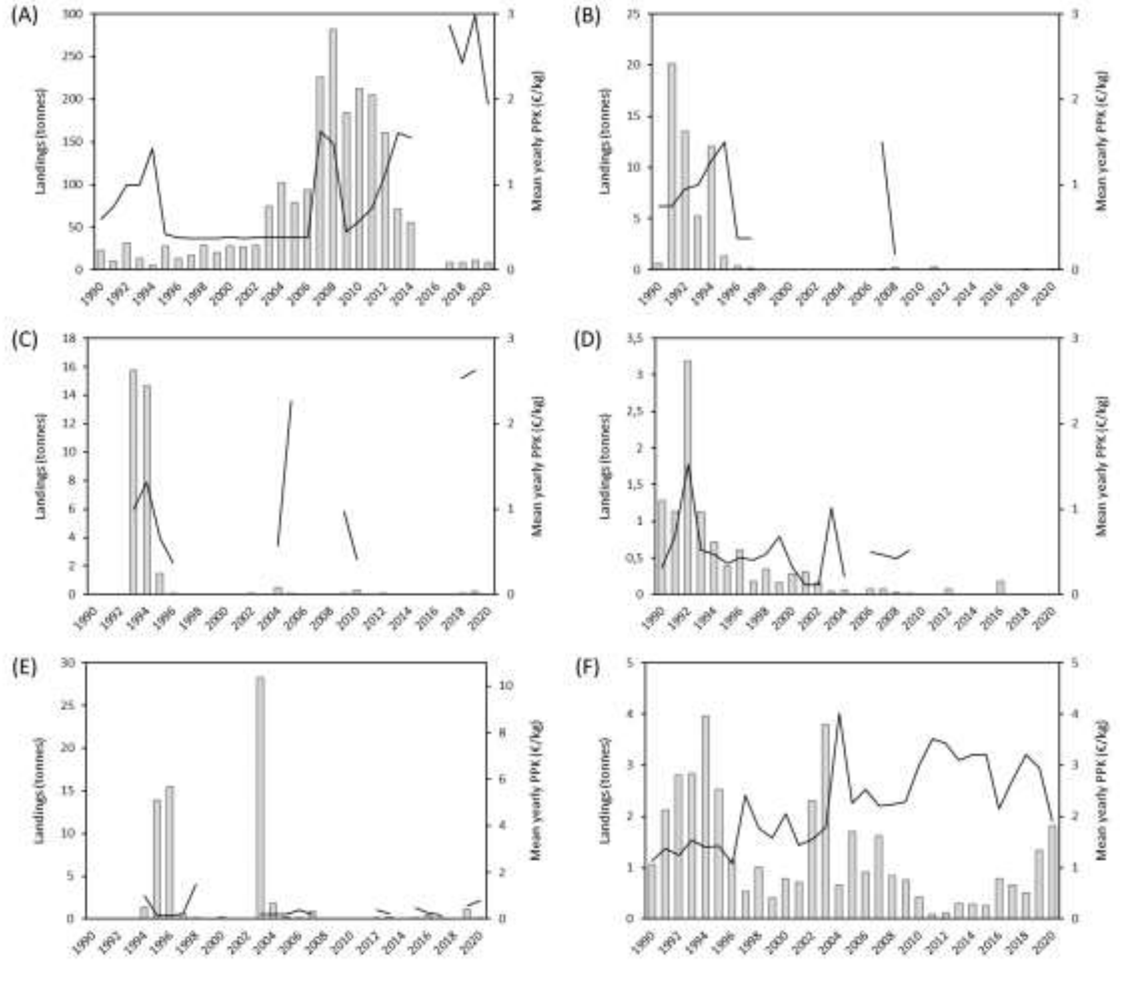

Figure 5. Annual elasmobranch landings by species, in tonnes and mean annual price per kilogram in euros, between 1990 and 2020 for catches performed by mid-water drifting longlines. A) *Centrophorus squamosus,* B) *Dalatias licha,* C) *Centroscymnus* spp.**,** D) *Centrophorus granulosus,* E) *Prionace glauca* and F) *Isurus oxyrinchus.*

Between 1990 and 2020, the cumulative volume of elasmobranch species landed by BLL/PLL/HL was dominated by *G. galeus* (*ca.* 47 t; *ca.* €41,000) (Figure 6A). Annual landings of *G. galeus* were higher in the nineties. In fact, the catch peak occurred in 1998 (*ca.* 5 t). Overall, from 2000 to 2017 catches were mostly low (< 1 t) and from 2018 onwards, catches increased to approximately 3 t. In general, the mean price increased with the decrease in landings. The analysis showed that there were statistically significant differences in the quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Raja spp. (*ca.* 8 t; *ca.* €3,000), *S. zygaena* (*ca.* 7 t; *ca.* €6,000) and *M. mustelus* (*ca.* 7 t; *ca.* €6,000) were also relevant species for the same study period.

Raja spp. data revealed higher annual landings from 1990 to 2000 (*ca.* 76 % of the total), corresponding to a mean price of €0.35 kg^{-1} (Figure 6B). From 2001 onwards, landings for this species corresponded to approximately 0.1 t (*ca.* €0.55 kg^{-1}). Annual analysis showed statistically significant differences in quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and in mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

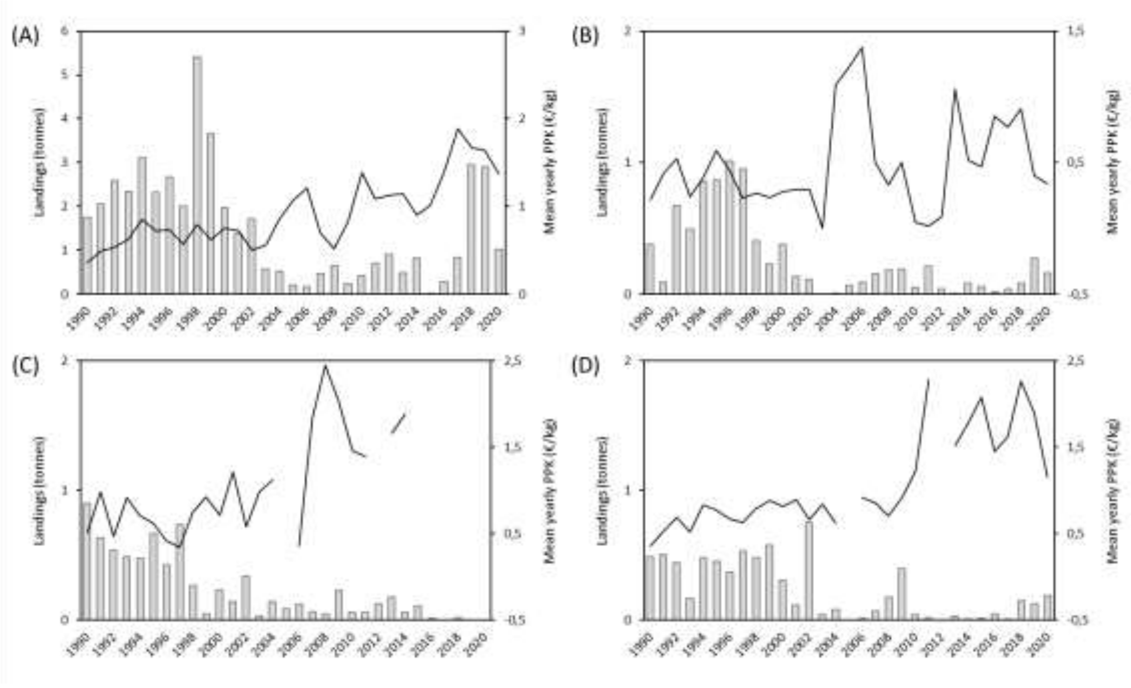

Figure 6. Annual elasmobranch landings by species, in tonnes and mean annual price per kilogram in euros, between 1990 and 2020 for catches performed by bottom longliners/pelagic longliners/handliners. A) *Galeorhinus galeus*, B) *Raja* spp., C) *Sphyrna zygaena* and D) *Mustelus mustelus*.

Landings of *S. zygaena* and *M. mustelus* showed a similar pattern during the study period. In general, landings were high until 2002 (Figures 6C and 6D). Afterwards, and until present, landings sharply decreased. As expected, the mean price showed an opposite trend. Annual analysis showed statistically significant differences in quantity landed for both species (Kruskal-Wallis test followed by Dunn's, $p<0.05$). Concerning the mean price, differences were only observed for *M. mustelus* (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Monthly analysis

Results revealed that landings fluctuate throughout the year for both fishing gears considered. The elasmobranchs tonnage landed by mid-water drifting longlines was higher in March (*ca.* 225 t) and October (*ca.* 227 t), contrarily to mean price which was superior in June (€0.97 kg^{-1}) and December (€0.99 kg^{-1}) (Figure 7A). The observed oscillations were statistically significant for the landed quantities (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal- Wallis test followed by Dunn's, $p<0.05$).

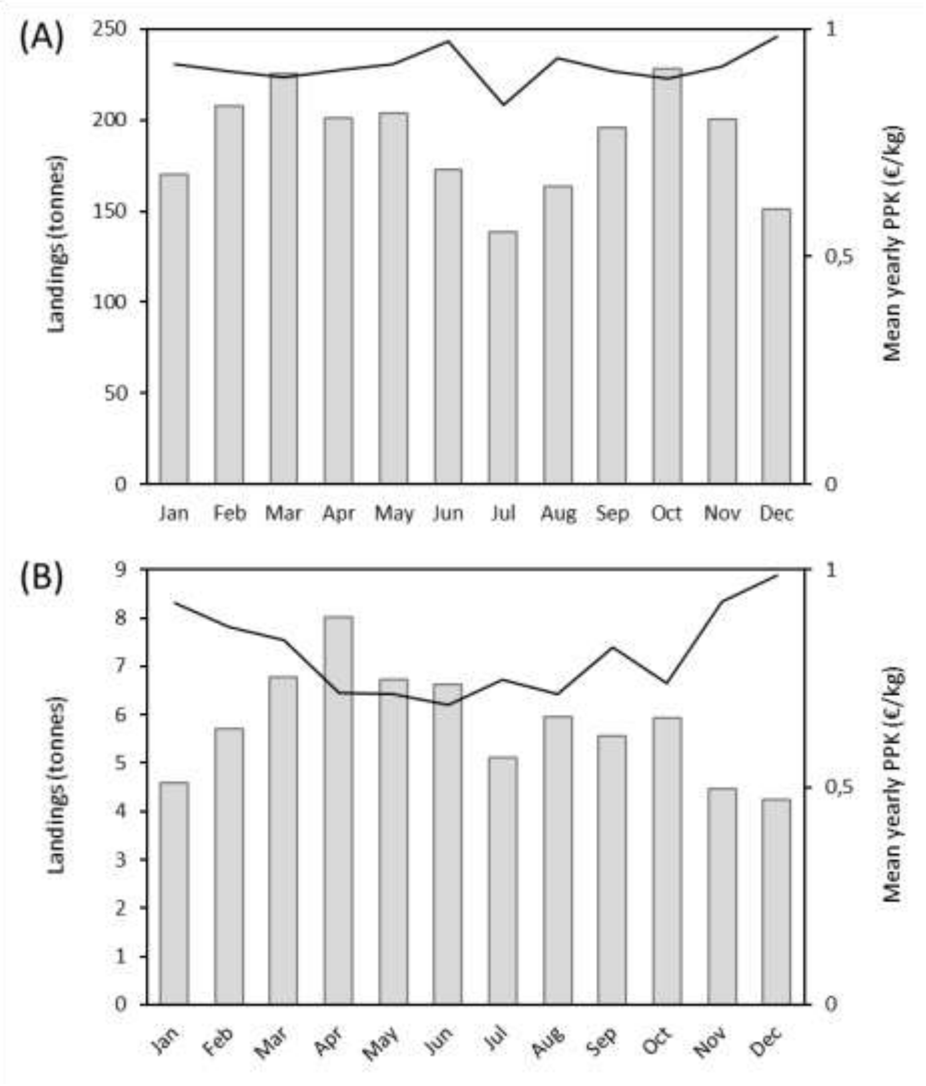

Figure 7. Monthly elasmobranch landings in tonnes and mean price per kilogram in euros between 1990 and 2020. A) Mid-water drifting longlines, B) Bottom longlines/ pelagic longlines/ handlines.

Regarding catches performed by bottom and pelagic longliners and handliners an increase in landings from January (*ca.* 5 t) to April (*ca.* 8 t) was observed (Figure 7B). The mean price followed an opposite trend, with higher values in January and December (> €0.92 kg^{-1}). Results demonstrated statistically significant differences both in monthly quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Monthly analysis showed that *C. squamosus* is landed throughout the year, with two major peaks in October (*ca.* 213 t) and in March (*ca.* 200 t) (Figure 8A). In general, the mean price was similar between January and March (*ca.* €0.90 kg^{-1}) and increased until June (*ca.* €1.0 kg^{-1}). The lowest mean price was verified in July (*ca.* €0.82 kg^{-1}). In

December a decrease in landings led to an increase in mean price. Results revealed statistically significant differences both in monthly quantity landed (Kruskal-Wallis test followed by Dunn's, 276 $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Monthly landings of *D. licha* showed higher values between January and April (> 5 t per month) (Figure 8B), with a peak occurring in February with approximately 9 t. Overall, mean price increased from January (*ca.* €0.8 kg^{-1}) to July (*ca.* €1.1 kg^{-1}), and then decreased until December (*ca.* €0.90 kg^{-1}). The analysis showed significant difference in monthly quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Data analysis of *Centroscymnus* spp. revealed higher landing values between March and June (> 3 t) (Figure 8C), with a major peak occurring in April with more than 6 t. In general, mean price showed an opposite trend to landings. However, no statistically significant differences were observed regarding neither monthly quantity landed (Kruskal-Wallis test followed by Dunn's, $p>0.05$) nor mean price (Kruskal-Wallis test followed by Dunn's, $p>0.05$).

With regards to *C. granulosus*, monthly differences were not statistically significant neither for monthly landed quantity (Kruskal-Wallis test followed by Dunn's, $p<0.05$) nor for mean price (Kruskal-Wallis test followed by Dunn's, $p>0.05$) (Figure 8D).

Concerning *P. glauca* landings' values revealed that this species was predominantly caught from February to May (> 6 t per month) with a peak in April (*ca.* 18 t) (Figure 8E). Mean price showed an opposite pattern in relation to landings, with a higher mean value in October (*ca.* €0.50 kg^{-1}) and the lowest mean value in December (*ca.* €0.10 kg^{-1}). The analysis showed significant differences in monthly quantity landed (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Regarding *I. oxyrinchus*, most landings occurred from October to April (*ca.* 71%) (Figure 7F). The highest mean price was observed in January (*ca.* €2.51 kg^{-1}) and the lowest in June (*ca.* €1.16 kg^{-1}). Monthly observed differences were not statistically significant for quantity landed (Kruskal-Wallis test followed by Dunn's, $p>0.05$) contrarily to mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

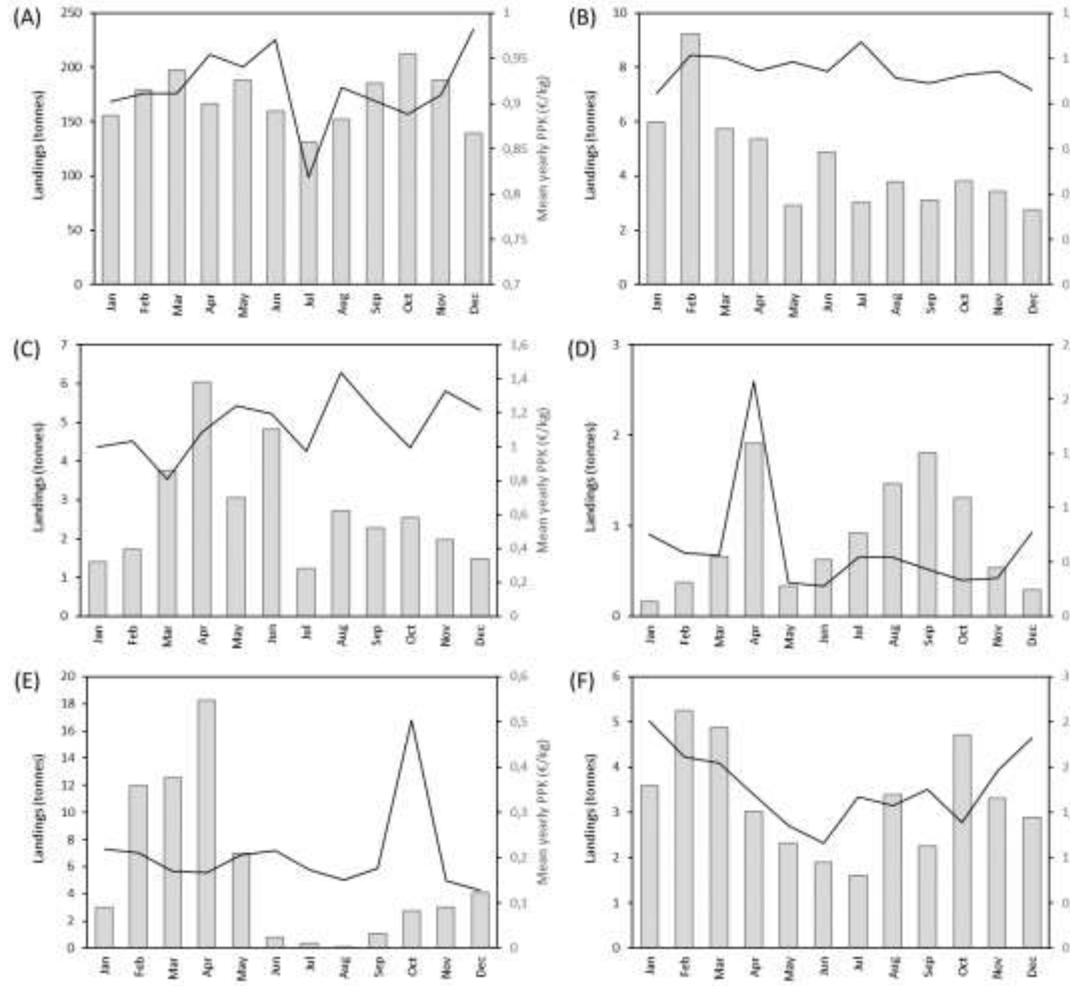

Figure 8. Monthly elasmobranch landings by species, in tonnes and mean annual price per kilogram in euros, between 1990 and 2020 for catches performed by mid-water drifting longlines. A) *Centrophorus squamosus*, B) *Dalatias licha*, C) *Centroscymnus* spp.**,** D) *Centrophorus granulosus*, E) *Prionace glauca* and F) *Isurus oxyrinchus*.

Results on *G. galeus* analysis showed significant difference in monthly landings (Kruskal-Wallis test followed by Dunn's, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn's, $p<0.05$) (Figure 9A). This species was predominantly landed from March to June (> 4.5 t per month). On the contrary, mean price revealed an opposite trend, showing the highest value over the month of October, simultaneously characterised by the lowest landed quantity (*ca.* €1.0 kg^{-1}).

Data analysis of *Raja* spp. data demonstrated that 42% of total landings occurred from February to April (Figure 9B). Mean price showed an opposite trend in relation to landings. The highest mean price was observed in June (*ca.* €0.50 kg^{-1}) and the lowest in November (*ca.* €0.28 kg^{-1}). The analysis showed significant differences in monthly quantity landed (Kruskal-Wallis test followed by Dunn’s, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn’s, $p<0.05$).

Monthly data examination of *S. zygaena* demonstrated that 62% of total landings occurred from August to October (Figure 9C). The highest mean price was verified in January (*ca.* €1.73 kg^{-1}) and the lowest in June (*ca.* €0.56 kg^{-1}). Statistically significant difference in monthly quantity landed (Kruskal-Wallis test followed by Dunn’s, $p<0.05$) and mean price (Kruskal-Wallis test followed by Dunn’s, $p<0.05$) were verified.

Concerning, *M. mustelus* 58% of total landings occurred from March to July. In general, mean price revealed an opposite trend to landings (Figure 9D). The monthly observed differences were not statistically significant for quantity landed (Kruskal-Wallis test followed by Dunn’s, $p>0.05$) nor mean price (Kruskal-Wallis test followed by Dunn’s, $p>0.05$).

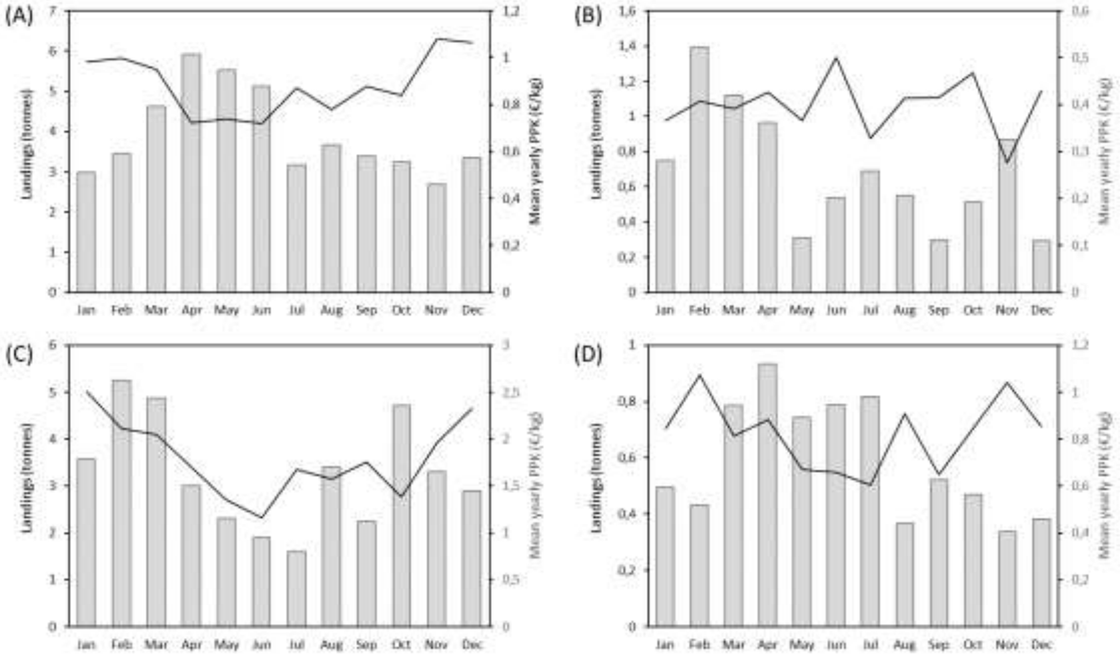

Figure 9. Monthly elasmobranch landings by species, in tonnes 330 and mean price per kilogram in euros, between 1990 and 2020 for catches performed by bottom longliners, pelagic longliners /handliners. A) *Galeorhinus galeus*, B) *Raja* spp., C) *Sphyrna zygaena* and D) *Mustelus mustelus*.

Vessel size analysis

The relationship between total annual landings in weight and vessel size allowed to verify two opposite trends for the study period related to catches performed by the mid-water drifting longlines (Figure 10A). In general, from 1990 to 2002 most catches were performed by small vessels (<12 m), with a peak in 1991 (*ca.* 84%). Contrarily to the trend verified from 2003 onwards, most catches were landed by bigger vessels (12>18 m) with a peak in 2010 (*ca.* 85%). Analysis by vessel size showed statistically significant differences for quantity landed by vessel size over the years (Kruskal-Wallis test followed by Dunn's, p<0.05).

Concerning the species caught by BLL/PLL/HL, it was verified that most catches were achieved by small vessels (<12 m), except for 1997, 2001 and 2015 (Figure 10B). The observed differences were statistically significant (Kruskal-Wallis test followed by Dunn's, p<0.05).

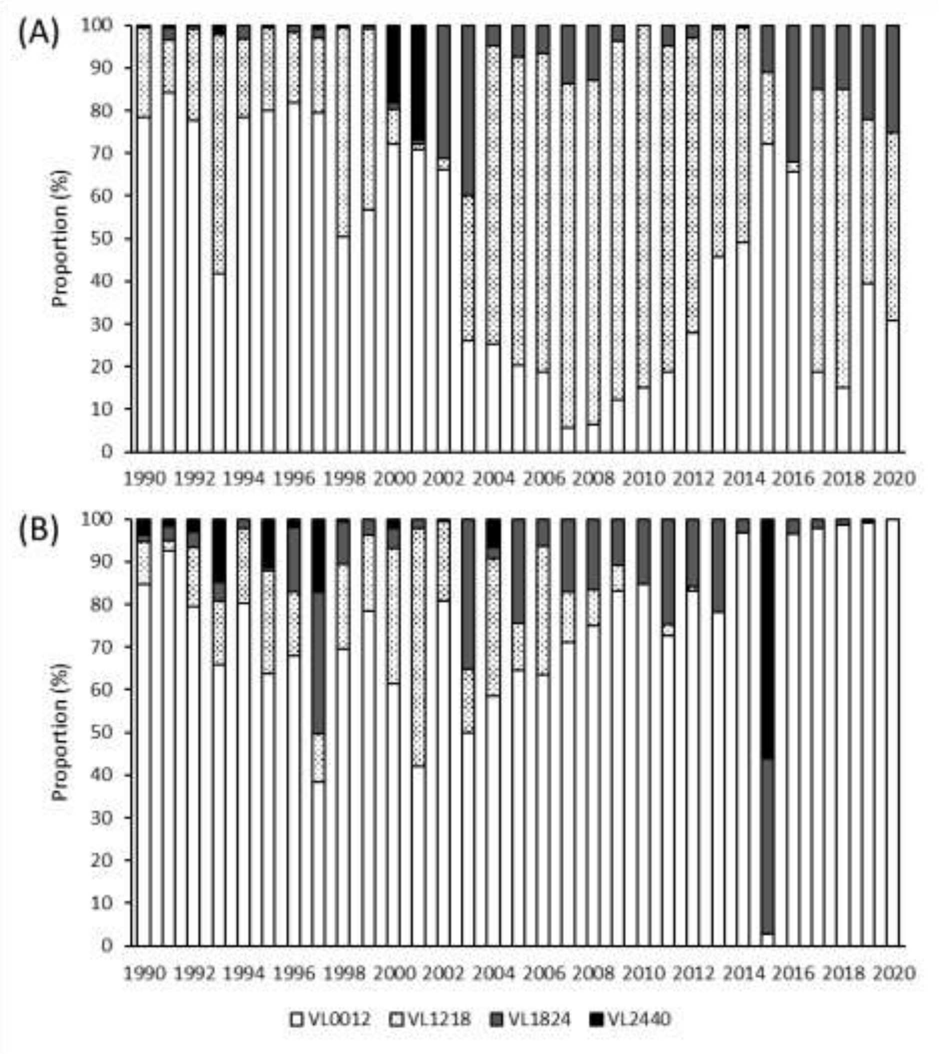

Figure 10. Landings by species and vessel size, in tonnes and mean annual price per kilogram in euros between 1990 and 2020. A) Mid-water drifting longlines, B) Bottom longlines/pelagic longlines/handlines.

Two opposite trends were observed in landings by vessel size per year for *C. squamosus* (Figure 11A). From 1990 to 2002, most catches was made by small vessels (<12 m), while from 2003 onwards most catches were performed by vessels between 12 and 18 m. Differences in the landings by vessel size per year were statistically significant (Kruskal-Wallis test followed by Dunn's, p<0.05).

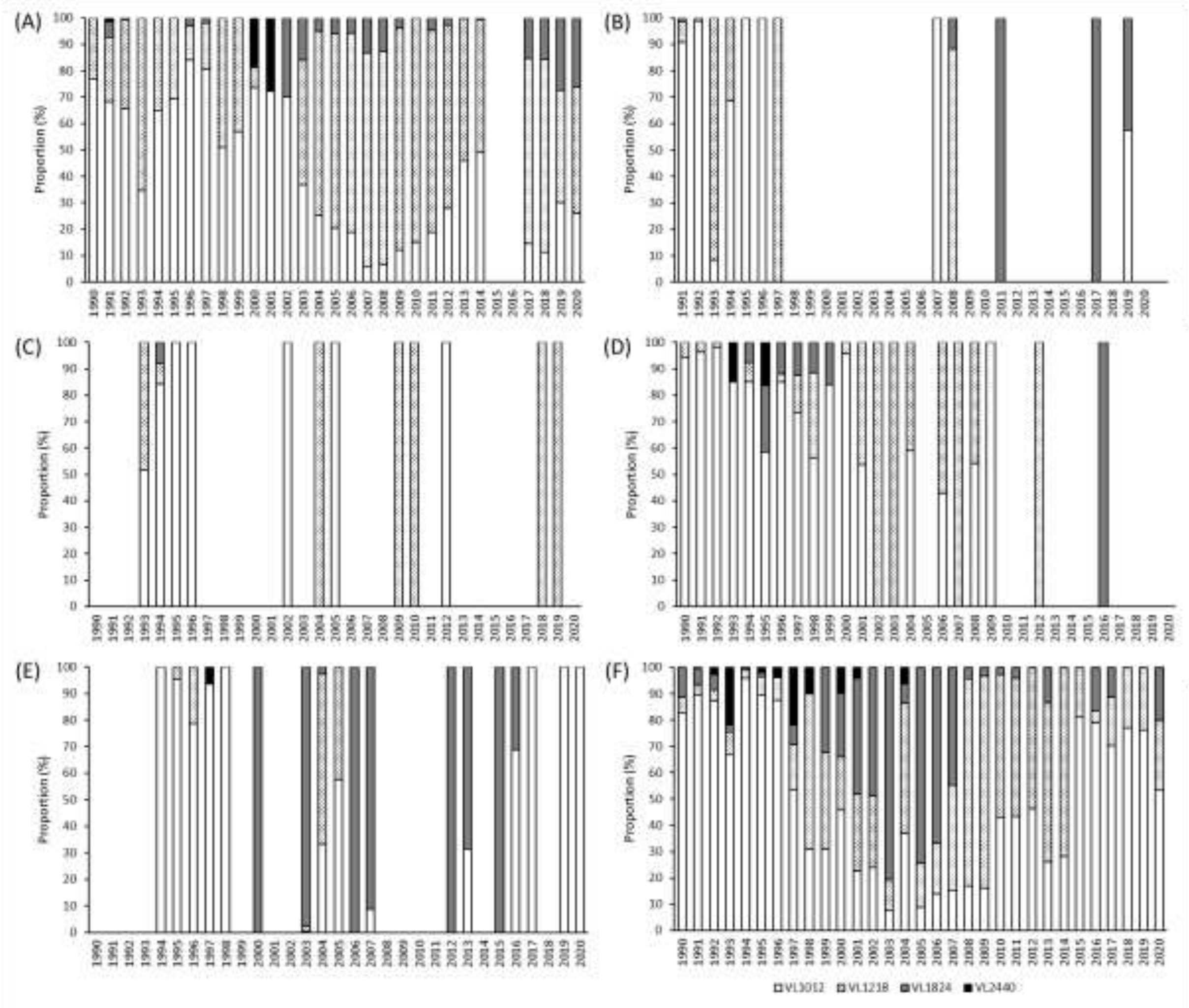

Figure 11. Landings by species and vessel size between 1990 and 2020 for catches performed by mid-water drifting longlines. A) *Centrophorus squamosus*, B) *Dalatias licha*, C) *Centroscymnus* spp.**,** D) *Centrophorus granulosus,* E) *Prionace glauca* and F) *Isurus oxyrinchus.*

Overall, *D. licha* was landed by small vessels between 1990 to 1996 and by bigger vessels from 1997 onwards (12<24 m) (Figure 11B). Analysis by vessel size allowed to verify statistically significant differences for landings by vessel over the years (Kruskal-Wallis test followed by Dunn's, p<0.05).

Centroscymnus spp. were landed by small vessels from 1993 to 1995 (<12 m) and by bigger vessels from 2002 onwards (12<24 m) (Figure 11C). The verified differences in the landings by vessel size were statistically significant (Kruskal-Wallis test followed by Dunn’s, p<0.05).

Regarding *C. granulosus* catches, it was observed that this species was predominantly landed by vessels with size between 12 and 18 m (Figure 11D). No significant differences were observed in the landings of *C. granulosus* by vessel size per year (Kruskal-Wallis test followed by Dunn’s, p>0.05).

Results on *P. glauca* landings, showed that catches were mostly performed by small vessels (<12m) between 1994 to 1998. In general, from 2000 to 2015 it was observed a reversed trend with catches being frequently made by bigger vessels (12<24 m) (Figure 11E). From 2016 onwards, the total catches were made by small vessels (<12 m). The observed differences in the catches by vessel size were statistically significant (Kruskal-Wallis test followed by Dunn’s, p<0.05).

Concerning *I. oxyrinchus,* catches were predominantly performed by small vessels over the course of two periods, from 1990 to 1997 and from 2016 to 2020. Landings by bigger vessels (12<24 m) were mostly concentrated between 1998 and 2015 (Figure 11F). Analysis by vessel size allowed to verify statistically significant differences for quantity landed by vessel over the years (Kruskal-Wallis test followed by Dunn’s, p<0.05).

The analysis for *G. galeus* indicated that catches were predominantly carried out by smaller vessels (< 12 m), except for the years 2001 (12<18 m) and 2015 (18<24 m) (Figure 12A). The observed differences were not statistically significant (Kruskal-Wallis test followed by Dunn’s, p>0.05).

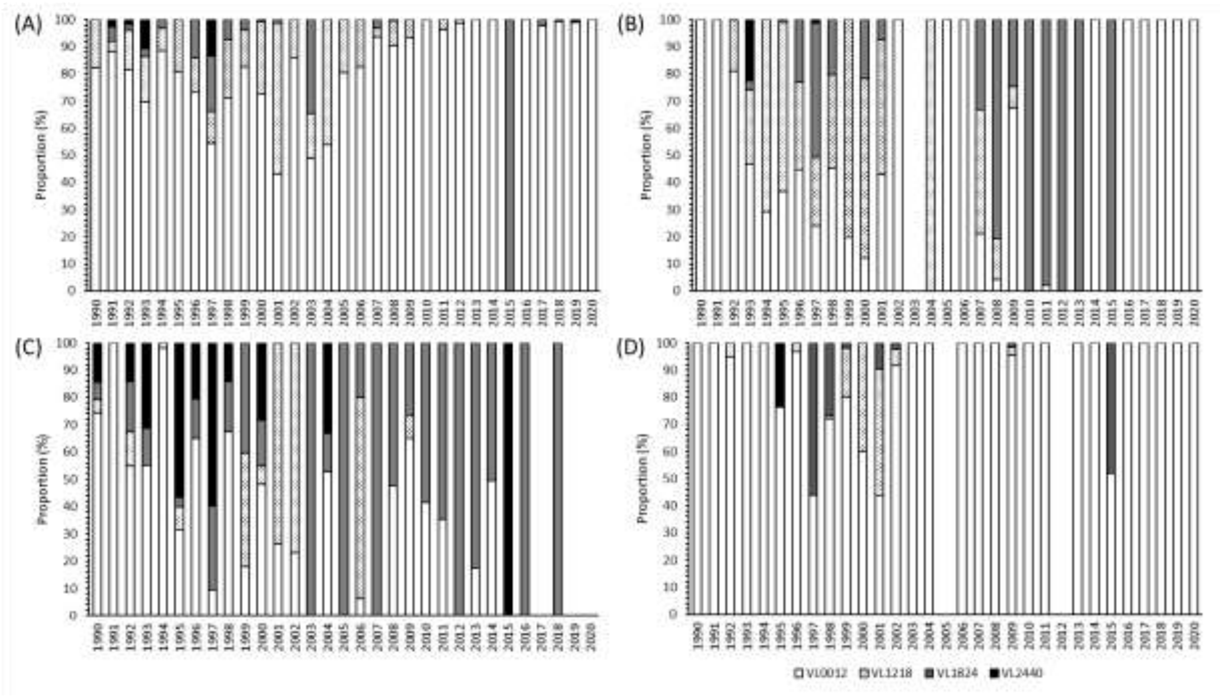

Figure 12. Landings by species and vessel size between 1990 and 2020 for catches performed by mid-water drifting longlines. A) *Galeorhinus galeus*, B) *Raja* spp., C) *Sphyrna zygaena* and D) *Mustelus mustelus*.

Landings of *Raja* spp. were carried out by small vessels from 1990 to 1994 and from 2016 to 2020 (< 12 m) (Figure 12B). From 1995 to 2015 no clear trend was observed. Analysis by vessel size allowed to verify statistically significant differences for landings by vessel over the years (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Catches of *S. zygaena* were conducted by small vessels from 1990 to 1996 (<12 m), while from 2003 onwards were predominantly made by vessels between 12 and 24 m length (Figure 12C). The observed differences were statistically significant (Kruskal-Wallis test followed by Dunn's, $p<0.05$).

Finally, *M. mustelus* landings were predominantly carried out by small vessels (<12 m) for the study period (Figure 12D). Analysis by vessel size did not show statistically significant differences for landings by vessel over the years (Kruskal-Wallis test followed by Dunn's, $p>0.05$).

Discussion

In the North Atlantic, the fisheries management system was not primarily designed with the management or conservation of elasmobranchs in mind (Clarke, 2008). The poor quality of the reported data, the unknown discard rates, species' misidentification, and the lack of knowledge on elasmobranchs' biology and ecology represent the main issues related with the under-assessment of the health status of Chondrichthyes' stocks (Large et al., 2003). More precisely, information on species-specific biological processes, recruitment, stock identity and fish behaviour are still lagging behind (Large et al., 2003), particularly for elasmobranchs whose life history characteristics make them more susceptible to overfishing than most teleost fishes (Bonfil, 1994; Large et al., 2003). Sharks are K-selected species, characterised by slow-growth rates, late attainment of sexual maturity, very low productivity, and high longevity (OSPAR, 2000; Stevens *et al.,* 2000; Denney *et al.,* 2002; Large et al., 2003; ICES 2007; Clark *et al.,* 2010). Furthermore, information on both the impact resulting from the selective removal of predator or prey at an ecosystem level, and on the enhancement of food supply through discards is still very scarce and should be included in fisheries management and conservation plans (Stevens et al., 2000).

The conservation status of the most important commercially exploited elasmobranch species in Madeira archipelago is of concern. From the 13 *taxa* landed over the study period, two are classified as Critically Endangered (*C. granulosus, O. ferox*), two as Endangered (*C. squamosus* and *D. licha*) and two as Vulnerable (*G. galeus* and *M. mustelus*) on the European Red List of Marine Fishes (Nieto et al., 2015).

This study reports the first fisheries landings analysis of elasmobranchs in Madeira archipelago. In this region, elasmobranchs are mainly caught as bycatch species in the mid-water drifting longline fisheries targeting black scabbardfishes. Elasmobranch annual landings showed a dominance of deep-water sharks which account for more than 90% of the total elasmobranch species landed between 1990 and 2020. In Madeira archipelago, the majority of deep-water shark species' bycatch is associated with the black and intermediate scabbard fishery. The harvesting of these species is performed using mid-water drifting longlines and represents approximately 50% of the region's total fisheries (Delgado et al., 2013).

Overall, a pattern of supply and demand was apparent when looking into annual landed tonnage and mean price values, i.e., a significant decrease in landings translated into an increasing market value over time. As expected, this trend is characteristic for species with commercial value (Copes et al., 1970).

Concerning the landed tonnage of deep-water sharks by mid-water drifting longlines, there is a significant period of 10 years (2004 to 2014) marked by landings over 50 t, which is a substantial amount considering the artisanal nature of this fishery in Madeira archipelago for unmanaged elasmobranch species at the time. Nevertheless, it is important to highlight that both deep-water and pelagic species were bycaught in their majority by mid-water drifting longlines. When looking further into species level within this fishery, it was clear that *C. squamosus* was the most representative species over the study period. This fact might be explained by the depth at which the fishing gear is deployed in the scabbardfish fishery, which overlaps with the depth range in which this species is more abundant (800-1300 m depth). In fact, the catch peak for 2008 corresponded to the catch peak for the scabbard fish (3,109 t) and is derived from an increase in fishing effort, namely of the number of fishing vessels and fishing trips (ICES, 2021). In addition, and taking into account the overlap between the depth range of deepwater sharks and scabbardfish, experimental fishing trips are being planned by the Regional Directorate for the Sea (DRM).These will aim to investigate this overlap as a steppingstone to reduce deep-water sharks' bycatch in the scabbard fishery.

Nonetheless, pelagic sharks' landings by mid-water drifting longlines also seemed to have some expression between 1990 and 2004, reaching a catch peak of more than 30 t in 2003, explained by the increasing market demand for blue shark *P. glauca.* Interestingly enough, this species' catch peaks were coincident with data reported by Roxo et al. (2017) for Portugal and are in line with a pattern of offer and demand. Likewise, shark finning was banned by the EU in 2003 (Council Regulation (EC) No 1185/2003 of 26 June 2003), which explains a reduction in *P. glauca* landings in Madeira Archipelago.

From 2015 until present, landed values do not reflect accurately the harvested weight of deep-water shark species. In particular, the observed decrease in total elasmobranch landings in 2015 and 2016 is explained by EU regulations, specifically by the imposition of 0 t established by Council Regulation (EU) 1367/2014 on 15 December 2014. Hence, even if sharks were bycaught over this period, all individuals were mandatorily discarded.

Since 2017, a maximum TAC of 10 t for the exclusive exploitation of deep-sea sharks was established by the Council Regulation (EU) 2016/2285 on 12 December 2016. This regulation only applies to bycatch in the fishery for scabbard fish species using longline in EU waters of CECAF regions 34.1.1, 34.1.2 and 34.2. after on, between 2019 and 2020, the TAC was adjusted to 7 t 471 by the Council Regulation (EU) 2018/2025 on 17 December 2018.

The main purposes of this TAC were 1) to reduce bycatch and 2) to gather robust data on the species' biology and population dynamics. Currently, in 2021, deep-sea sharks' landings are strictly forbidden, and all accidental catches must be discarded. At first sight, this might seem to be a good conservation measure. However, as fishing gears remain unchanged, this legislation still fails to accurately acknowledge the significance of the unintentional capture of elasmobranch species in Madeira archipelago. Additionally, this restriction would benefit from further scientific studies on species' survival rates upon discard, which are presumably scarce, since it is widely agreed upon by fishermen that most individual deep-water sharks do not survive to the hauling of the fishing gear. Changes in pressure are highly likely to guarantee that discarded individuals will not survive (Large et al., 2003). Moreover, studies on the enhancement of food supply through fisheries discards are still missing, even though it is highly likely that this input may alter the dynamics of marine food webs.

The total cumulative volume of elasmobranch *taxa* caught by bottom longliners/pelagic longliners/handliners was dominated by *G. galeus*, other elasmobranchs like *Raja* spp., *S. zygaena* and *M. mustelus* also showed a consistent landings' trend throughout the years, with greater expression until 2002 and again from 2017 onwards. In addition, the landed tonnage and mean market price for *G. galeus* described in this study were similar to the one revealed by Torres et al. (2016) for the Azores, with a catch peak in 1998. This event might be explained by this species dynamic migratory behaviour, with routes coming close to the Atlantic archipelagos in some years, and in other periods moving towards other areas in the Northeast Atlantic. Nonetheless, this hypothesis is poorly investigated as studies on *G. galeus* migratory patterns are still missing, though previous ones have shown that most individuals do not venture beyond a 500 km radius (Thorburn et al., 2019).

In general, and similarly to the offer and demand pattern observed for the drifting longline fishery, an increase in landed weight led to a decrease in species' mean price.

Elasmobranch monthly landings fluctuate throughout the year for both fishing gears considered, although a clear pattern does not seem to exist when looking into data for mid-water drifting longlines. This fishery is mainly operated by vessels bigger than 12 m in length, normally better equipped to deal with all year-round meteorological conditions. However, higher landings for the scabbard fishery were reported mainly for winter and autumn months, most likely due to the coastal pattern of migrations characteristic of these species during spawning season. This ecological trait has been previously studied by Vasconcelos et al. (2020) for the Archipelago of Madeira. On the other hand, regarding bottom longliners/pelagic longliners/handliners, there is marked evidence of higher catches during springtime. This might be explained by better sea conditions between April and June, especially given that this kind of fishery is mostly performed by smaller vessels, with reduced autonomy and poorer basic conditions.

When looking further into species level monthly analysis, the observed pattern for *C. squamosus* follows the same trend as the one reported for the whole bycatch of landings performed by midwater drifting longlines. With regards to *D. licha*, higher landings were registered for the winter months, and for *Centroscymnus* spp. during springtime. However, *C. granulosus* landed tonnage showed no clear pattern as values fluctuate throughout the year. Nonetheless, these observed results might be misleading when attempting to draw conclusions, as overall catch values were relatively low throughout the study period.

Regarding species' monthly values performed by bottom longliners/pelagic longliners/handliners, data revealed more prominent landings for most species during springtime, with the sole exception of *S. zygaena*. This species landing pattern showed that it is predominantly harvested during late summer and early autumn months.

In relation to landings according to vessel size, two different trends became clear for elasmobranchs caught by mid-water drifting longlines. Until 2002, most species were caught by vessels smaller than 12 m in length. From 2003 onwards, a shift became apparent, and elasmobranchs were predominantly harvested by vessels with sizes comprised between 12 and 18 m. During this period, a reduction in total number of vessels was verified. This decrease was most pronounced for vessels under 12 m in length, which is in line with this study's findings (DRP, 2021). In turn, this alteration might be consistent with the increase of subsidies for the decommissioning of fishing vessels funded by the EU.

Concerning bottom longliners/pelagic longliners/handliners data, only 5 years stand out from the entire study period. Overall, landings were mostly performed by smaller vessels (< 12 m), which usually catch more pelagic shark species, especially during the deployment and hauling of the fishing gear.

When looking further into species level, it becomes obvious that *C. squamosus* is the main bycatch species associated with the use of mid-water drifting longlines. The observed overall pattern overlaps with that of the whole bycatch of landings performed by mid-water drifting longlines. However, and given the reduced landed tonnage for *D. licha*, *Centroscymnus* spp. and *C. granulosus* over the study period, no continuous pattern could be reported. Because the scabbard fishery is the oldest deep-sea fishery, dating back to the 17th century, fleets have progressively moved to new fishing grounds further offshore and away from coastal areas as resources have become increasingly scarce. Additionally, fishing boats have also suffered technological improvements and are currently better equipped to withstand rougher seas and longer fishing trips. Hence, new fishing grounds have been increasingly explored. The combination of these factors is likely to have led to a decrease in the bycatch of *D. licha* and *Centroscymnus* spp. as these species might be less abundant in the new fishing grounds, farther away from shore, and to an increase in the landed tonnage of *C. squamosus*. Moreover, species misidentification among deep water sharks could be an explaining factor and should be accounted for.

As far as *G. galeus* and *M. mustelus* are concerned, data showed a predominance of landings performed by vessels with sizes under 12 m in length, which usually catch more pelagic shark species, especially during the deployment and hauling of the fishing gear. About *I. oxyrinchus*, an interesting pattern revealed itself when looking at landed tonnage by vessel size. In the early nineties and from 2014 onwards, landings were mainly performed by smaller vessels (< 12 m). However, and between 1996 and 2014, this species was mostly harvested by vessels with sizes bigger than 12 m in length.

Conservation measures aiming to reduce bycatch post-release mortality would benefit from forthcoming experimental fishing cruises focusing on pairing type and size of hook to infer about species-specific survival rates, as well as fishing gears' soak time.

Additionally, and to accurately gather robust information on mortality rates, a fisheries observer programme for the Archipelago of Madeira ought to be implemented soon.

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Chapter 11

Long-term population status of the commercially exploited shark *Centrophorus squamosus* in an oceanic archipelago

CHAPTER 11 - Long-term population status of the commercially exploited shark *Centrophorus squamosus* in an oceanic archipelago

Abstract

Deep-sea commercial exploited species are very susceptive to overexploitation. *Centrophorus squamosus* a deep-sea shark is the most important species caught as bycatch in the artisanal black scabbard fishery in the archipelago of Madeira, but rarely studied in this region. Currently, knowledge on this species distribution and stock structure is highly deficient, and as such a comparative study considering two time-series (1996-1997 and 2018-2019) was performed to determine biological parameters and to evaluate the fishing pressure on exploited populations over a period of 22 years. Specimens larger than 100 cm were dominant in both time-series. The asymptotic length was estimated between 118.27 and 139.39 cm for males and females respectively. *C. squamosus* is considered a long-living species, presenting a maximum age of 39 years for this region. The spawning season occurs between July and December and sex-ratio of males outnumber females (> 80%). The size at first capture was higher than size at first maturity in the second time-series. The total mortality was higher for males than for females in both time series. Natural and fishing mortality (F) exerts similar pressure on the exploited populations. The pressure of fishing targets mainly males and did not cause crucial changes in the biological parameters of the species over 22 years.

Keywords

Life history, North-eastern Atlantic, *Centrophorus squamosus*, sustainable exploitation, management.

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Introduction

Sharks play a key role in the ecological balance of the ecosystems due to their position in the marine food chains. These marine predators mediate trophic cascades as top or meso predatory species and maintain the ecosystem vitality (Myers et al., 2007). However, these predators do have not evolved in terms of resistance strategies against rapid fluctuations in mortality caused by anthropogenic pressures such as overfishing. Thus, proper conservation strategies based on the knowledge of the biology and ecology of these species are essential to maintain their success in the marine ecosystem (Stevens et al., 2000).

Centrophorus squamosus (Bonnaterre, 1788) (Chondrichthyes: Centrophoridae), the leafscale gulper shark is a deep-sea demersal dogfish of the outer continental shelves and upper slopes at depths between 128 and 2400 m. This species has a wide geographic distribution, including the eastern Atlantic (from Iceland to South Africa), Indian Ocean, western and central Pacific and Australia (Acuña-Marrero et al., 2013; Ebert et al., 2013; Kühlmann, 1986; Last et al., 2009).

Like most deep-water species, *C. squamosus* is extremely susceptible to overexploitation. This is mainly due to its particular k-selected life-history strategy, characterized by slow growth, late attainment of sexual maturity, very low productivity and high longevity (Clarke et al., 2001; Denney et al., 2002; International Council for the Exploration of the Sea et al., 2007; OSPAR Commission, 2000; Stevens et al., 2000). High vulnerability of *C. squamosus* to the fishing pressure led the International Union for Conservation of Nature to classify *C. squamosus* as Endangered in the European IUCN Red List (IUCN, 2003), and therefore even a limited fishing activity can result in a risk to its conservation. According to OSPAR (2020) the current knowledge on deep-water shark species' distribution and stock structure is highly deficient and as such life history and biological information for these species should be updated.

Deep-sea fisheries usually target highly vulnerable species. In Madeira Archipelago, *C. squamosus* is caught as bycatch by the artisanal drifting longline fishery for the black and intermediate scabbardfishes (*Aphanopus carbo* Lowe, 1839 and *Aphanopus intermedius* Parin, 1983), in a depth range between 800 and 1300 m (Delgado et al., 2018). In 2019, it represented around 38% of the total bycatch of these species. Black scabbardfish fishery is one of the oldest worldwide exploitations of deep-sea marine resources dating back to the 19th century (Noronha and Sarmento, 1948). It is also one of the most profitable commercial activities on small scale fisheries in this region, reaching in 2019 annual landings of up to 2292 tonnes, yielding a total first sale value of ca. 7.7 M€ (Regional Fisheries Department of Madeira). These species are part of the gastronomic cultural heritage of the region, appreciated by the local population and tourists, and has a high social and economic importance.

Centrophorus squamosus is commercially exploited as a bycatch of the black scabbard fishery for both human consumption (dried-salted or fresh) and for squalene extraction from its liver.

Landings of leafscale gulper shark in the archipelago of Madeira peaked in 2008 at 282 tons, corresponding to a first sale value of approximately 0.4 M€. Data from 2015 to 2019 are in line with EU restrictive Total Allowable Catch (TAC) (Fig. 1). Since 2017, a maximum TAC of 10 tons, for the exploitation of deep-sea sharks exclusively for bycatch in fisheries for black scabbard fish using longline for Union waters of CECAF 34.1.1, 34.1.2 and 34.2, was established by the Council Regulation (EU) 2016/2285 of 12 December 2016. This has been adjusted to 7 tons, from 2019 to 2020, by the Council Regulation (EU) 2018/2025 of 17 December 2018. For 2021 landings for deep-sea sharks are forbidden and all the accidental catches must be discarded.

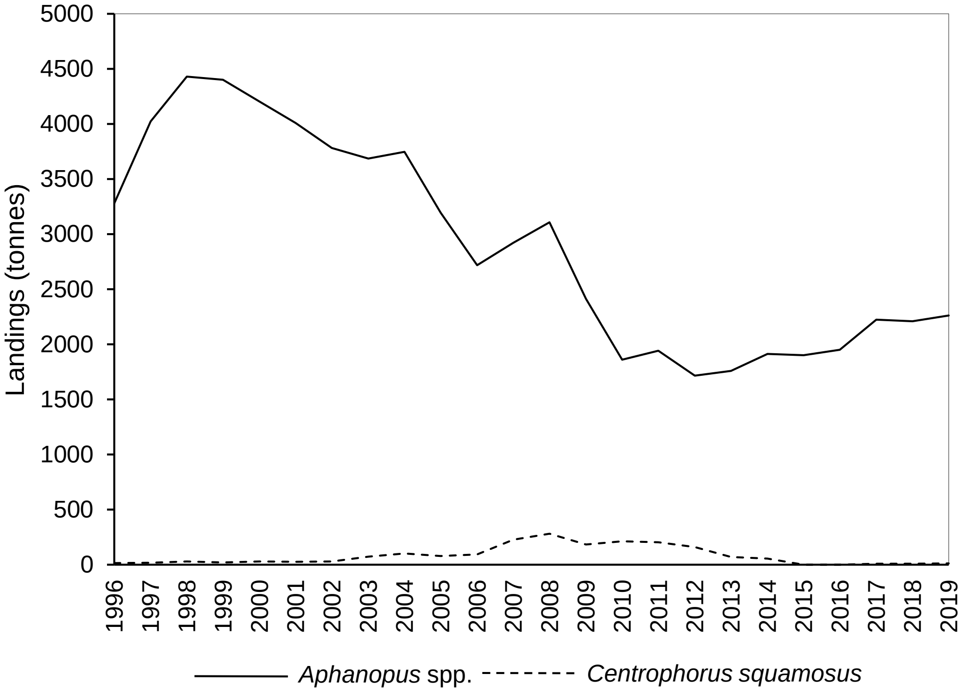

Figure 1. Representation of landings (tonnes) for *Aphanopus* spp. and *Centrophorus squamosus*, from 1996 to 2019, in the archipelago of Madeira.

It is likely that long-term exploitation of leafscale gulper sharks in the archipelago of Madeira, dating back to the early 19th century, have caused changes on its biology and population dynamics, namely in abundance, size structure and life history traits. Despite the absence of scientific evidence, this exploitation may have also promoted imbalances at the community level by the removal of a top predator from the food chain. Thus, conservation and management should follow accurate data on catch/effort and discards, as well as on biological parameters.

The lack of biological information about *C. squamosus* and the evolution of its exploitation status in the Economic Exclusive Zone of the archipelago of Madeira led to this study, which was developed as a first approach to verify the effects of this long-term exploitation on the biology and population dynamics of this important apex shark on the Madeira waters ecosystem. Thus, a comparative study was carried out considering two time series, separated by a period of over 20 years in order to verify whether fishing pressure has caused changes in the biology and population dynamics of this species.

The information obtained from this study is essential to assess the black scabbardfish fishery impact on *C. squamosus* population dynamics in the Northeast Atlantic Ocean.

This will lead to the development of suitable management strategies to preserve this species, specifically the populations under pressure by the Madeiran longline artisanal fishery.

Materials and methods

Data collection

Monthly specimens of *C. squamosus* were collected from the landings of the Madeiran commercial drifting longline fishery for black scabbard-fish, in the north-eastern Atlantic Ocean, Madeira archipelago. Same sampling design was applied in two different time-series: time-series 1 (TS1) between September 1996 and august 1997 and time-series 2 (TS2) from September 2018 and August 2019. All fishes were measured for total length (L) using a beam compass to the nearest centimetre and weighed with an electronic scale (± 0.01 g) for total (W), liver and gonad weight. Primary sex identification was based on the presence/absence of claspers and maturity stages were assigned after dissection by macroscopic inspection of the gonads following the scale described by Stehmann (2002). In males the length, weight, number of testis and the presence or absence of seminal fluid were also recorded. Regarding females, the ovaries length and weight, condition of the uteri, egg diameter and number of ripe eggs were registered. In pregnant females the number of embryos and their total length and weight were recorded.

Data analysis

The data were analysed for deviations to the parametric assumptions of analysis of variance (ANOVA). Normality of the distribution of the sample was verified by the Kolmogorov-Smirnov two-sample test and homogeneity of variance was tested using Levene’s statistics. The existence of differences in mean length between sexes was determined using an ANOVA (Sokal and Rohlf, 2012). All ANOVA’s were performed considering the Brown-Forsythe F test, when the variance of the data was not homogeneous.

For size frequency analysis, specimens were grouped into 5 cm intervals. The differences between size-classes were tested using the Pearson’s chi square test.

Relative growth

The relationship between weight (W) and length (L) was determined adjusting the data to a power relationship as $W = aL^b$ (Bagenal and Tesch, 1978), where W is the total weight of fishes (g), a is the coefficient related to body shape, L is the total length (cm) and b is the relative growth rate). The parameters a and b were calculated by linear regression analysis fitted by the least-squares method over log-transformed data ($log\ W = \log a + b\ log\ L$). The coefficient of determination (r^2) was used as an indicator of the quality of the linear regression. A Student's t-test (King, 1995) was used to test the hypothesis of an isometric relationship (H_0: b = 3; H_1: b $\neq 3$, at the 5% significance level).

Absolut growth and age

Absolut growth was calculated from the modal class progression analysis in the monthly length frequency distributions, applying Bhattacharya method available in the package FISAT II (Fish Stock Assessment Tools FAO-ICLARM), VER 1.2.0 (Gayanilo et al., 2005). The identified size age groups resulted from at least three consecutive points and was based on the separation index values (>2) for the different age groups and the number of individuals per age group (Sparre and Venema, 1997). NORMSEP by Hasselblad & Tomlinson (1971) was applied to decompose the mixtures of normal distributions based on Hasselblad's maximum likelihood method (Hasselblad, 1966).

The von Bertalanffy growth parameters were estimated using ELEFAN I routine available in FISAT II (Gayanilo et al., 1997) by means of the Gulland and Holt method (Gulland and Holt, 1959) for non-linear parameter estimation according the equation $Lt = L_\infty \{1 - exp\ [-k(t - t_0)]\}$ (Gulland and Holt, 1959), where L_t is the mean total length at age t (mm), L_∞ is the asymptotic length (cm), K is the growth coefficient (year^{-1}), t is the age (years), and t_0 is the hypothetical age determined applying the equation: $log_{10}- t_0 = -0.3922 - 0.2752 \times log10\ L_\infty - 1.038\ log_{10}\ K$.

The growth performance index (ϕ') was used for the comparison of the estimated growth parameters L_∞ and K through the application of the equation $\phi' = log_{10}(K) + 2\ log_{10}(L_\infty)$ (Pauly and Munro, 1984).

The age at length was determined according to the inverse von Bertalanffy growth equation ($t = t_0 \, (1/k) \ln (1 - L_t/L_\infty)$) (King, 1995) and the potential longevity ($A_{0.95}$) was estimated from $A_{0.95} = t_0 + 2.996/K$ (Taylor, 1958).

Reproduction

The sex ratio (males: females) was calculated and tested for the existence of differences in the proportion of sexes in the studied population using a Chi-square test (Zar, 1996) and between months using Pearson's Chi-square, considering a significance level of 0.05 under the null hypothesis a 1:1 sex ratio. The proportion of immatures and matures was determined considering specimens in A and B maturity stages as immatures and as mature in the remaining stages (Stehmann, 2002). The differences in the proportion of immatures and matures specimens by size classes within and between time-series was tested using the Pearson's chi-square test.

The gonadosomatic index (GSI) was determined according to the equation: GSI = (Gonad weight/Total body weight) × 100 and the hepatosomatic index (HSI) using the formula (Liver weight/Total body weight) × 100. Differences in the mean GSI and HSI values between sexes and among months were assessed using an analysis of variance (ANOVA) considering a significance level of 0.05. The differences between time-180 series were tested using ANOVA.

Maturation ogives for females and males were fitted to the proportion using the logistic model (King, 1995). Size at sexual maturity (Lm_{50}) corresponds to the size at which 50% of all specimens in a stock are mature and was determined from the relationship between the proportion of mature individuals and length, according to the logistic equation: $P = 1/(1 + exp^{-(a+bL)})$ (Sparre and Venema, 1997), where P is the balanced probability, a and b are the equation parameters. The mean size at maturity was defined as the size at which 50% of the population is mature, when P = 0.5, then $Lm_{50}=(-a)/b$ (King, 1995).

The existence of differences in size-at-maturity between sexes and time-series was identified by comparing the slopes of maturity curves using an analysis of covariance (ANCOVA).

Mortality, exploitation rate and probability of capture

Total mortality (Z) was calculated applying the length-converted catch curve method. Natural mortality (M) was estimated based on the assumption that M is the level of natural mortality required to reduce the recruited population to 1 % of its initial value: $M = -ln(0.01)/Maximum\ age$ and by Paulynls-T estimator $M = 4.118K^{0.73} \times L_{\infty}^{-0.33}$. Fishing mortality ($F$) was calculated as the difference between Z and M, and the exploitation rate (E) was determined applying the equation: $E = F/Z$ (Gulland, 1971).

The probability of capture was determined by applying the logistic transformation of the probabilities obtained from the lower-sized, using the left hand-side of the length-converted catch curve, by plotting the cumulative probability of capture against middle length of class intervals.

The length at first capture (Lc_{50}), that corresponds to the cumulative probability of 50%, was assessed from the resultant curve according to Sparre & Venema (1997): $SL = 1/[1 + \exp(S1 - S2 \times L)]$, where SL is the logistic curve, $S1$ and $S2$ are constants in the formula for length-based logistic curve and L is the length.

The existence of differences in size at first capture between sexes and time-series was identified by comparing the slopes of capture curves using ANCOVA.

Results

A total of 894 specimens were sampled including 131 females and 763 males. The size-frequency showed that the sampled specimens had a normal distribution for both time-series ($Z=0.311$, $p<0.05$; $Z=0.333$, $p<0.05$). However, size did not exhibit homogenous variance for TS1($W=0.719$; $p=0.397$). In regard to weight the sampled specimens were normally distributed ($Z=0.096$, $p<0.05$; $Z=0.210$, $p<0.05$) and not homogeneous for both time-series ($W=9.758$, $p<0.05$; $W=208.501$; $p<0.05$).

In TS1, the size of specimens varied from 88.00 to 132.00 cm ($\bar{x} = 106.55 \pm 12.29$ cm) in females and from 80.90 to 115.80 cm ($\bar{x} = 103.83 \pm 6.70$ cm) in males. Concerning TS2, the size varied from 90.00 to 136.20 cm ($\bar{x} = 118.75 \pm 9.58$ cm) in females wile males ranged between 74.80 and 122.30 cm ($\bar{x} = 108.60 \pm 5.26$ cm) (Fig. 2).

The observed differences in mean length (F=0.001; p=0.095) and mean weight (F=5.050; p=0.270) between groups, in TS1, were not statistically significant. Regarding TS2 the differences between females and males were statistically significant for mean length (F=5.050; p<0.05) and mean weight (F=202.112, p<0.05). The mean size between TS1 and TS2 were statistically significant for females (F=26.384, p<0.05) and males (F=134.227, p<0.05).

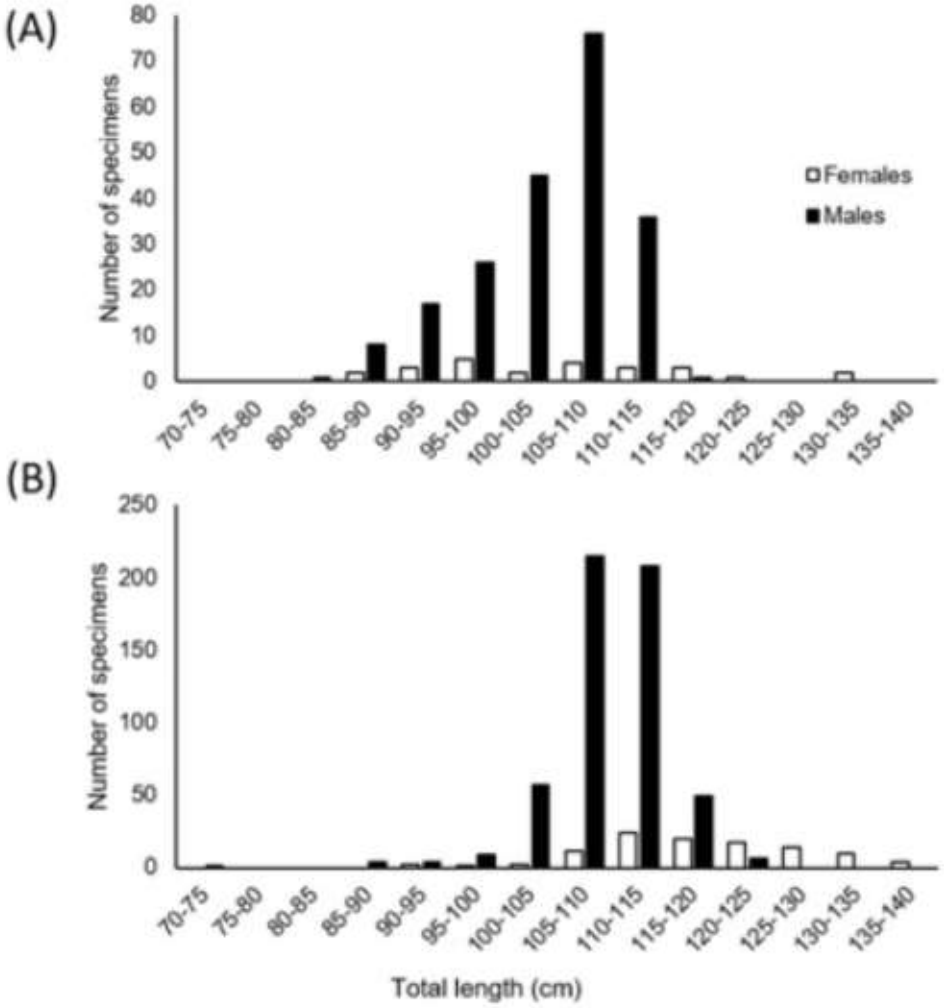

Figure 2 - Size composition of *Centrophorus squamosus* off the archipelago da Madeira, for females and males. A – TS1 (1997-1997), B – TS2 (2018-2019).

The size distribution of specimens in both time-series showed that larger sizes (> 100 cm) were dominant with 74% in TS1 and 85% in TS2. The frequency of the specimens by size class was statistically significant within TS1 (χ_2=50.100, p<0.05) and TS2 (χ_2=183.165, p<0.05). Differences in size-classes between the time-series were significant (χ_2=217.442, p<0.05).

Relative growth

The relation between total length and total weight showed a similar pattern for males in both time series. Concerning females, differences between time-series were observed (Table 1). The *b* coefficient returned values inferior to 3 for males and superior for females in TS2. The differences were highly significant ($p<0.05$) indicating negative allometric pattern for males and positive allometric for females in TS2.

Table 1. Parameters of the relationship between total length and total weight for females (F) and males (M) of *Centrophorus squamosus* caught in the archipelago of Madeira (n - sample size; a and b = parameters of equation $W=aL^b$; r^2 - coefficient of determination and t – test t).

	Sex	n	a	b	SE (b)	r^2	TL range (cm)	TW range (g)	t
TS1	F	25	0.0757	3.14	0.164	0.94	88.00-132.00	3500-13900	0.87
	M	210	0.0239	2.57	0.010	0.76	80.90-115.80	2800-8100	4.30
TS2	F	106	0.0171	3.87	0.197	0.85	90.00-136.20	3757-18721	4.41
	M	553	0.4201	2.30	0.119	0.75	74.80-122.30	1946-8592	5.88

Absolut growth and age

The estimated von Bertalanffy growth parameters are presented in Table 2. The L_∞ varied between 125.38 and 139.39 cm for females whereas for males L_∞ ranged from 118.27 to 135.18 cm. The growth coefficient was slightly higher for both females (K = 0.082 $year^{-1}$) and males (K = 0.093 $year^{-1}$) in TS1, in comparison to TS2. The growth performance index ranged from 3.12 for males and 3.18 for females in TS1.

Table 2. Von Bertalanffy growth parameters estimated for *Centrophorus squamosus* caught in the archipelago of Madeira between 1996 and 2019 (L_{∞} - asymptotic length, K – growth coefficient), growth performance index (ϕ'), t_0 is the "age" the fish would have had length zero, $A_{0.95}$ the potential longevity, M – males and F – females).

	Sex	L_{∞} (cm)	K (year^{-1})	ϕ'	t_0	$A_{0.95}$
TS1	F	135.16	0.082	3.18	-1.31	35.28
	M	118.27	0.095	3.12	-1.17	30.37
TS2	F	139.39	0.074	3.16	-1.43	39.05
	M	125.38	0.093	3.16	-1.16	30.98

Centrophorus squamosus showed a predominance of individuals in the higher age classes, with more than 90% of all specimens from the studied population being >15 years, except for the females from TS1, with approximately 70% with >15 years. The most representative age classes were 20-25 years, representing 36% to 48% of the studied specimens and the age classes 15-20 years, representing 32% for the females from TS1.

Potential longevity was determined to vary between 30.37 (males – TS1) and 39.05 years (females – TS2). Females presented a higher potential longevity than males in both time-series. Moreover, it is possible to verify an increase of this parameter between time-series for both females (from 35.28 to 39.05) and males (from 30.37 to 30.98).

Reproduction

The overall ratio between females and males favoured the males in both time series. 11% of specimens were females and 89% were males in TS1, whereas in TS2 16% of the total individuals were females and 84% males. The observed differences in the sex proportion were significant for both time-series (χ_2=145.638, $p<0.05$; χ_2=346.501, $p<0.05$). The monthly analysis of the sex-ratio showed that males were predominant all year round in both time-series (χ_2=21.103, $p<0.05$; χ_2=25.656, $p<0.05$).

The proportion of immatures was smaller than matures in both time-series. In TS1 of the total of sampled specimens 10.60% were immature and 89.40% were matures. The same pattern was observed in TS2 with 14.60% of specimens being immatures and 85.40% matures. The differences in the proportions by size class, within each time-series were statistically significant for TS1 (χ_2=30.745, $p<0.05$) and TS2 (χ_2=188.181, $p<0.05$). The comparison in the proportion by size-class between time-series was not statistically significant for immatures (χ_2=116.912, p=0.106) neither for matures (χ_2=143.498, p=0.080).

Centrophorus squamosus specimens had relatively large livers representing approximately 19% of total body weight in females and 21% in males. The HSI values (Fig. 3) differ significantly between sexes for both time-series (F=73.177, $p<0.05$; F=18.04, $p<0.05$). The average HSI of females increases from March to June/July corresponding to an increase of 3% in TS1 and 4% in TS2. The highest HSI values for females occurred in August, with 19.94%, in TS1 and in July, with 21.43%, in TS2. However, the observed differences were not statistically significant neither for TS1 (F=0.880, p=0.565) nor for TS2 (F=1.158, p=0.340).

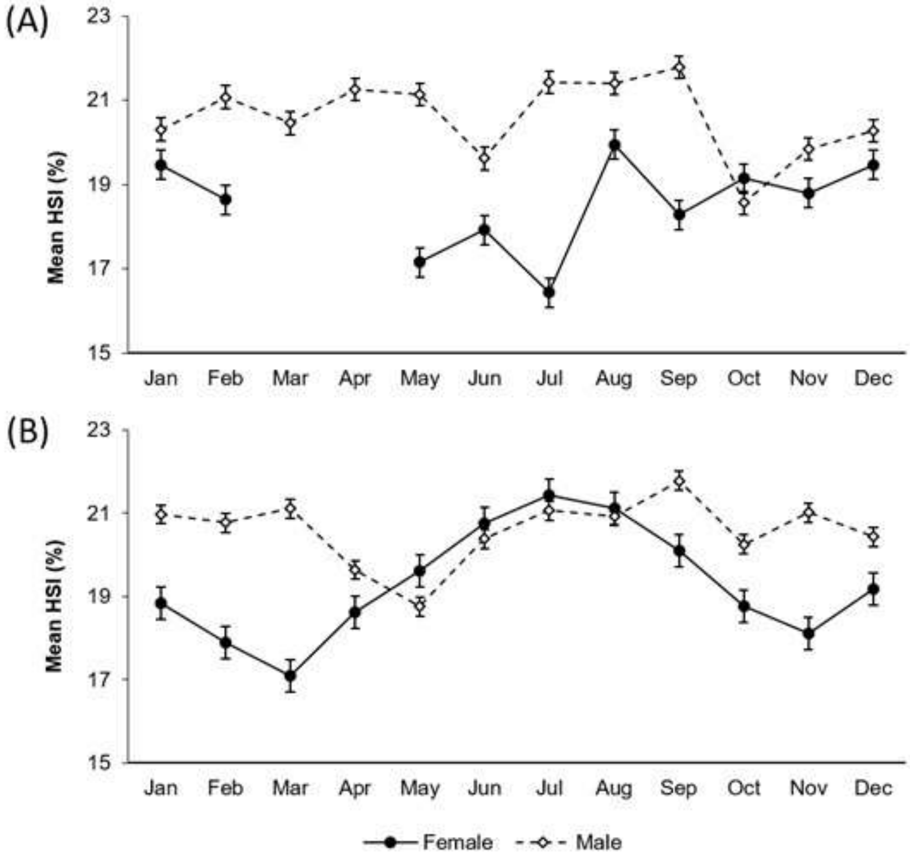

Figure 3 - Hepatosomatic index of *Centrophorus squamosus* caught off the archipelago da Madeira, for females and males. (A) – TS1 (1996-1997), (B) – TS2 (2018-2019).

Concerning males, HSI ranged from 18.55 to 21.78% in TS1 and from 19.64 to 21.78% in TS2. The observed differences were statistically significant in both time-series (F=2.215, p<0.05; F=2.511, p<0.05). Differences in HSI between time-series was not statistically significant for both females (χ_2=79.370, p=0.988) and males (χ_2=143.466, p=0.08).

Regarding the relation between gonads and total weight, GSI values 280 (Fig. 4) showed significant differences between females and males in both time-series (F=19.982, p<0.05; F=18.520, p<0.05). Monthly evolution of GSI revealed a similar trend for females and males in both time series. An increase in the GSI values from 0.11 to 0.39% (May to September) and from 0.35 to 0.54% (March to July/August) was observed for females and males respectively in TS1.

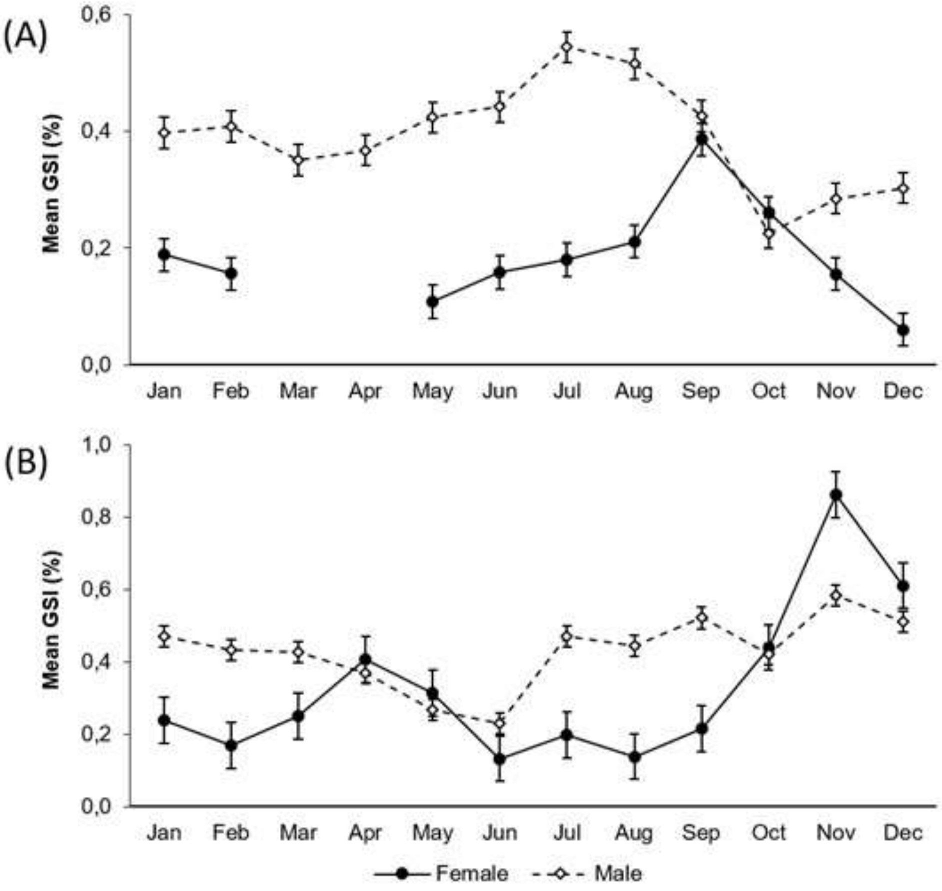

Figure 4 - Gonadosomatic index of *Centrophorus squamosus* caught off the archipelago da Madeira for females and males. (A) – TS1 (1996-1997), (B) – TS2 (2018-2019).

Regarding TS2, GSI increased from June to November for both females (0.13- 0.86%) and males (0.23-0.58%). The highest GSI values for females occurred in September (0.39%) and November (0.86%) for TS1 and TS2, respectively. Concerning males, the highest values were found in July/August (0.54%) and November (0.58%). The GSI values showed significant differences between months within females (F=1.522, $p<0.05$; F=2.289, $p<0.05$) and males (F=3.641, $p<0.05$; F=2.691, $p<0.05$) in both time-series.

Differences in GSI between TS1 and TS2 was not statistically significant for females (χ_2=64.421, p=0.898) but showed to be significant for males (χ_2=214.453, $p<0.05$).

Immature and mature specimens were present all year round in both time-series. A predominance of females and males in stages A, B and C was observed in all months. Females differentiating and expecting (stages E and F, respectively) were only found from October to December and the embryos total length varied from 10.70 to 35.80 cm ($\bar{x}$ = 19.85±11.65 cm). The number of embryos ranged from 3 to 9 per female ($\bar{x}$ = 5.67±3.06 cm). All pups had external yolk sac. The mean size at sexual maturity was higher for females in both time series (Table 3) in comparison with males. Lm_{50} ranged from 99.13 in males to 105.83 in females in TS1 and from 95.38 (males) to 109.94 (females) in TS2, corresponding to 14.09 and 19.43 years respectively.

Table 3. Mortality (Z – total mortality, M – natural mortality, F – fishing mortality), exploitation rate (E), Lm_{50} – length at first maturity and length (Lc_{50}) and age (A_{50}) at first capture estimated for *Centrophorus squamosus* caught in the archipelago of Madeira between 1996-1997 (TS1) and 2018-2019 (TS2) for females (F) and males (M).

	Sex	Z (year)	M (year)*	M (year)**	F (year)	E	Lm_{50} (cm)	Lc_{50} (cm)	A_{50} (year)
TS1	F	0.18	0.13	0.09	0.09	0.50	105.83	96.13	15.15
	M	0.24	0.15	0.10	0.14	0.57	99.13	97.22	18.17
TS2	F	0.09	0.12	0.08	0.01	0.11	109.94	113.54	22.77
	M	0.37	0.15	0.10	0.27	0.73	95.38	102.18	18.02

Estimated according to *Rago *et al.*, 1998) and to **Paulynls-T estimator.

The observed differences in Lm_{50} between females and males were not statistically significant in TS1 (F=2.413, p=0.135) neither in TS2 (F=0.853, p=0.435).

Lm_{50} was higher for females in TS2 and for males in TS1. The observed differences in Lm_{50} between females and males were not statistically significant for TS1 (F=2.413; p=0.135) and TS2 (F=0.082, p=0.778).

Regarding the comparison between time-series, differences were not statistically significant for both females (F=0.138, p=0.714) and males (F=0.126, p=0.726).

Relative growth

Total mortality (Z), natural mortality (M) and fishing mortality (F) presented a similar pattern for both females and males in the two time-series (Table 3). Similar values were obtained in the estimation of M by the two considered methods. However, the best fitted model was Paulynls-T estimator. M was estimated at 0.08 and 0.09 per year for females for TS2 and TS1 respectively, and at 0.10 for males in both time-series. For the estimation of Z and E, were considered the values from the M best fitted model (Paulynls-T estimator). F was similar to M in TS1 with ranging from 0.09 to 0.14 per year and higher for males in TS2 with 0.27 per year. The highest Z was estimated for males in TS2 (Z=0.37).

The lowest exploitation rate (E) was observed for females, in both time series with 0.11 (TS2) and with 0.50 (TS1).

The probability of capture returned an estimate of the length at first capture (Lc_{50}) higher in TS2 for both females and males. The observed differences in Lc_{50} were statistically significant for females (F=5.466; $p<0.05$) whereas for males were not significant (F=0.731, p=0.495).

The Lc_{50} was estimated as 96.13 for females and 97.22 cm for males and corresponded to 15.15 and 18.17 years of age respectively, in TS1. Concerning TS2, the Lc_{50} was calculated as 113.54 for females (A_{50}=22.77 years) and 102.18 cm for males (A_{50}=18.02 years).

Differences in Lc_{50} between females and males were not statistically significant for TS1 (F=2.413; p=0.135) and TS2 (F=0.853, p=0.435).

Discussion

In Madeira archipelago exploited deep-sea fish stocks are dominated by the black and intermediate scabbard fishes (*A. carbo* and *A. intermedius*). This fishery represents approximately 50% of total fisheries in the region (Delgado et al., 2013). *C. squamosus* is the most important species from the bycatch of this fishery, representing around 0.4% of the total catches of black scabbard fish in 2020 (Regional Fisheries Department of Madeira).

The knowledge of the biology of commercial deep-sea species is pivotal to develop integrative management actions aiming a sustainable exploitation, mainly in susceptible species as *C. squamosus* because of their slow growth and late maturity.

The size distribution of the studied specimens is in accordance with those reported for *C. squamosus* in West of Britain (Girard and Du Buit, 1999), Ireland and Scotland (Clarke et al., 2001), Galicia (Bañón et al., 2006), Portugal mainland (Figueiredo et al., 2008), New Zealand (Parker and Francis, 2012) and Madeira archipelago (Severino et al., 2009). The majority of the sampled specimens were comprised in a size ranged from 100 to 115 cm.

The overall results of this study indicate that frequency distribution by size class and mean length of the specimens differed between time series, however a similar length range was observed. Catches are composed mostly by males with a small fraction of females in both time series. This is in line with that described by Clarke et al. (2001) who stated that males outnumbered females at shallower depths (<1300 m). Since black scabbardfish fishery is carried out at depths between 800 and 1300 m, females' bycatch is less likely to occur.

Males were always higher in number than females until 115-120 cm. This trend changes in the 120-125 cm class and from 125 cm onwards only females occurred. This translates into the existence of a sexual dimorphism, with females having a total length greater than males. Sexual dimorphism is commonly reported for most deep-sea sharks of Squalidae family, where mature males are smaller than mature females (Aranha et al., 2009; Clarke et al., 2002; Jakobsdóttir, 2001; Sion et al., 2003; Yano and Tanaka, 1983). This pattern was also verified for *Deania profundorum* (Smith & Radcliffe, 1912) in the same region of the present study (Sousa et al., 2009).

The highly significant correlation between length and weight showed an opposite trend in the relative growth of the studied groups. Females reach larger sizes (total length) and are heavier (total weight) than males of a similar length. Males presented a negative allometric growth trend, whereas females have a positive and isometric allometric growth trend, resulting in a differential growth. This implies a disproportionate increase in total weight, in relation to the increase in length for females. Kohler et al. (1995) reported that there are several factors that can influence the weight of sharks of the same size, mainly stomach contents, the state of maturity and biological condition of the shark. Thus, males possibly allocate more energy to growth than to reproduction. The opposite seems to be true for females.

The comparison between time series showed no differences in the growth pattern of males, the main group caught as bycatch in the black scabbardfish fishery even after more than twenty years.

There is a pattern of higher asymptotic growth for females than for males, in both time series (approximately 12 and 10% respectively), being consistent with the length of the largest sampled specimens. However, when comparing groups between time-series it is possible to verify a similarity in the values for females and for males. Analogous biological parameters were estimated for this species in Ireland and Scotland (Clarke et al., 2001).

In Madeira archipelago *C. squamosus* is considered a long-living species, presenting a maximum age of 39 years. Similar longevity (43 years) was estimated by Parker & Francis (2012) for specimens caught in New Zealand, however Clarke *et al.* (2002) reported a much higher maximum age at 70 years for specimens caught in Ireland and Scotland.

Distinct sex ratio was observed in both time-series favouring the males. The same pattern was reported for specimens caught off Galicia (Bañón et al., 2006) and for Ireland and Scotland (Clarke et al., 2001). However, an opposite pattern was verified for the British Isles area where females were more numerous (Girard and Du Buit, 1999), probably related to differences in fishing depths.

Segregation by sex and state of maturity is described in several studies with sharks of the squalid family, in which pregnant or mature females occur in different depth strata than the rest of the population (Yano & Tanaka, 1988; Yano, 1991; Yano, 1995). In the northeastern Atlantic vertical segregation according to sex and state of maturity was reported for the genus *Centrophorus* (Muñoz-Chápuli and Ramos, 1984), *Deania* (Sousa et al., 2009) and *Etmopterus* (Aranha et al., 2009). Regarding maturity, there was a similar trend in both time series, with only 10 to 15% of the individuals being immature and the absence of juveniles with less than 70 cm. Thus, black scabbardfish fishery depth range seems not to match with any nursery grounds. Probably juveniles occupy different areas from the rest of the population (Yano and Tanaka, 1988). This hypothesis his corroborated by the fact that specimens of *Etmopterus pusillus* (Lowe, 1839) with sizes inferior than 40 cm are simultaneously caught by the same gear in the Madeiran black scabbard fishery (Severino et al., 2009). Thus, the selectivity of the hooks is not a major factor in the absence of *C. squamosus* juveniles in the catches.

The presence of mature females and males was verified throughout the year. However, the breeding season appears to occur between July and December. The appearance of differentiating females (stage E) and expecting (stage F) only in November corroborates this hypothesis. Post natal females (stage G) were only caught at the end of November and beginning December.

Females with embryos in the terminal state of development were sporadically sampled in the course of this study. Earlier studies on elasmobranchs indicate that low fishing mortality on mature females may favor the population growth rate (Simpfendorfer, 1999). According to Yano & Tanaka (1988) the expecting females of *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864 and *Centroscymnus owstonii* Garman, 1906 do not feed and migrate to other areas. This may justify the decrease in HSI during reproductive season, suggesting that females invest their energy in embryonic development.

HSI tends to be higher for males than for females, except during breeding season. Since squalene confers buoyancy, greater HSI results in greater buoyancy, explaining the fact that males are found in shallower regions than females.

As males mature, an increase in GSI occurs. As demonstrated by Clarke *et al.* (2001) also in the present study the presence of maturing individuals (stage B) was verified between March and June. A relationship between HSI and GSI was more pronounced for females in TS2. It was observed that as vitellogenesis increases, an increase in GSI and a decrease in HSI occurs. Yano (1995) also reported that *Centroscyllium fabricii* (Reinhardt, 1825) maintains a balance between buoyancy of liver and gonads.

Size at 50% maturity was grater in females, comparing with males. This trend was observed for both time series and could be explained by the need for females to attain a larger size to support pups and to a lesser investment in growth in favor of reproduction, which would translate into the delayed onset of sexual maturity in females. The same pattern was observed for specimens caught in Galicia (Bañón et al., 2006), Ireland and Scotland (Clarke et al., 2001), British Isles (Girard and Du Buit, 1999) and New Zealand (Parker and Francis, 2012).

In terms of size at first maturation, although there is a similar trend between females and males in both time series (with females presenting a size at first maturation higher than males), it was found that in TS2 the size at first capture is greater than the size at first maturation for both sexes, suggesting that the bulk of capture occurs after sexual maturity for both sexes This seems to ensure reproduction of the species, implying that at least 50% of the total population reproduces before being captured, contributing to the population's fitness.

The total mortality was higher for males in both time-series. Natural and fishing mortality exerts similar pressure on the exploited populations. However, males seem to be more susceptive to be caught by the drifting long line, once fishing mortality was higher for this group mainly in TS2.

Results for fishing mortality in TS2 must be carefully analyzed, once the estimation of the mortality was limited by the TAC of 7 tons, imposed for deep-sea sharks in this region (Council Regulation (EU) 2018/2025 of 17 December 2018). The small occurrence of females with embryos in the terminal state of development leads us to believe that the fishing pressure in Madeira archipelago on this species does not significantly affect pregnant females neither immature individuals. This might be because females seem to occupy other areas or depths which are different from the fishing areas or depths operated by the black scabbard gear.

This observation drives us to the conclusion that fishing pressure in Madeira archipelago is attenuated for these groups (gravid females and immatures) (Clarke et al., 2002;

Hasselblad and Tomlinson, 1971; Kohler et al., 1995; Parker and Francis, 2012; Sparre and Venema, 1997; Stehmann, 2002; Yano, 1995; Yano and Tanaka, 1988).

Conclusions

The *C. squamosus* bycatch resulting from artisanal scabbard fishing in Madeira target mainly on adult males, constituting low pressure on differentiating and expecting females. The comparative study between time series showed that over 22 years the pressure of fishing did not cause crucial changes in the biological parameters of the species. In the near future a study including different fishing depth range (500 to 2000 m) must be carried out in order to confirm the hypothesis of vertical segregation in the archipelago of Madeira and to allocate the different groups (juveniles and gravid females) to the corresponding depth strata.

The application of a 7 tones TAC does not contribute efficiently for the *C. squamosus* sustainable exploitation. Since no modifications have been made to the black scabbard fishing gear, similar amounts of sharks are caught. *C. squamosus* specimens which are caught above the TAC are not landed. According to fishermen, sharks reach the surface already dead, ended up discarded without being accounted by the local authorities. However, to accurate estimation regarding mortality rates of these specimens during the fishing gear hauling, an onboard observer program should be implemented.

In the current scenario, with the application of the TAC (0 tons), specimens are not landed, making it impossible to quantify the catches and to estimate biological parameters, which hinds the scientific knowledge on the species.

The existence of landings is of paramount importance to allow the collection of data and to complement the ongoing scientific studies of the species.

Although fishing in Madeira archipelago does not seem to influence the sustainability of the exploited populations, international stock management is necessary. As this species is considered by several authors to be highly migratory, it is caught in other regions, in several depth strata, by different fishing gear influencing other populational groups, including juveniles and gravid females.

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Chapter 12

Length-weight relationships for eight Chondrichthyes from the north-eastern Atlantic Ocean

CHAPTER 12 - Length-weight relationships for eight Chondrichthyes from the north-eastern Atlantic Ocean

Abstract

Length-weight relationships (LWRs) are pivotal for comparative life-history studies, conservation strategies and ecosystem modelling among regions. They provide essential information on the growth, fitness and wellbeing of a population in an ecosystem. Length and weight relationships and descriptive statistics for eight Chondrichthyes, caught off the Madeira archipelago between 2004 and 2019 from depths ranging from 350 to 2500 m, are herein reported. A total of 767 specimens was studied and it was observed that the parameter b (relative growth rate) oscillated between 2.558 for males of *Centrophorus squamosus* and 3.494 for females of *Etmopterus princeps*. This study is the first to include the LWRs for these 8 Chondrichthyes species in Madeira waters.

Keywords

Chondrichthyes, growth, weight-length relationships, Madeira archipelago

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Introduction

Knowledge on recruitment, mortality and growth rates of fish resources are essential to a proper management plan for the conservation of exploited species in a given ecosystem (Froese & Binohlan, 2003).

Length-weight relationships (LWRs) allow the determination of the average weight at a given length in a particular region (Ferreira, Sousa, Delgado, Carvalho, & Chada, 2008). Therefore, LWRs are considered an important tool with wide application in fishery sciences. These relationships might vary between habitats and geographic areas. The accurate determination of local parameters is pivotal for the elaboration of comparative studies provided a standardized sampling procedure is employed by all investigators (Vaz-dosSantos & Gris, 2016). The LWRs are commonly used for comparison of life-history studies, population dynamics, biomass estimation, ecosystem modelling, stock assessment and to implement conservation strategies among regions (Erzini, 1994; Jisr, Younes, Sukhn, & El-Dakdouki, 2018; King, 1995; Lteif et al., 2016; Santos, Gaspar, Vasconcelos, & Monteiro, 2002). Furthermore, LWRs are also used to quantify the physical wellbeing of a population through the application of the condition factor (Bagenal & Tesch, 1978; Rochet, 2000).

Chondrichthyan species, especially sharks and rays are highly vulnerable to overexploitation either as a target or as bycatch species due to their intrinsic biological and ecological features. These apex predators are pivotal to preserve the balance of the ecosystems. However, they have not evolved in terms of strategies to resist rapid fluctuations in mortality (Stevens, Bonfil, Dulvy, & Walker, 2000). Thus, proper conservation strategies based on the knowledge of the biological parameters of the studied species are central to their success.

In Madeira archipelago, only few Chondrichthyan species were studied in terms of LWRs. These include *Galeus melastomus, Mustelus mustelus* and *Deania profundorum* (Ferreira et al., 2008; Sousa, Ferreira, Chada, Delgado, & Carvalho, 2009). This study aims to increase the information on the LWRs and condition factor of eight chondrichthyan species caught in this area of the north-eastern Atlantic Ocean. To the best knowledge, this is the first report from the populations of these species in Madeira archipelago. It will therefore contribute to complement data provided from Azorean archipelago (Morato et al., 2001; Rosa, Menezes, Melo, & Pinho, 2006) and the mainland

Portuguese coast (Borges, Olim, & Erzini, 2003; Gonçalves et al., 1997; Mendes, Fonseca, & Campos, 2004; Santos et al., 2002).

For most of the species under study, accurate information regarding systematics and taxonomy is available (Biscoito, Ribeiro, & Freitas, 2018), but a biological information gap still exists. As such the LWRs herein presented stand as a pioneer towards the increase of the knowledge in these elasmobranchs.

Materials and methods

Data collection

The specimens used in this study were collected in the northeastern Atlantic Ocean, around Madeira archipelago (Exclusive Economic Zone). Fish were obtained from research surveys and commercial fishery, collected at depths ranging from 350 to 2500 m, between 2004 and 2019.

All fishes were measured for total length (TL) using a beam compass to the nearest cm, and weighed with a digital balance to the nearest gram for total weight (TW). The presence or absence of claspers allowed the primary sex identification. Maturity stages were assigned after dissection by macroscopic inspection of the gonads following the scale proposed by Stehmann (2002)). Species identification was done following Compagno, Dando, & Fowler (2005), Ebert & Stehmann (2013), Kühlmann (1986). Whitehead, Bauchot, Hureau, Nielsen, & Tortonese (1986) and checked with FishBase (Froese & Pauly, 2021).

Most of the specimens measured are deposited in the Funchal Natural History Museum (MMF).

Data analysis

The LWRs were determined applying the equation W ¼ aL^b (Bagenal & Tesch, 1978), where W is the total weight (g), L is the length (cm), a is the condition factor and b is the relative growth rate. Parameters a and b were calculated by linear model fitted by the least-squares method over log-transformed data ($\log W = \log a + b\log L$), subsequently, the use of log–log plots to detect and exclude outliers (Froese, 2006), where b is the slope and log a is the intercept of the relationship (Bagenal & Tesch, 1978).

The coefficient of determination (r^2) was applied to evaluate the correlation between L and W (King, 1995) and a Student's t-test was used to test the existence of an isometric relationship (H_0: $b = 3$; H_1: $b \neq 3$, at the 5% significance level). The statistical analyses were assessed through SPSS v.24.0 (IBM Corp, 2016), considering a statistical significance when $P < 0.05$.

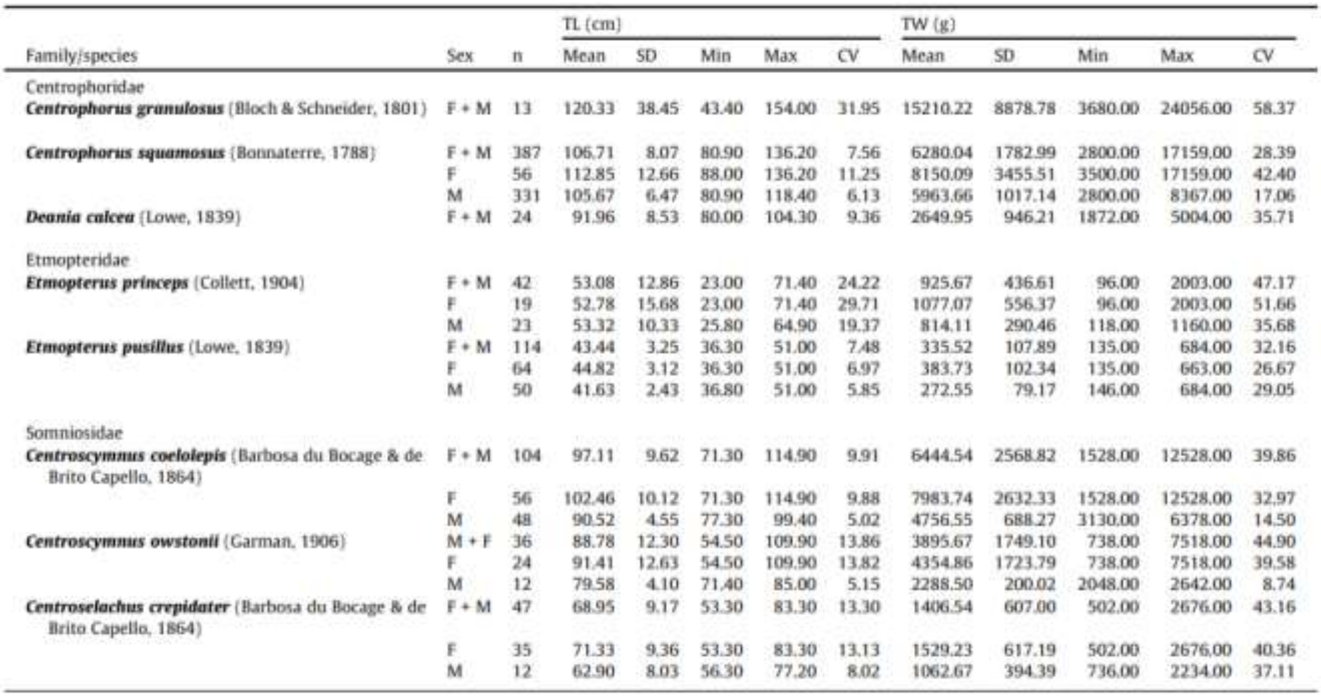
Results

A total of 767 elasmobranch specimens was studied in the present work. The LWRs and related statistics for eight of the studied species are presented in Tables 1 and 2. In almost all species, males were smaller than females in terms of length and weight, except for *Etmopterus princeps* that showed larger and heavier males. The relative growth rate varied between 2.558 (*Centrophorus squamosus* - males) and 3.494 (*E. princeps* - females).

The growth pattern was similar between males and females for *E. princeps* and *Centroselachus crepidater*. Concerning the other species, differential growth between males and females was observed.

Table 1 - Descriptive statistics for eight chondrichthyan species in the north-eastern Atlantic Ocean, Madeira archipelago (n - sample size; S.D. - standard deviation; Min - minimum; Max - maximum; CV - coefficient of variation (%); TL - total length; TW – total weight).

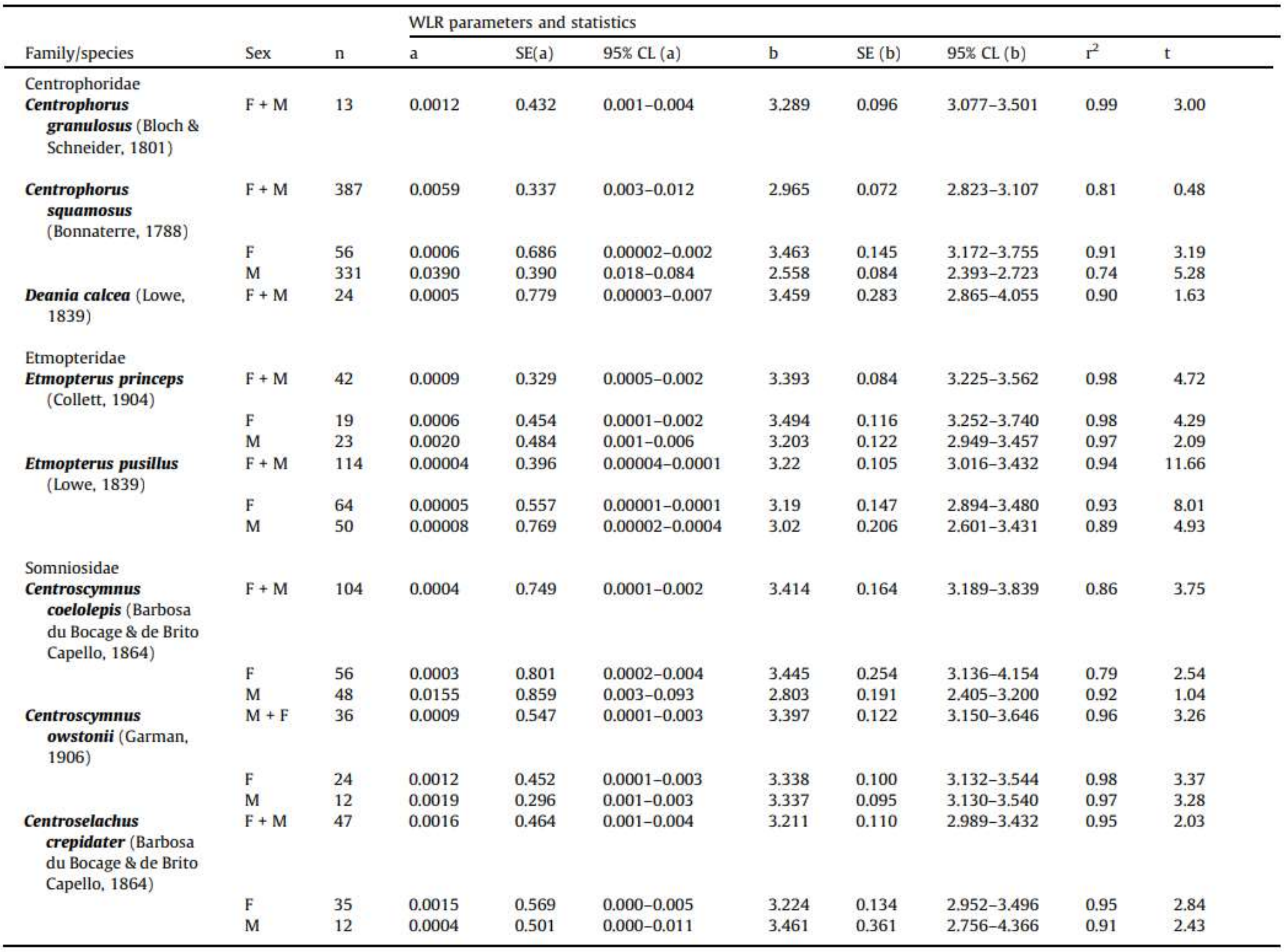
Discussion



			TL (cm)					TW (g)				
Family/species	Sex	n	Mean	SD	Min	Max	CV	Mean	SD	Min	Max	CV
Centrophoridae												
Centrophorus granulosus (Bloch & Schneider, 1801)	F + M	13	120.33	38.45	43.40	154.00	31.95	15210.22	8878.78	3680.00	24056.00	58.37
Centrophorus squamosus (Bonnaterre, 1788)	F + M	387	106.71	8.07	80.90	136.20	7.56	6280.04	1782.99	2800.00	17159.00	28.39
	F	56	112.85	12.66	88.00	136.20	11.25	8150.09	3455.51	3500.00	17159.00	42.40
	M	331	105.67	6.47	80.90	118.40	6.13	5963.66	1017.14	2800.00	8367.00	17.06
Deania calcea (Lowe, 1839)	F + M	24	91.96	8.53	80.00	104.30	9.36	2649.95	946.21	1872.00	5004.00	35.71
Etmopteridae												
Etmopterus princeps (Collett, 1904)	F + M	42	53.08	12.86	23.00	71.40	24.22	925.67	436.61	96.00	2003.00	47.17
	F	19	52.78	15.68	23.00	71.40	29.71	1077.07	556.37	96.00	2003.00	51.66
	M	23	53.32	10.33	25.80	64.90	19.37	814.11	290.46	118.00	1160.00	35.68
Etmopterus pusillus (Lowe, 1839)	F + M	114	43.44	3.25	36.30	51.00	7.48	335.52	107.89	135.00	684.00	32.16
	F	64	44.82	3.12	36.30	51.00	6.97	383.73	102.34	135.00	663.00	26.67
	M	50	41.63	2.43	36.80	51.00	5.85	272.55	79.17	146.00	684.00	29.05
Somniosidae												
Centroscymnus coelolepis (Barbosa du Bocage & de Brito Capello, 1864)	F + M	104	97.11	9.62	71.30	114.90	9.91	6444.54	2568.82	1528.00	12528.00	39.86
	F	56	102.46	10.12	71.30	114.90	9.88	7983.74	2632.33	1528.00	12528.00	32.97
	M	48	90.52	4.55	77.30	99.40	5.02	4756.55	688.27	3130.00	6378.00	14.50
Centroscymnus owstonii (Garman, 1906)	M + F	36	88.78	12.30	54.50	109.90	13.86	3895.67	1749.10	738.00	7518.00	44.90
	F	24	91.41	12.63	54.50	109.90	13.82	4354.86	1723.79	738.00	7518.00	39.58
	M	12	79.58	4.10	71.40	85.00	5.15	2288.50	200.02	2048.00	2642.00	8.74
Centroselachus crepidater (Barbosa du Bocage & de Brito Capello, 1864)	F + M	47	68.95	9.17	53.30	83.30	13.30	1406.54	607.00	502.00	2676.00	43.16
	F	35	71.33	9.36	53.30	83.30	13.13	1529.23	617.19	502.00	2676.00	40.36
	M	12	62.90	8.03	56.30	77.20	8.02	1062.67	394.39	736.00	2234.00	37.11

LWRs are very useful to provide a baseline for conservation strategies, particularly in species susceptible to overexploitation as elasmobranchs. Herein, we presented the LWRs for eight chondrichthyan species from the NE Atlantic Ocean. All LWRs obtained in this study were estimated for the first time for the Madeira region and could be applied in studies regarding fisheries and management in the Madeiran Economic Exclusive Zone.

Table 2 - Length-weight relationships for eight chondrichthyan species in the north-eastern Atlantic Ocean, Madeira archipelago (n - sample size; a and b = parameters of equation $W = aL^b$; S.E. - standard error; CL95% - confidence limits; r^2 - coefficient of determination; t – t-test).



			WLR parameters and statistics							
Family/species	Sex	n	a	SE(a)	95% CL (a)	b	SE (b)	95% CL (b)	r^2	t
Centrophoridae										
Centrophorus granulosus (Bloch & Schneider, 1801)	F + M	13	0.0012	0.432	0.001–0.004	3.289	0.096	3.077–3.501	0.99	3.00
Centrophorus squamosus (Bonnaterre, 1788)	F + M	387	0.0059	0.337	0.003–0.012	2.965	0.072	2.823–3.107	0.81	0.48
	F	56	0.0006	0.686	0.00002–0.002	3.463	0.145	3.172–3.755	0.91	3.19
	M	331	0.0390	0.390	0.018–0.084	2.558	0.084	2.393–2.723	0.74	5.28
Deania calcea (Lowe, 1839)	F + M	24	0.0005	0.779	0.00003–0.007	3.459	0.283	2.865–4.055	0.90	1.63
Etmopteridae										
Etmopterus princeps (Collett, 1904)	F + M	42	0.0009	0.329	0.0005–0.002	3.393	0.084	3.225–3.562	0.98	4.72
	F	19	0.0006	0.454	0.0001–0.002	3.494	0.116	3.252–3.740	0.98	4.29
	M	23	0.0020	0.484	0.001–0.006	3.203	0.122	2.949–3.457	0.97	2.09
Etmopterus pusillus (Lowe, 1839)	F + M	114	0.00004	0.396	0.00004–0.0001	3.22	0.105	3.016–3.432	0.94	11.66
	F	64	0.00005	0.557	0.00001–0.0001	3.19	0.147	2.894–3.480	0.93	8.01
	M	50	0.00008	0.769	0.00002–0.0004	3.02	0.206	2.601–3.431	0.89	4.93
Somniosidae										
Centroscymnus coelolepis (Barbosa du Bocage & de Brito Capello, 1864)	F + M	104	0.0004	0.749	0.0001–0.002	3.414	0.164	3.189–3.839	0.86	3.75
	F	56	0.0003	0.801	0.0002–0.004	3.445	0.254	3.136–4.154	0.79	2.54
	M	48	0.0155	0.859	0.003–0.093	2.803	0.191	2.405–3.200	0.92	1.04
Centroscymnus owstonii (Garman, 1906)	M + F	36	0.0009	0.547	0.0001–0.003	3.397	0.122	3.150–3.646	0.96	3.26
	F	24	0.0012	0.452	0.0001–0.003	3.338	0.100	3.132–3.544	0.98	3.37
	M	12	0.0019	0.296	0.001–0.003	3.337	0.095	3.130–3.540	0.97	3.28
Centroselachus crepidater (Barbosa du Bocage & de Brito Capello, 1864)	F + M	47	0.0016	0.464	0.001–0.004	3.211	0.110	2.989–3.432	0.95	2.03
	F	35	0.0015	0.569	0.000–0.005	3.224	0.134	2.952–3.496	0.95	2.84
	M	12	0.0004	0.501	0.000–0.011	3.461	0.361	2.756–4.366	0.91	2.43

The size ranges of the specimens obtained are in accordance with studies already described in literature for other regions. For *C. squamosus*, *C. crepidater*, *Centroscymnus coelolepis* and *Centroscymnus owstonii*, noticeable sexual dimorphism was observed, with larger females. This might be due to differential morphological development, reproductive investment, and habitat preference (King, 1995).

The estimated values of b (Table 1) varied between 2.558 (*C. squamosus* – males) and 3.494 (*E. princeps* – females) and the determined values of a between 0.00004 (*E. pusillus* - total) and 0.0390 (*C. squamosus* - males). Overall, the b values varied between 2 and 4, being within the range of values usually reported for fishes (Bagenal & Tesch, 1978). Furthermore, because all the b values are within the range of 2.5 to 3.5, this indicates normal growth dimensions and/or healthy populations (Carlander, 1969; Froese, 2006; King, 1995).

This indicates that the linear regression methodology used for the analysed species possesses high predictability and is suitable to estimate weight from the length of specimens with comparable length ranges. However, because most of the elasmobranchs considered in this study were collected over a prolonged period of time, these data do not represent a particular season or a time of the year.

The practical condition index LWR might vary temporally according to several factors, namely the availability of food, feeding rate and reproduction, b parameter does not vary significantly throughout the year (Bagenal & Tesch, 1978). Together with a (condition factor), mean annual values can be considered, as reported previously (Santos et al., 2002). Therefore, the estimated values of the parameters of the LWRs should be regarded as mean annual values, and be treated with caution, since there were not considered hypothetic seasonal variations related to environmental, biological, and temporal factors in the populations studied.

Authors know the limitation of data for the estimation of some LWR in this study. However, due to the lack of knowledge regarding these species, the present study reveals to be important in the management of these Chondrichthyes in this region.

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Chapter 13

Assemblages of deep-sea fishes on the middle slope off Northwest Africa (26°–33° N, eastern Atlantic)

CHAPTER 13 - Assemblages of deep-sea fishes on the middle slope off Northwest Africa (26°–33° N, eastern Atlantic)

Abstract

The structure and composition of deep-sea fish assemblages living on the middle slope off NW Africa (26–33° N) were investigated. Data were collected by six commercial trawlers during experimental fishing (1027 hauls) at depths between 800 and 1515 m. A total of 1,115,727 fish specimens, belonging to 37 families and 96 species (24 Elasmobranchii, 5 Holocephali, and 67 Actinopteri) were collected with bottom trawls. The deep-sea demersal fish fauna off NW Africa is dominated by fishes of the family Macrouridae, followed by the Moridae and Alepocephalidae families. The main abundant species were *Trachyrincus scabrus*, *Bathygadus favosus*, *Mora moro*, *Alepocephalus productus*, *Nezumia aequalis* and *Bathygadus melanobranchus*. PERMANOVA analysis showed differences in demersal fish assemblages among bottom types, depth strata and between areas (north and south of parallel 30° N), with the area being the most influential factor followed by the type of substrate. PERMANOVAs computed separately for each area showed significant differences among the bottom types and depths in both areas. SIMPER analysis revealed that *B. melanobranchus* and *B. favosus*, which occurred at higher abundances in the area ≥30° N, were the species that were best discriminated between areas; whilst *T. scabrus* and *M. moro* occurred at higher abundances in the area < 30° N. *N. aequalis*, *B. favosus*, *B. melanobranchus*, *Deania hystricosa*, *Aphanopus intermedius*, *Coelorinchus labiatus* and *Halosaurus johnsonianus* were restricted or more abundant in the area ≥30° N, and functioned as the discriminating species that most contributed to the average dissimilarity between areas. *T. scabrus*, *M. moro*, *Alepocephalus productus* and *Alepocephalus bairdii* were more abundant in the area < 30° N. The standardized mean abundance (in number of individuals/km2) showed a decreasing pattern: i) with depth in both areas, north and south of parallel 30° N, and ii) with depth on each type of substrate, except on cold coral bottoms. *Hydrolagus mirabilis*, *Gadomus dispar*, *Nettastoma melanurum*, *Halosaurus ovenii*, *Chimaera opalescens*, *A. productus*, *Hoplostethus mediterraneus*, *Apristurus laurussonii* and *Trachyscorpia cristulata echinata* showed a deeper Center of Gravity at latitudes ≥30° N, with differences in depths from 299 to 110 m compared to the area at latitudes < 30° N. *T. scabrus*, *Anoplogaster cornuta*, *B. favosus*, *Centrophorus squamosus*, *B. melanobranchus* and *A. bairdii* showed a similar depth Center of Gravity, with differences in depths lower than 21 m.

Keywords

Assemblages, fishes, abundance, distribution, diversity, upwelling, Africa.

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Introduction

The northwestern coast of Africa is located in the Canary Current System, which is one of the Large Marine Ecosystems of the World, forming one of the primary eastern boundary coastal upwelling systems of the world occurring over a shelf and shelf break (Hagen, 2001; Carr, 2002; Eberwein and Mackensen, 2006; Chavez and Messié, 2009; Wilke et al., 2009); these systems are characterized by their singular hydrography and productivity and their ability to support high biomasses of marine populations. The northwestern African coast occupies a key position with respect to marine biogeochemical cycles, especially carbon export to the sea floor (Pelegrí et al., 2005a, 2005b).

It is one of the most important and productive fishing areas of the world, characterized by important fishing grounds (Arístegui et al., 2009). The fishery catches in this area reach more than 2.5 million tons per year. From 1950, the small-sized pelagic species represented 32% of the average annual catch followed by medium-sized pelagic species with 29% and cephalopods with a mean annual catch of 5%. According to FAO (2012, 2015) more than 40% of the fisheries in this area are currently in a senescent phase providing approximately 10% of the total catches, and the rest are in a mature phase providing approximately 90% of the total catches, mainly of small and medium pelagic species (Arístegui et al., 2009).

Coastal demersal and coastal pelagic resources in the northwestern coast of Africa are highly sought after due to their generally elevated market value, showing a general decreasing trend in the catches since 1999 (FAO, 2012). These resources are exploited by artisanal and industrial fleets (national and foreign) of cephalopod freezer trawlers, seiners, coastal trawlers and longliners, and artisanal boats in a multipurpose fishery with benthic fish species being the bycatch of other fisheries (FAO, 2012). However, the deep demersal species are secondary resources in the area, and for this reason their scientific information is scarce. The spatial patterns, abundances and biomasses of the deep-sea fish assemblages that support these fisheries, as well as their relationship with environmental variables, are still far from being fully understood because the fishery information is deficient, and this region has a complex topography and oceanography with the presence of several water masses that can influence the deep-sea fauna (Arístegui et al., 2009; Chavez and Messié, 2009).

The majority of the studies on demersal fish communities have been conducted in the first 800 m of depth, where biological resources are more widely exploited (Follesa et al., 2011). The current knowledge of demersal fish assemblages below this depth indicate that the assemblages are less diverse, abundance is less frequent and assemblages are usually fragmented (Follesa et al., 2011). The demersal fish fauna of deep-sea habitats appear to be more widespread than in shallower ecosystems (Ross and Quattrini, 2009), which has been attributed to the existence of fewer physical barriers in the deep-sea, mainly horizontally, and relatively uniform environmental conditions with respect to temperature and salinity (Gage and Tyler, 1991; Merrett and Haedrich, 1997; Ross and Quattrini, 2009).

On the slope, vertical zonation is more pronounced than latitudinal zonation (Haedrich et al., 1980; Jacob et al., 1988; Bianchi, 1992a; Carney, 2005; Ross and Quattrini, 2009). The deep-sea faunal assemblages along the slopes usually change with depth (Jacob et al., 1988; Bianchi, 1992a) and with environmental factors, such as the water mass, temperature, salinity or oxygen content, which also vary with depth (Snelgrove and Haedrich, 1985; Hecker, 1990; Bianchi, 1992a, 1992b; Koslow, 1993; Stefanescu et al., 1993; Pajuelo et al., 2015). Koslow (1993) suggested the existence of horizontal faunal zones at depths below 1500 m, which were less apparent in deeper areas. The existence of these boundaries independent of depth have usually been related to changes in biotic or abiotic conditions, such as the productivity, latitudinal changes in temperature or salinity or heterogeneity of the substrate (Ross and Quattrini, 2009; Ingels et al., 2011; De Leo et al., 2012). On the slope below the 1500 m depth, the uniformity of environmental parameters produces an increase of the uniformity of the demersal fish fauna horizontally over large areas (Ross and Quattrini, 2009). However, on the upper slope, the demersal fish fauna are usually not continuous over large horizontal areas and may generate different fish assemblages (Koslow, 1993; Ross and Quattrini, 2009). Horizontal and vertical demersal fish assemblages have been recorded on the slope of different Atlantic areas (Markle and Musick, 1974; Merrett et al., 1991a; Bianchi, 1992a, 1992b; Koslow, 1993; Gordon et al., 1996; Bergstad et al., 1999; Menezes et al., 2006; Ross and Quattrini, 2007, 2009). However, in many cases, the habitat influence has remained undetected because trawl samplings were made on relatively homogeneous bottoms (Ross and Quattrini, 2007, 2009).

The abundance and distribution of the deep-sea demersal fish assemblages in the western coast of Africa have been studied at some shelf and slope locations on several occasions (Fager and Longhurst, 1968; Maurin, 1968; Merrett and Marshall, 1981; Merrett and Domanski, 1985a, 1985b; Bianchi, 1992a, 1992b). Most of these studies have been focused in the areas of the upwelling of the Cape Blanc (20°–21° N) or towards southern waters (Merrett and Marshall, 1981; Roel et al., 1985; Bianchi, 1992a, 1992b), and have been less frequently focused in the area between Cape Bojador and Cape Juby or towards the areas further north, such as Cape Ghir (Merrett and Domanski, 1985a, 1985b).

The main goal of this study is to describe the deep-sea fish assemblages on the upper part of the slope off NW Africa (26°–33° N) from the data from commercial trawlers during experimental fishing, as well as to identify the primary factors influencing these boundaries.

Materials and methods

2.1. Study area and sampling procedure

The study area extends off the north-western coast of Africa (26°– 33° N) between depth of 800 and 1515 m. In this area, the slope is characterized by the presence of a large submarine canyon located in front of Agadir (approximately at 30° N) that breaks the continuity of the continental slope. In this region, the Canary Current flows towards the Equator from 33° N to 20° N where it separates from the coast, producing an upwelling system (Mittelstaedt, 1983, 1991). The upwelling events occur year round with seasonal variations, which are strongest in late summer (Mittelstaedt, 1991; Arístegui et al., 2009) in the subregion located between Cape Sim and Cape Blanc, 21°–33° N (Arístegui et al., 2009). One of the main phenomena observed in the NW Africa upwelling system region of Cape Bojador and Cape Juby (26°–28° N) is the formation of filament structures from the coastal upwelling system, merging approximately 100 km offshore and connecting the coastal upwelling with the open sea (García-Muñoz et al., 2004; Arístegui et al., 2009). The filaments exist throughout the year with a width of approximately 25 km and a separation of approximately 200 km to both the south and north (off Cape Ghir) (Barton et al., 1998). From Cape Ghir to Cape Juby, the morphology of the Moroccan Atlas Mountains, together with the concave shape of the coastline, modify winds locally and reduce upwelling during the summer (Pelegrí et al., 2005a). The NW African coast is also characterized by the presence of several deep water masses. North Atlantic Central Waters (NACW) can be found from the surface to a depth of approximately 700 m (Knoll et al., 2002; Pelegrí et al., 2005a). Under this water mass, two other water masses can be found, the Mediterranean Water (MW) and the Antarctic Intermediate Water (Hernández-Guerra et al., 2001; Knoll et al., 2002; Pelegrí et al., 2005a). North Atlantic Deep Water is the deepest water mass found in the area, and is located under the MW at approximately below 1600 m (Knoll et al., 2002; Pelegrí et al., 2005a).

Data were collected by six commercial trawlers during experimental fishing trips organized by the Spanish and Moroccan Ministries for Fisheries that were conducted from November to December 2005 within the 33°–29° N area and from the end of January to mid-March 2006 within the 29°–26° N area on the continental slope, comprising a total of 1027 hauls (Fig. 1). Hauls were performed between 800 and 1515 m of depth. Trawls were operated with nominal codend mesh size of 50 and 70 mm, mean hauling time of 3.60 h and mean distance of 10.64 nautical miles at mean tow speeds of 2.95 knots. Bottom trawls were used for all vessels in the whole area. Tow duration was timed from the moment of the arrival of the net on the sea-bottom to the liftoff time, recorded with echo sounder. The mean doorspread was 204.14 m recorded by a Scanmar device mounted on wing trawl, and the mean trawled area was 4.02 km2/haul. The groundrope was composed by rubber wheel bobbins with a section of wire or rockhopper discs (González et al., 2014). For each haul, data on the bottom type, depth, latitude and longitude, number of specimens and their total weight were recorded. Five bottom types - muddy, muddy-rocky, rocky, individual colonies of cold coral, and mixed bottoms of muddy, rocky, and cold coral - were established; these substrates were confirmed by echo-sounding (single beam echo-sounders model ES80 or EA-400 by Simrad) on the fishing ground of the nautical chart of the vessel master. In addition to regular depth sounding, these echosounders were employed for side looking sonar surveying. One single 200 kHz side looking transducer with 38 kHz bottom detector line was utilized for accurate surveying of the operation areas. Information on seabed obtained was firstly validated by means of the evidences provided by trawl nets, such as cold corals, muddy, rocks, and/or sponges, and then checked by the chart atlas of bottom types and bathymetry (characterized with dredges) of the National Institute for Fisheries Research of Morocco (INRH, 2009). Specimens were identified at the species level. Taxonomical arrangement followed the WoRMS Editorial Board (2016). For each collected species, the combined weight of all individuals caught was taken for each haul.

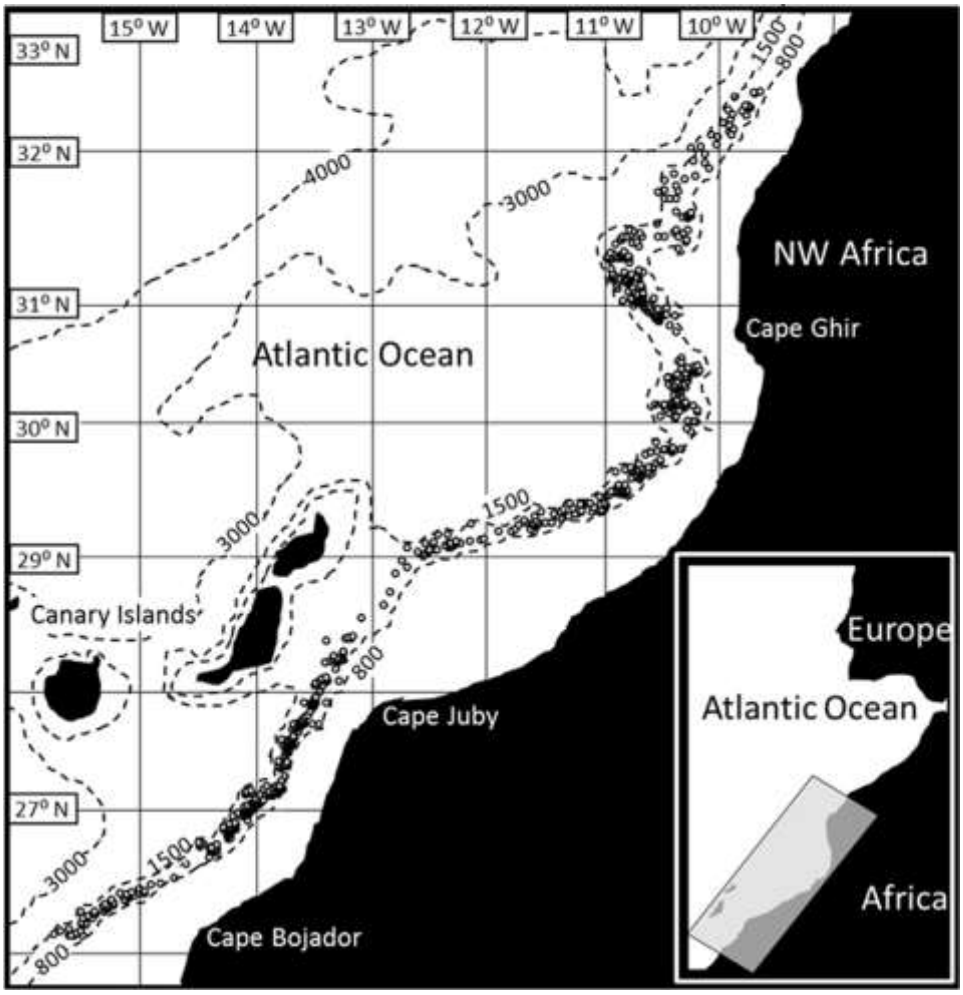


Fig. 1. Study area off the northwestern coast of Africa (26°–33° N) between the isobaths of 800 and 1500 m of depth; the location of the 1027 studied hauls are also presented.

2.2. Data analysis

Analyses were focused on demersal fish species, excluding all pelagic fish species and other groups, such as cephalopods, shrimps or crabs. For each haul, the demersal species composition and the abundance (expressed as the number of individuals/km^2) were estimated.

Species with one individual present in all samples were removed from analysis (Fanelli et al., 2007, 2011; Cartes et al., 2014). Standardization and logarithmic transformation were applied to the data prior to the analysis (Clarke and Warwick, 2001), after which a resemblance matrix using the Bray-Curtis similarity index was constructed (Clarke and

Warwick, 2001; Clarke and Gorley, 2006). The factors considered to explain the ordination of the hauls were area, depth, bottom type, and mesh size. The fish assemblages were analysed using distance-based permutational multivariate analysis of variance, PERMANOVA (Anderson et al., 2008). PERMANOVA was performed to evaluate four null hypotheses of no differences among the demersal fish assemblages between the two areas separated by the Agadir Canyon (northwards or southwards of the parallel 30° N); among the five types of substrata (muddy, muddy-rocky, rocky, individual colonies of cold coral, and mixed bottoms of muddy, rocky, and cold coral); among three depths strata (800–1000, 1001–1200, and 1201– 1500 m); and between the mesh size used as sampling gear (50 and 70 mm). The experimental design was a four-way crossed design with fixed levels for each factor: area (with two levels), depth (with three levels), mesh size (with two levels) and bottom type (with five levels).

The permutation method used was the permutation of residuals under a reduced model with a maximum number of permutations of 9999 due to their good empirical results in the maximum discriminant power (Anderson and Legendre, 1999; Anderson and ter Braak, 2003). For each factor, a pseudo-F test (p-F) and a pairwise test for significant effects were estimated. Non-parametric multidimensional scaling ordination (nMDS) was used to examine the haul's relationships on a two dimensional ordination plane using the standardized abundance data (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The Similarity Percentage analysis procedure (SIMPER) was used to identify the main species that characterize each assemblage (Clarke and Warwick, 1994, 2001). Statistical analyses were performed by using Primer v.6 with PERMANOVA+ software (Clarke and Warwick, 1994; Anderson et al., 2008).

The measures of species diversity were estimated for each haul with the Shannon-Wiener diversity index (H′), the species richness (S), and the Pielou evenness index (J′) using the DIVERSE subroutine within the Primer v.6 software. Measures of species diversity were tested using PERMANOVA (Anderson et al., 2008). PERMANOVA was performed to evaluate the same four null hypotheses of no differences among the two areas separated by the Agadir canyon; the five types of substrata; the three strata depths; and the two mesh sizes, with the same experimental design of a four-way crossed design with fixed levels for each factor. For each factor, a pseudo-F test (p-F) and pairwise test for significant effects were estimated.

The spatial trends of the standardized mean abundance (number of individuals/km2) and diversity indices were explored as functions of depth with Generalized Additive Models (GAM) (Hastie and Tibshirani, 1990). Models were built using smoothing splines of depth as explanatory variables (as a continuous variable) for each area and bottom type. This amounts to include two interactions (depth × area; depth × substrata) that allow to describe relationships of abundance and diversity with depth potentially differing among levels of the factors. GAM and smoothing splines were used to explore curvilinear relationships with depth. Models for the abundance were tried with Gaussian (this with log-transformed abundance as the response variable), Poisson and negative binomial errors (these with raw abundance), and their adequacy gauged according to both the percentage of the total deviance explained by the model (%DE) and the Akaike Information Criterion (AIC) (Akaike, 1970) and after inspection of the diagnostic plots. No further model selection were pursued. Models for the indexes of diversity were built with Gaussian errors and examined as for the abundance models. These procedures were performed with R (R Core Team, 2014, version 3.1.1) and the specialized package mgcv (Wood, 2006).

To compare the depth and latitudinal distribution of the species with the highest standardized mean abundance recorded, the Center of Gravity (CoG) was estimated (Stefanescu et al., 1992; Cartes et al., 2011). The CoG was tested for differences among species using an ANOVA test. This analysis was used to evaluate the null hypothesis of equality of CoG with depth and with latitude among species, at the significance level of 5% (α=0.05).

The standardized mean abundance (in number of individuals/km^2) data of each haul was used to estimate maps of abundances in the area by means of the geostatistical analysis. This tool was applied to detect, model, and estimate the fishes' spatial pattern using the GS+ version 9 software (Robertson, 2008). Analyses were developed using two techniques, the variographic and the conditional simulation methods.

The variographic technique is a structural analysis in which the spatial correlation among the observations is modelled (Robertson, 1987). Theoretical models (spherical, exponential, Gaussian, and linear) were fitted to the experimental semivariograms. The semivariogram is defined by several parameters, namely the nugget (C0), the sill (C0+C), and the range (A0). The nugget is a discontinuity at the origin of the semivariogram due to small-scale spatial phenomena and can be attributed to measurement errors, white noise, microscale variability, or small-scale spatial structure (Cressie, 1991; Maynou, 1998). The sill can be defined as the maximum variability point beyond which the semivariance values become asymptotic, and the range represents the distance within which the data remain autocorrelated (Maynou, 1998).

The proportion of variance explained by the spatially structured component (C/[C0+C]), the coefficient of determination (r^2), and the residual sum of squares (RSS) were defined as criteria for the goodness of fit (Cressie, 1991; Robertson, 2008). The conditional simulation technique is an advanced interpolation technique whereby abundance estimates are based on a form of stochastic simulation in which measured data values are honoured at their locations (Robertson, 1987).

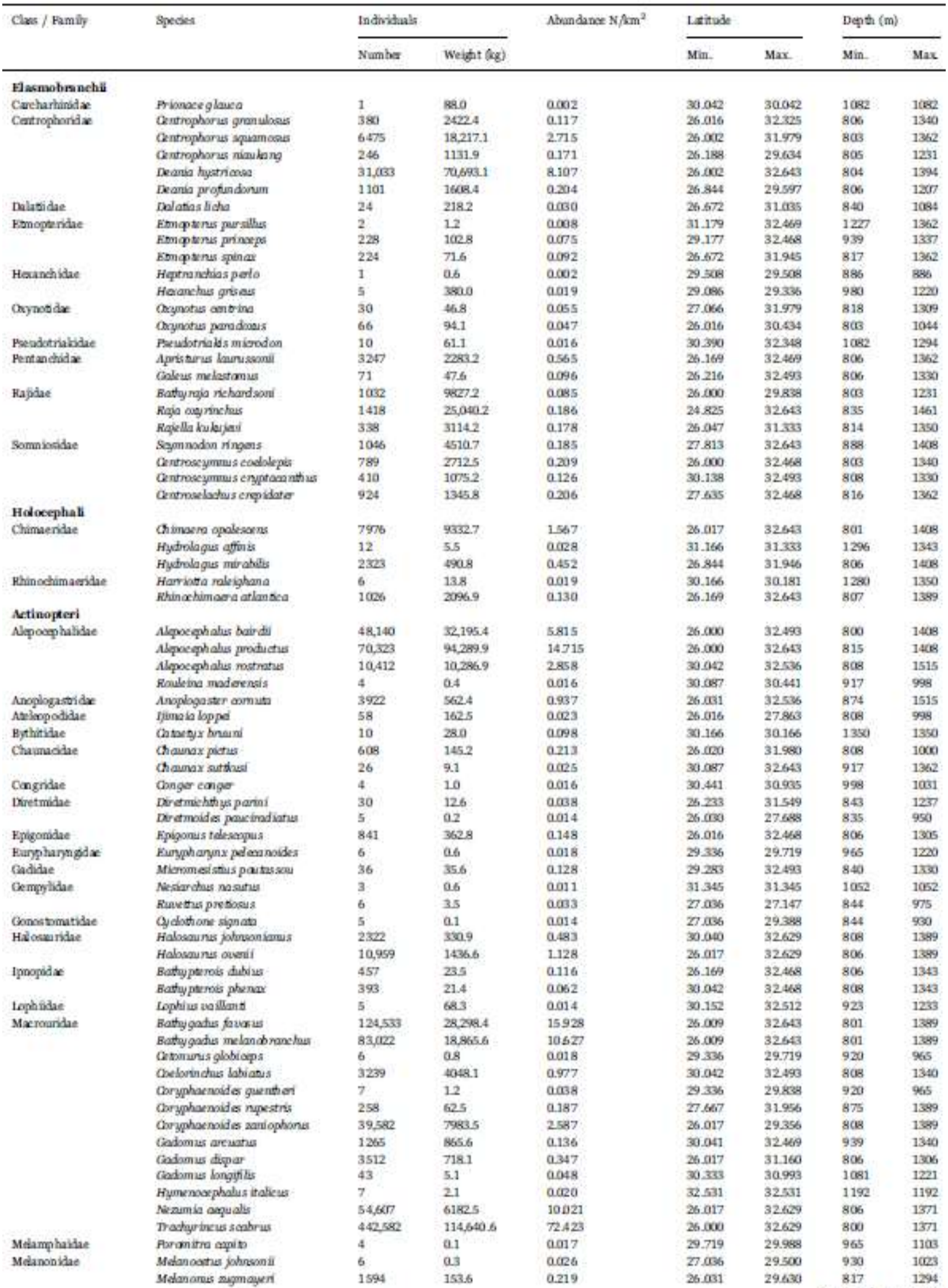
Results

A total of 1,115,727 individuals (650.1 t) representing 96 fish species were recorded: 24 species of Elasmobranchii (belonging to 10 families and representing 4.40% of the individuals caught), five species of Holocephali (2 families and 1.02%), and 67 species of Actinopterygii (25 families and 94.53%) (Table 1). The deep-sea demersal fish fauna is dominated by fishes of the family Macrouridae, followed by the Moridae and Alepocephalidae families. *Trachyrincus scabrus*, *Bathygadus favosus*, *Mora moro*, *Alepocephalus productus*, *Nezumia aequalis* and *Bathygadus melanobranchus* were the most abundant species. Elasmobranchs, with 49,101 individuals, showed a low abundance in the hauls, although their importance increases when the data were analysed by weight, reaching 22.31% (145.1 t), with *Deania hystricosa* being the fourth species in importance.

The results of PERMANOVA indicated significant differences in the demersal fish assemblage among bottom types (pseudo-F=26.86, $p < 0.0001$) and depth strata (p-F=3.13, p=0.001) and between areas (p- F=114.88, $p < 0.0001$), with the area being the most influential factor followed by the bottom type (Table 2). Pair-wise comparisons showed that the hauls (assemblages) among the bottom types were significantly different ($t > 2.43$, $p < 0.0005$), except those of muddy and mixed bottoms (t=1.04, $p < 0.3597$). The assemblages among the depth strata were significantly different between the two shallowest (t=2.21, $p < 0.0005$) strata, but similar between the two deepest strata (t=0.88,

$p < 0.5975$). No significant differences were observed between the mesh sizes (p-F=0.56; p=0.7614) or between the mesh sizes crossed with other factors (p-F < 1.66, $p > 0.0511$). Significant differences were found for the following crossed factors: bottom type and area (p-F=41.96, $p < 0.0001$), depth strata and area (p-F=3.40, p=0.0008), and bottom type, area and depth strata (p-F=1.55, p=0.0230).

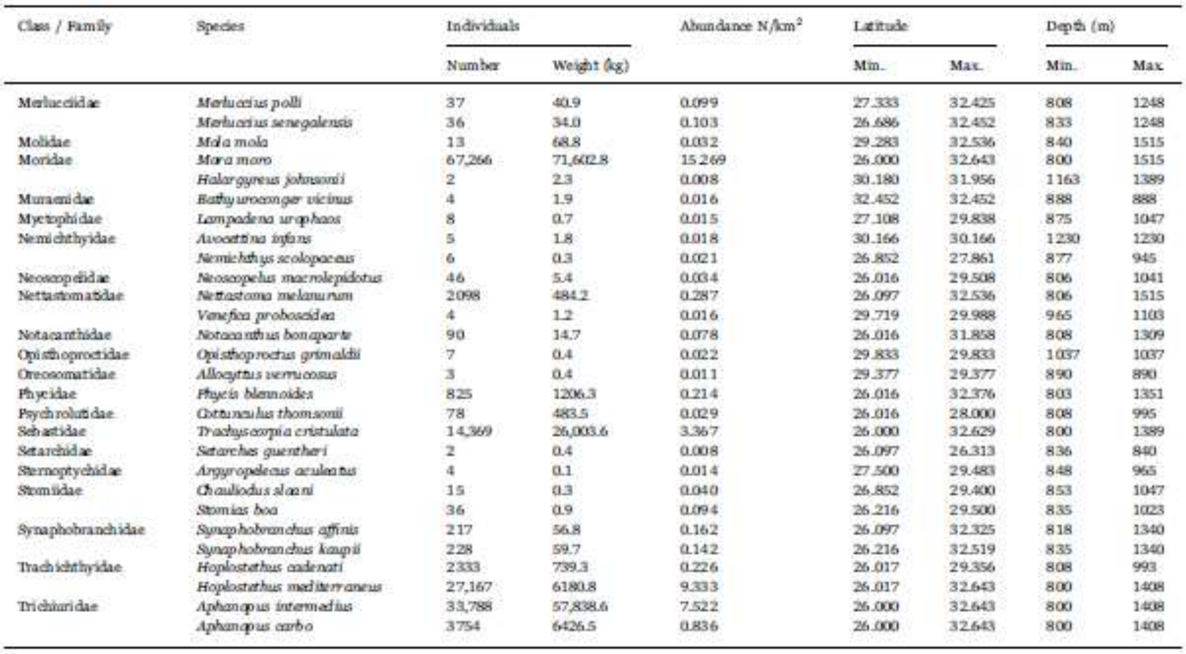
Table 1 - List of species arranged by families, indicating the number of individuals and weight (kg) collected, depth (m) of capture (minimum and maximum), latitude of capture (minimum and maximum) and mean standardized abundance in number of individuals per km^2.



Class / Family	Species	Individuals		Abundance N/km^2	Latitude		Depth (m)	
		Number	Weight (kg)		Min.	Max.	Min.	Max.
Elasmobranchii								
Carcharhinidae	*Prionace glauca*	1	88.0	0.002	30.042	30.042	1082	1082
Centrophoridae	*Centrophorus granulosus*	380	2422.4	0.117	26.016	32.325	806	1340
	Centrophorus squamosus	6475	18,217.1	2.715	26.002	31.979	803	1362
	Centrophorus niaukang	246	1131.9	0.171	26.188	29.634	805	1231
	Deania hystricosa	31,033	70,693.1	8.107	26.002	32.643	804	1394
	Deania profundorum	1101	1608.4	0.204	26.844	29.597	806	1207
Dalatiidae	*Dalatias licha*	24	218.2	0.030	26.672	31.035	840	1084
Etmopteridae	*Etmopterus pusillus*	2	1.2	0.008	31.179	32.469	1227	1362
	Etmopterus princeps	228	102.8	0.075	29.177	32.468	939	1337
	Etmopterus spinax	224	71.6	0.092	26.672	31.945	817	1362
Hexanchidae	*Heptranchias perlo*	1	0.6	0.002	29.508	29.508	886	886
	Hexanchus griseus	5	380.0	0.019	29.086	29.336	980	1220
Oxynotidae	*Oxynotus centrina*	30	46.8	0.055	27.066	31.979	818	1309
	Oxynotus paradoxus	66	94.1	0.047	26.016	30.434	803	1044
Pseudotriakidae	*Pseudotriakis microdon*	10	61.1	0.016	30.390	32.348	1082	1294
Pentanchidae	*Apristurus laurussonii*	3247	2283.2	0.565	26.169	32.469	806	1362
	Galeus melastomus	71	47.6	0.096	26.216	32.493	806	1330
Rajidae	*Bathyraja richardsoni*	1032	9827.2	0.085	26.000	29.838	803	1231
	Raja oxyrinchus	1418	25,040.2	0.186	24.825	32.643	835	1461
	Rajella kukujevi	338	3114.2	0.178	26.047	31.333	814	1350
Somniosidae	*Scymnodon ringens*	1046	4510.7	0.185	27.813	32.643	888	1408
	Centroscymnus coelolepis	789	2712.5	0.209	26.000	32.468	803	1340
	Centroscymnus cryptacanthus	410	1075.2	0.126	30.138	32.493	808	1330
	Centroselachus crepidater	924	1345.8	0.206	27.635	32.468	816	1362
Holocephali								
Chimaeridae	*Chimaera opalescens*	7976	9332.7	1.567	26.017	32.643	801	1408
	Hydrolagus affinis	12	5.5	0.028	31.166	31.333	1296	1343
	Hydrolagus mirabilis	2323	490.8	0.452	26.844	31.946	806	1408
Rhinochimaeridae	*Harriotta raleighana*	6	13.8	0.019	30.166	30.181	1280	1350
	Rhinochimaera atlantica	1026	2096.9	0.130	26.169	32.643	807	1389
Actinopteri								
Alepocephalidae	*Alepocephalus bairdii*	48,140	32,195.4	5.815	26.000	32.493	800	1408
	Alepocephalus productus	70,323	94,289.9	14.715	26.000	32.643	815	1408
	Alepocephalus rostratus	10,412	10,286.9	2.858	30.042	32.536	808	1515
	Rouleina maderensis	4	0.4	0.016	30.087	30.441	917	998
Anoplogastridae	*Anoplogaster cornuta*	3922	562.4	0.937	26.031	32.536	874	1515
Ateleopodidae	*Ijimaia loppei*	58	162.5	0.023	26.016	27.863	808	998
Bythitidae	*Cataetyx bruuni*	10	28.0	0.098	30.166	30.166	1350	1350
Chaunacidae	*Chaunax pictus*	608	145.2	0.213	26.020	31.980	808	1000
	Chaunax suttkusi	26	9.1	0.025	30.087	32.643	917	1362
Congridae	*Conger conger*	4	1.0	0.016	30.441	30.935	998	1031
Diretmidae	*Diretmichthys parini*	30	12.6	0.038	26.233	31.549	843	1237
	Diretmoides pauciradiatus	5	0.2	0.014	26.030	27.688	835	950
Epigonidae	*Epigonus telescopus*	841	362.8	0.148	26.016	32.468	806	1305
Eurypharyngidae	*Eurypharynx pelecanoides*	6	0.6	0.018	29.336	29.719	965	1220
Gadidae	*Micromesistius poutassou*	36	35.6	0.128	29.283	32.493	840	1330
Gempylidae	*Nesiarchus nasutus*	3	0.6	0.011	31.345	31.345	1052	1052
	Ruvettus pretiosus	6	3.5	0.033	27.036	27.147	844	975
Gonostomatidae	*Cyclothone signata*	5	0.1	0.014	27.036	29.388	844	930
Halosauridae	*Halosaurus johnsonianus*	2322	330.9	0.483	30.040	32.629	808	1389
	Halosaurus ovenii	10,959	1436.6	1.128	26.017	32.629	806	1389
Ipnopidae	*Bathypterois dubius*	457	23.5	0.116	26.169	32.468	806	1343
	Bathypterois phenax	393	21.4	0.062	30.042	32.468	808	1343
Lophiidae	*Lophius vaillanti*	5	68.3	0.014	30.152	32.512	923	1233
Macrouridae	*Bathygadus favosus*	124,533	28,298.4	15.928	26.009	32.643	801	1389
	Bathygadus melanobranchus	83,022	18,865.6	10.627	26.009	32.643	801	1389
	Cetonurus globiceps	6	0.8	0.018	29.336	29.719	920	965
	Coelorinchus labiatus	3239	4048.1	0.977	30.042	32.493	808	1340
	Coryphaenoides guentheri	7	1.2	0.038	29.336	29.838	920	965
	Coryphaenoides rupestris	258	62.5	0.187	27.667	31.956	875	1389
	Coryphaenoides zaniophorus	39,582	7983.5	2.587	26.017	29.356	808	1389
	Gadomus arcuatus	1265	865.6	0.136	30.041	32.469	939	1340
	Gadomus dispar	3512	718.1	0.347	26.017	31.160	806	1306
	Gadomus longifilis	43	5.1	0.048	30.333	30.993	1081	1221
	Hymenocephalus italicus	7	2.1	0.020	32.531	32.531	1192	1192
	Nezumia aequalis	54,607	6182.5	10.021	26.017	32.629	806	1371
	Trachyrincus scabrus	442,582	114,640.6	72.423	26.000	32.629	800	1371
Melamphaidae	*Poromitra capito*	4	0.1	0.017	29.719	29.988	965	1103
Melanonidae	*Melanocetus johnsonii*	6	0.3	0.026	27.036	29.500	930	1023
	Melanonus zugmayeri	1594	153.6	0.219	26.031	29.630	817	1294

(continued on next page

Table 1 (continued)



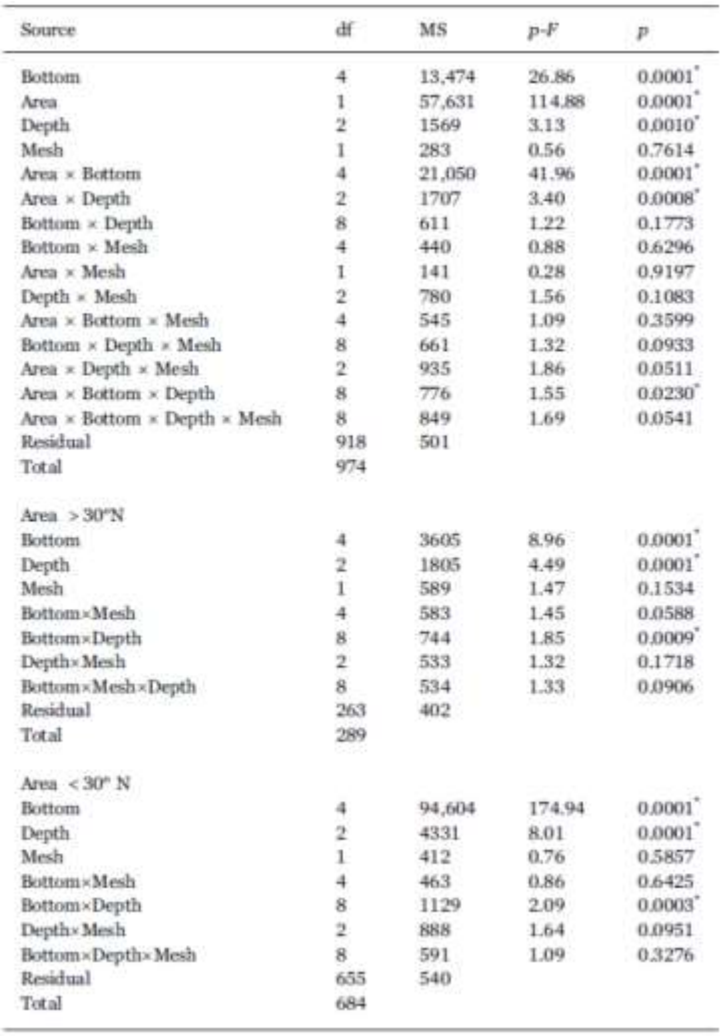
Class / Family	Species	Individuals		Abundance N/km²	Latitude		Depth (m)	
		Number	Weight (kg)		Min.	Max.	Min.	Max.
Merlucciidae	*Merluccius polli*	37	40.9	0.099	27.333	32.425	808	1248
	Merluccius senegalensis	36	34.0	0.103	26.686	32.452	833	1248
Molidae	*Mola mola*	13	68.8	0.032	29.283	32.536	840	1515
Moridae	*Mora moro*	67,266	71,602.8	15.269	26.000	32.643	800	1515
	Halargyreus johnsonii	2	2.3	0.008	30.180	31.956	1163	1389
Muraenidae	*Bathyuroconger vicinus*	4	1.9	0.016	32.452	32.452	888	888
Myctophidae	*Lampadena urophaos*	8	0.7	0.015	27.108	29.838	875	1047
Nemichthyidae	*Avocettina infans*	5	1.8	0.018	30.166	30.166	1230	1230
	Nemichthys scolopaceus	6	0.3	0.021	26.852	27.861	877	945
Neoscopelidae	*Neoscopelus macrolepidotus*	46	5.4	0.034	26.016	29.508	806	1041
Nettastomatidae	*Nettastoma melanurum*	2098	484.2	0.287	26.097	32.536	806	1515
	Venefica proboscidea	4	1.2	0.016	29.719	29.988	965	1103
Notacanthidae	*Notacanthus bonaparte*	90	14.7	0.078	26.016	31.858	808	1309
Opisthoproctidae	*Opisthoproctus grimaldii*	7	0.4	0.022	29.833	29.833	1037	1037
Oreosomatidae	*Allocyttus verrucosus*	3	0.4	0.011	29.377	29.377	890	890
Phycidae	*Phycis blennoides*	825	1206.3	0.214	26.016	32.376	803	1351
Psychrolutidae	*Cottunculus thomsonii*	78	483.5	0.029	26.016	28.000	808	995
Sebastidae	*Trachyscorpia cristulata*	14,369	26,003.6	3.367	26.000	32.629	800	1389
Setarchidae	*Setarches guentheri*	2	0.4	0.008	26.097	26.313	836	840
Sternoptychidae	*Argyropelecus aculeatus*	4	0.1	0.014	27.500	29.483	848	965
Stomiidae	*Chauliodus sloani*	15	0.3	0.040	26.852	29.400	853	1047
	Stomias boa	36	0.9	0.094	26.216	29.500	835	1023
Synaphobranchidae	*Synaphobranchus affinis*	217	56.8	0.162	26.097	32.325	818	1340
	Synaphobranchus kaupii	228	59.7	0.142	26.216	32.519	835	1340
Trachichthyidae	*Hoplostethus cadenati*	2333	739.3	0.226	26.017	29.356	808	993
	Hoplostethus mediterraneus	27,167	6180.8	9.333	26.017	32.643	800	1408
Trichiuridae	*Aphanopus intermedius*	33,788	57,838.6	7.522	26.000	32.643	800	1408
	Aphanopus carbo	3754	6426.5	0.836	26.000	32.643	800	1408

PERMANOVAs computed separately for each area showed significant differences among the bottom types and depth in both areas (Table 2). No significant differences were observed between the mesh sizes (p-F < 1.46, p > 0.1534) or between the mesh size crossed with the bottom type or depth strata (p-F < 1.664, p > 0.0588) in both areas. At latitudes ≥30° N, pair-wise comparisons showed that hauls (assemblages) among the bottom types (t > 1.69, p < 0.0066) or among the depth strata (t > 1.89, p < 0.0034) were significantly different in all cases. Pair-wise comparisons between the bottom types within the depth strata also showed significant interactions among the factors.

Significant differences in the assemblage among bottom types were mainly restricted to the mid (1001–1200 m, t > 1.99, p < 0.0011) and deepest strata (1201–1500 m, t > 1.98, p < 0.0488), with the exception between the cold coral and mixed bottoms (t=1.68, p=0.1188) in the last strata. In the shallower strata, differences among bottom types were not observed (t < 1.60, p > 0.3288), with the exception of the difference between muddy and muddy-rocky bottoms (t=2.10, p=0.0293) and between cold coral and mixed bottoms (t=1.71, p=0.0265). At latitudes < 30°N, pair-wise comparisons showed that the assemblages among bottom types (t > 5.48, p < 0.0001) or depth strata (t > 1.72, p < 0.0216) were significantly different in all cases. The bottom-type assemblages differed significantly in the shallowest (800– 1000 m, t > 4.24, p < 0.0001), mid (1001–1200 m, t

> 2.46, p < 0.0016) and deepest strata (1201–1500 m, t > 2.15, p < 0.0111), with the exception between muddy and mixed bottoms in the last stratum (t=1.19, p=0.174).

Table 2. Results of the PERMANOVA analysis as a whole and for each area separately. *values indicate significant differences at p < 0.05. df, degrees of freedom; MS, mean squares; p- F, pseudo F value; p, p value.



Source	df	MS	*p-F*	*p*
Bottom	4	13,474	26.86	0.0001^{*}
Area	1	57,631	114.88	0.0001^{*}
Depth	2	1569	3.13	0.0010^{*}
Mesh	1	283	0.56	0.7614
Area × Bottom	4	21,050	41.96	0.0001^{*}
Area × Depth	2	1707	3.40	0.0008^{*}
Bottom × Depth	8	611	1.22	0.1773
Bottom × Mesh	4	440	0.88	0.6296
Area × Mesh	1	141	0.28	0.9197
Depth × Mesh	2	780	1.56	0.1083
Area × Bottom × Mesh	4	545	1.09	0.3599
Bottom × Depth × Mesh	8	661	1.32	0.0933
Area × Depth × Mesh	2	935	1.86	0.0511
Area × Bottom × Depth	8	776	1.55	0.0230^{*}
Area × Bottom × Depth × Mesh	8	849	1.69	0.0541
Residual	918	501		
Total	974			
Area >30°N				
Bottom	4	3605	8.96	0.0001^{*}
Depth	2	1805	4.49	0.0001^{*}
Mesh	1	589	1.47	0.1534
Bottom×Mesh	4	583	1.45	0.0588
Bottom×Depth	8	744	1.85	0.0009^{*}
Depth×Mesh	2	533	1.32	0.1718
Bottom×Mesh×Depth	8	534	1.33	0.0906
Residual	263	402		
Total	289			
Area <30° N				
Bottom	4	94,604	174.94	0.0001^{*}
Depth	2	4331	8.01	0.0001^{*}
Mesh	1	412	0.76	0.5857
Bottom×Mesh	4	463	0.86	0.6425
Bottom×Depth	8	1129	2.09	0.0003^{*}
Depth×Mesh	2	888	1.64	0.0951
Bottom×Depth×Mesh	8	591	1.09	0.3276
Residual	655	540		
Total	684			

A nMDS performed separately for each area confirmed these assemblage patterns (Fig. 2). In the area ≥30° N, nMDS showed five not well-defined assemblages that basically aggregated as a function of the bottom type. Each assemblage is formed by the hauls made on one type of bottom at all depths strata (Fig. 2a). The nMDS plot did not show high separation (degree of dissimilarity) among the assemblages, confirming the absence of significant differences at the shallowest stratum among all bottom types obtained with PERMANOVA. In the area < 30° N, nMDS confirmed the type of bottom as the first key factor, showing five well-defined assemblages separated by bottom types, each one formed by hauls made on one type of bottom at all depths strata (Fig. 2b). The nMDS plot showed high separation (degree of dissimilarity) among assemblages from the cold coral bottoms (left side of plot), rocky bottoms (center of plot) and muddy-rocky bottoms (right side of plot), as well as the other two bottoms, mixed and muddy (left-bottom side of plot). The last two assemblages, the mixed and muddy bottoms, are very close in the plot, confirming the absence of significant differences at the deepest stratum obtained with PERMANOVA.

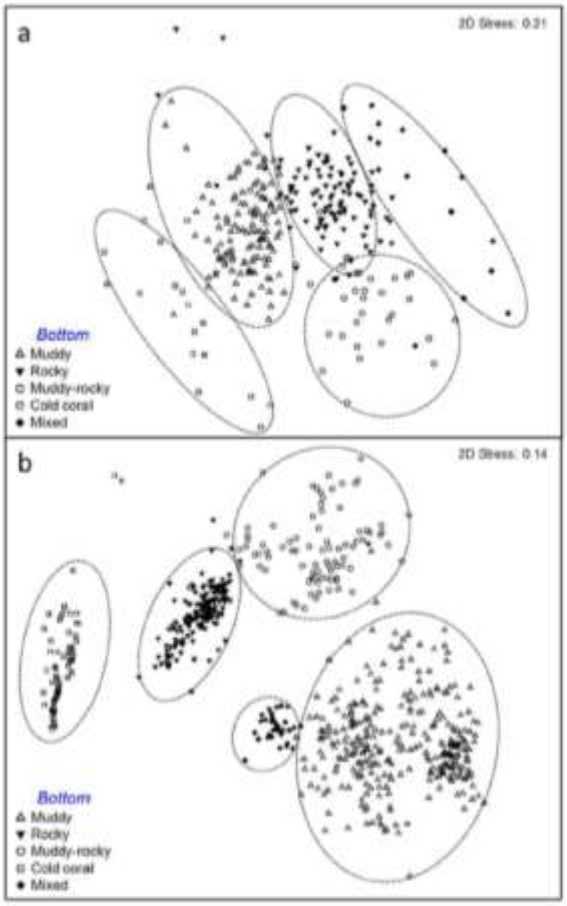
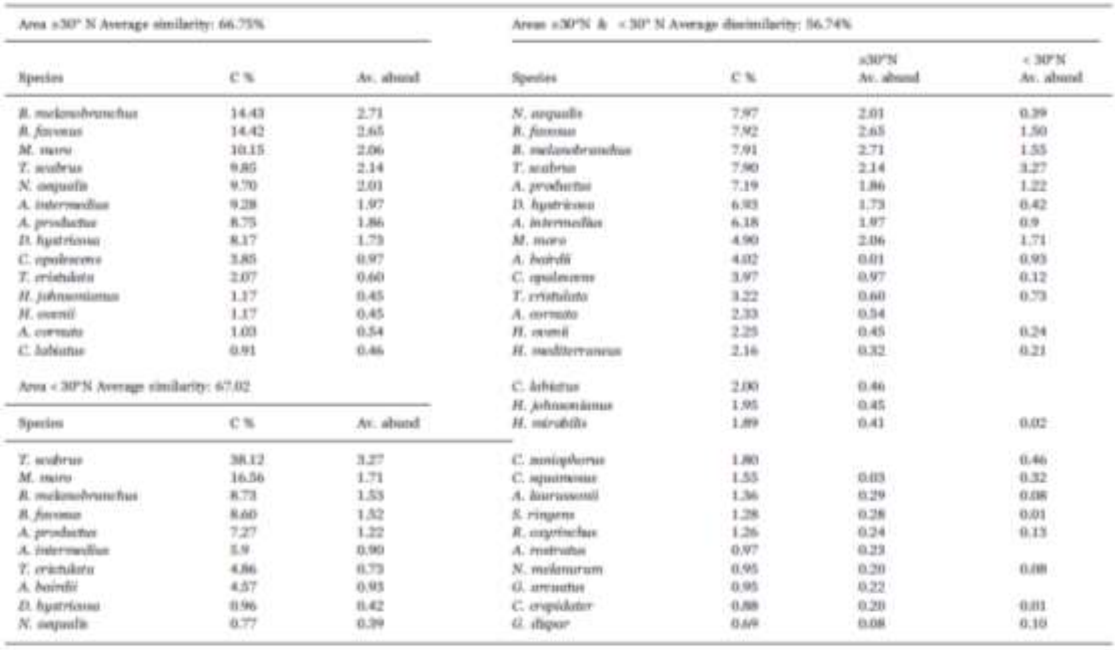


Fig. 2. Non-parametric multidimensional scaling ordination (nMDS) analysis performed on fish abundance (individuals/km2) along the continental slope in the area, (a) ≥30° N, (b) < 30° N, off the northwestern coast of Africa. S, Stress.

The results of the SIMPER analysis revealed the most important species contributing to the similarity and dissimilarity among areas or bottom types found as significantly different by PERMANOVA (Table 3). *B. melanobranchus* and *B. favosus* were the species that better discriminated between the areas, which occurred at higher abundances in the area ≥30° N, whilst *T. scabrus* and *M. moro* occurred at higher abundances in the area < 30° N. *N. aequalis*, *B. favosus*, *B. melanobranchus*, *Deania hystricosa*, *Aphanopus intermedius*, *Coelorinchus labiatus* and *Halosaurus johnsonianus* were restricted or more abundant in the area ≥30° N and were found to be the discriminating species that most contributed to the average dissimilarity between the areas. *T. scabrus*, *M. moro*, *T. cristulata* and *Alepocephalus bairdii* were more abundant in the area < 30° N. The results of SIMPER (Table 4) in areas located at latitudes ≥30° N, showed, as a general pattern, that at these latitudes, the contribution of higher number of species is necessary to define the assemblages than at latitudes < 30° N, with low values of dissimilarities between assemblages, ranging from 32.7% (between muddy and rocky bottoms) to 53.8% (between cold coral and muddy, rocky, cold coral mixed bottoms). Eight species, *B. melanobranchus*, *B. favosus*, *A. intermedius*, *M. moro*, *N. aequalis*, *T. scabrus*, *A. productus*, and *D. hystricosa*, provided the major contribution (> 86%) for defining the muddy bottoms assemblage. In the cold coral bottoms, *A. intermedius*, *M. moro*, *D. hystricosa*, *A. productus*, *B. favosus*, *B. melanobranchus*, *T. scabrus* and *Scymnodon ringens* were the most characteristic species, contributing > 84% of the average similarity. *B. favosus*, *B. melanobranchus*, *T. scabrus*, *N. aequalis*, *A. productus*, *M. moro*, *D. hystricosa* and *A. intermedius* were the main contributors to the average similarity (> 81%) for the rocky bottoms assemblage. For the muddy, rocky, cold coral mixed bottoms assemblage, nine species, *N. aequalis*, *B. favosus*, *B. melanobranchus*, *T. scabrus*, *D. hystricosa*, *M. moro*, *A. intermedius*, *Hoplostethus mediterraneus* and *Chimaera opalescens*, accounted for more than 79% of the average similarity. *N. aequalis*, *A. productus*, *M. moro*, *T. scabrus*, *D. hystricosa*, *A. intermedius*, *B. favosus*, *B. melanobranchus*, *C. opalescens* and *C. labiatus* were the main contributors to the average similarity of the muddy-rocky bottoms assemblage, accounting for more than 79% of the average similarity.

Table 3. Results of SIMPER routine for each area (north and south of parallel 30° N) analysing the contribution (C %; cut off=95%) of typifying species to within-group similarity and showing species that most contribute to dissimilarity. Av. abund. is the average abundance.



Area ≥30° N Average similarity: 66.75%

Species	C %	Av. abund
B. melanobranchus	14.43	2.71
B. favosus	14.42	2.65
M. moro	10.15	2.06
T. scabrus	9.85	2.14
N. aequalis	9.70	2.01
A. intermedius	9.28	1.97
A. productus	8.75	1.86
D. hystricosa	8.17	1.73
C. opalescens	3.85	0.97
T. cristulata	2.07	0.60
H. johnsonianus	1.17	0.45
H. ovenii	1.17	0.45
A. cornuta	1.03	0.54
C. labiatus	0.91	0.46

Area < 30°N Average similarity: 67.02

Species	C %	Av. abund
T. scabrus	38.12	3.27
M. moro	16.56	1.71
B. melanobranchus	8.73	1.53
B. favosus	8.60	1.52
A. productus	7.27	1.22
A. intermedius	5.9	0.90
T. cristulata	4.86	0.73
A. bairdii	4.57	0.93
D. hystricosa	0.96	0.42
N. aequalis	0.77	0.39

Areas ≥30°N & < 30° N Average dissimilarity: 56.74%

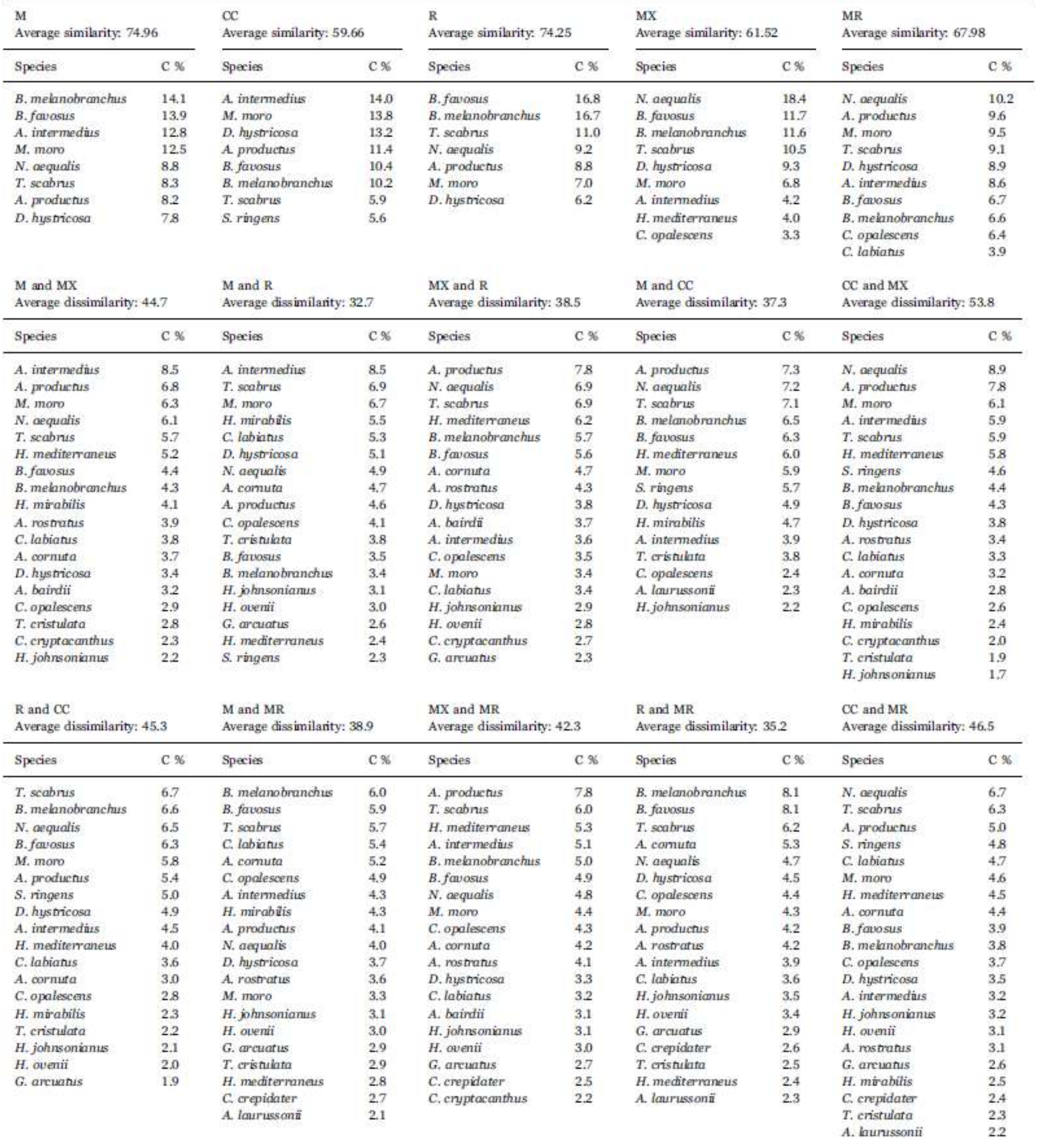
Species	C %	≥30°N Av. abund	< 30°N Av. abund
N. aequalis	7.97	2.01	0.39
B. favosus	7.92	2.65	1.50
B. melanobranchus	7.91	2.71	1.55
T. scabrus	7.90	2.14	3.27
A. productus	7.19	1.86	1.22
D. hystricosa	6.93	1.73	0.42
A. intermedius	6.18	1.97	0.9
M. moro	4.90	2.06	1.71
A. bairdii	4.02	0.01	0.93
C. opalescens	3.97	0.97	0.12
T. cristulata	3.22	0.60	0.73
A. cornuta	2.33	0.54	
H. ovenii	2.25	0.45	0.24
H. mediterraneus	2.16	0.32	0.21
C. labiatus	2.00	0.46	
H. johnsonianus	1.95	0.45	
H. mirabilis	1.89	0.41	0.02
C. moniophorus	1.80		0.46
C. squamosus	1.55	0.03	0.32
A. laurussonii	1.36	0.29	0.08
S. ringens	1.28	0.28	0.01
R. oxyrinchus	1.26	0.24	0.13
A. rostratus	0.97	0.23	
N. melanurum	0.95	0.20	0.08
G. arcuatus	0.95	0.22	
C. crepidater	0.88	0.20	0.03
G. dispar	0.69	0.08	0.10

The results of SIMPER (Table 5) showed that few species provided the major contribution for defining the assemblages at latitudes < 30°N, with the values of the dissimilarities ranging from 40.6% (between muddy and muddy, rocky, cold coral mixed bottoms) to 85.7% (between muddy and cold coral bottoms). Three species, *A. productus*, *M. moro* and *A. intermedius*, provided the major contribution (> 88%) for defining the cold coral bottoms assemblage. In the rocky bottoms, *T. scabrus*, *A. productus* and *M. moro* were the most characteristic species of the assemblage, which contributed > 85% of the average similarity. *T. scabrus*, *B. favosus*, *A. productus*, *B. melanobranchus* and *M. moro* were the main contributors to the average similarity (> 92%) of the muddy, rocky, cold coral mixed bottoms assemblages. For the muddy-rocky bottoms assemblage, three species, *T. scabrus*, *T. cristulata*, and *M. moro*, accounted for more than 82% of the average similarity. The main contributors of the average similarity to the muddy bottoms assemblage were *T. scabrus*, *B. favosus*, *B. melanobranchus* and *A. bairdii*, accounting for more than 80% of the average similarity.

PERMANOVA indicated significant differences in species richness and the Shannon-Wiener diversity index among bottom types (S, p-F=13.92, p < 0.0001; H′, p-F=9.37, p < 0.0001); in richness among the depth strata (p-F=2.92, p=0.0467); and in richness, diversity and evenness between the areas (S, p-F=328.39, p < 0.0001; H′, p-F=160.88, p=0.00091; J′, p-F=12.50, p=0.0009), with the area being the most influential factor in all cases (Table 6). Taking the areas into account, the greatest richness (S=19.71), diversity (H′=2.14) and evenness (J′=0.73) were found at latitudes higher than 30° N (Fig. 3). No significant differences in S, H′ or J′ were observed between the mesh sizes (p-F < 0.13; p > 0.8022) or between the mesh sizes crossed with other factors (p-F < 1.66, p > 0.1833). Significant differences in richness were found for the crossed factors bottom type and area (p-F=23.39, p < 0.0001).

PERMANOVAs computed separately for each area showed significant differences in S, H′ and J′ among the bottom types in the area ≥30° N. The area < 30° N also showed significant differences in the richness, diversity and evenness among the bottom types, and in diversity and evenness among the depth strata (Table 6). No significant differences in S, H′ and J′ were observed between the mesh sizes (p-F < 0.22, p > 0.6426) or between the mesh size crossed with bottom type and/or depth strata (p-F < 1.71, p > 0.1512) in both areas. At latitudes ≥30°, N pair-wise comparisons showed significant differences in S, H′ and J′ among the bottom types in all cases (t > 1.69, p < 0.0066) (Fig. 3), with the exception in richness between muddy and cold coral (t=1.61, p=0.104), muddy and rocky (t=1.63, p=0.0937), muddy-rocky and rocky (t=0.65, p=0.4509), rocky and mixed (t=0.36, p=0.7018) and mixed and muddy-rocky (t=0.36, p=0.7149); in diversity between muddy and rocky (t=0.44, p=0.6283), cold coral and mixed (t=0.67, p=0.5019), muddy-rocky and rocky (t=1.12, p=0.2062), and rocky and mixed (t=1.35, p=0.1432); and in evenness between muddy and cold coral (t=2.10, p=0.0399), muddy and rocky (t=2.15, p=0.0228), muddy and muddy-rocky (t=0.35, p=0.7460), cold coral and mixed (t=0.99, p=0.3321), rocky and mixed (t=1.55, p=0.1210), and rocky and muddy-rocky (t=0.87, p=0.3893). At latitudes < 30° N, pair-wise comparisons showed significant differences in S, H′ and J′ among the bottom types in all cases (t > 1.83, p < 0.044) (Fig. 3), with the exception of S between muddy-rocky and muddy bottoms (t=1.51, p=0.1358) and muddy-rocky and cold coral (t=1.83, p=0.0648); in diversity between muddy and cold coral (t=0.83, p=0.4068) and mixed and rocky (t=0.49, p=0.6707); and in evenness between muddy and rocky (t=0.63, p=0.5431), muddy and mixed (t=1.52, p=0.1267), and rocky and mixed bottoms (t=1.74, p=0.0786). The pair-wise comparisons showed significant differences in diversity among the depth strata in all cases (t > 2.33, p < 0.0127). Evenness differed significantly only between the two shallowest strata (t=2.54, p < 0.0089).

Table 4. Results of SIMPER routine for bottoms types in the area ≥30° N to analysing the contribution (C, in %; cut off=80%) of typifying species to within-group similarity and showing species that most contribute to dissimilarity. MX, muddy-rocky-cold coral mixed bottoms. R, rocky bottoms. MR, muddy-rocky bottoms. CC, cold coral bottoms. M, muddy bottoms.



M Average similarity: 74.96		CC Average similarity: 59.66		R Average similarity: 74.25		MX Average similarity: 61.52		MR Average similarity: 67.98	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
B. melanobranchus	14.1	*A. intermedius*	14.0	*B. favosus*	16.8	*N. aequalis*	18.4	*N. aequalis*	10.2
B. favosus	13.9	*M. moro*	13.8	*B. melanobranchus*	16.7	*B. favosus*	11.7	*A. productus*	9.6
A. intermedius	12.8	*D. hystricosa*	13.2	*T. scabrus*	11.0	*B. melanobranchus*	11.6	*M. moro*	9.5
M. moro	12.5	*A. productus*	11.4	*N. aequalis*	9.2	*T. scabrus*	10.5	*T. scabrus*	9.1
N. aequalis	8.8	*B. favosus*	10.4	*A. productus*	8.8	*D. hystricosa*	9.3	*D. hystricosa*	8.9
T. scabrus	8.3	*B. melanobranchus*	10.2	*M. moro*	7.0	*M. moro*	6.8	*A. intermedius*	8.6
A. productus	8.2	*T. scabrus*	5.9	*D. hystricosa*	6.2	*A. intermedius*	4.2	*B. favosus*	6.7
D. hystricosa	7.8	*S. ringens*	5.6			*H. mediterraneus*	4.0	*B. melanobranchus*	6.6
						C. opalescens	3.3	*C. opalescens*	6.4
								C. labiatus	3.9

M and MX Average dissimilarity: 44.7		M and R Average dissimilarity: 32.7		MX and R Average dissimilarity: 38.5		M and CC Average dissimilarity: 37.3		CC and MX Average dissimilarity: 53.8	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
A. intermedius	8.5	*A. intermedius*	8.5	*A. productus*	7.8	*A. productus*	7.3	*N. aequalis*	8.9
A. productus	6.8	*T. scabrus*	6.9	*N. aequalis*	6.9	*N. aequalis*	7.2	*A. productus*	7.8
M. moro	6.3	*M. moro*	6.7	*T. scabrus*	6.9	*T. scabrus*	7.1	*M. moro*	6.1
N. aequalis	6.1	*H. mirabilis*	5.5	*H. mediterraneus*	6.2	*B. melanobranchus*	6.5	*A. intermedius*	5.9
T. scabrus	5.7	*C. labiatus*	5.3	*B. melanobranchus*	5.7	*B. favosus*	6.3	*T. scabrus*	5.9
H. mediterraneus	5.2	*D. hystricosa*	5.1	*B. favosus*	5.6	*H. mediterraneus*	6.0	*H. mediterraneus*	5.8
B. favosus	4.4	*N. aequalis*	4.9	*A. cornuta*	4.7	*M. moro*	5.9	*S. ringens*	4.6
B. melanobranchus	4.3	*A. cornuta*	4.7	*A. rostratus*	4.3	*S. ringens*	5.7	*B. melanobranchus*	4.4
H. mirabilis	4.1	*A. productus*	4.6	*D. hystricosa*	3.8	*D. hystricosa*	4.9	*B. favosus*	4.3
A. rostratus	3.9	*C. opalescens*	4.1	*A. bairdii*	3.7	*H. mirabilis*	4.7	*D. hystricosa*	3.8
C. labiatus	3.8	*T. cristulata*	3.8	*A. intermedius*	3.6	*A. intermedius*	3.9	*A. rostratus*	3.4
A. cornuta	3.7	*B. favosus*	3.5	*C. opalescens*	3.5	*T. cristulata*	3.8	*C. labiatus*	3.3
D. hystricosa	3.4	*B. melanobranchus*	3.4	*M. moro*	3.4	*C. opalescens*	2.4	*A. cornuta*	3.2
A. bairdii	3.2	*H. johnsonianus*	3.1	*C. labiatus*	3.4	*A. laurussonii*	2.3	*A. bairdii*	2.8
C. opalescens	2.9	*H. ovenii*	3.0	*H. johnsonianus*	2.9	*H. johnsonianus*	2.2	*C. opalescens*	2.6
T. cristulata	2.8	*G. arcuatus*	2.6	*H. ovenii*	2.8			*H. mirabilis*	2.4
C. cryptacanthus	2.3	*H. mediterraneus*	2.4	*C. cryptacanthus*	2.7			*C. cryptacanthus*	2.0
H. johnsonianus	2.2	*S. ringens*	2.3	*G. arcuatus*	2.3			*T. cristulata*	1.9
								H. johnsonianus	1.7

R and CC Average dissimilarity: 45.3		M and MR Average dissimilarity: 38.9		MX and MR Average dissimilarity: 42.3		R and MR Average dissimilarity: 35.2		CC and MR Average dissimilarity: 46.5	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
T. scabrus	6.7	*B. melanobranchus*	6.0	*A. productus*	7.8	*B. melanobranchus*	8.1	*N. aequalis*	6.7
B. melanobranchus	6.6	*B. favosus*	5.9	*T. scabrus*	6.0	*B. favosus*	8.1	*T. scabrus*	6.3
N. aequalis	6.5	*T. scabrus*	5.7	*H. mediterraneus*	5.3	*T. scabrus*	6.2	*A. productus*	5.0
B. favosus	6.3	*C. labiatus*	5.4	*A. intermedius*	5.1	*A. cornuta*	5.3	*S. ringens*	4.8
M. moro	5.8	*A. cornuta*	5.2	*B. melanobranchus*	5.0	*N. aequalis*	4.7	*C. labiatus*	4.7
A. productus	5.4	*C. opalescens*	4.9	*B. favosus*	4.9	*D. hystricosa*	4.5	*M. moro*	4.6
S. ringens	5.0	*A. intermedius*	4.3	*N. aequalis*	4.8	*C. opalescens*	4.4	*H. mediterraneus*	4.5
D. hystricosa	4.9	*H. mirabilis*	4.3	*M. moro*	4.4	*M. moro*	4.3	*A. cornuta*	4.4
A. intermedius	4.5	*A. productus*	4.1	*C. opalescens*	4.3	*A. productus*	4.2	*B. favosus*	3.9
H. mediterraneus	4.0	*N. aequalis*	4.0	*A. cornuta*	4.2	*A. rostratus*	4.2	*B. melanobranchus*	3.8
C. labiatus	3.6	*D. hystricosa*	3.7	*A. rostratus*	4.1	*A. intermedius*	3.9	*C. opalescens*	3.7
A. cornuta	3.0	*A. rostratus*	3.6	*D. hystricosa*	3.3	*C. labiatus*	3.6	*D. hystricosa*	3.5
C. opalescens	2.8	*M. moro*	3.3	*C. labiatus*	3.2	*H. johnsonianus*	3.5	*A. intermedius*	3.2
H. mirabilis	2.3	*H. johnsonianus*	3.1	*A. bairdii*	3.1	*H. ovenii*	3.4	*H. johnsonianus*	3.2
T. cristulata	2.2	*H. ovenii*	3.0	*H. johnsonianus*	3.1	*G. arcuatus*	2.9	*H. ovenii*	3.1
H. johnsonianus	2.1	*G. arcuatus*	2.9	*H. ovenii*	3.0	*C. crepidater*	2.6	*A. rostratus*	3.1
H. ovenii	2.0	*T. cristulata*	2.9	*G. arcuatus*	2.7	*T. cristulata*	2.5	*G. arcuatus*	2.6
G. arcuatus	1.9	*H. mediterraneus*	2.8	*C. crepidater*	2.5	*H. mediterraneus*	2.4	*H. mirabilis*	2.5
		C. crepidater	2.7	*C. cryptacanthus*	2.2	*A. laurussonii*	2.3	*C. crepidater*	2.4
		A. laurussonii	2.1					*T. cristulata*	2.3
								A. laurussonii	2.2

The model for abundance built with negative binomial errors had good residual graphs (residuals versus predictive values and boxplot of residuals), without hints of heteroscedasticity, highest DE% (54.6%) and lowest AIC (12125), and thus was selected among the Poisson model (DE% =52.3%, AIC = 83,203) and the Gaussian model for logtransformed abundance (DE% =50.1%, AIC not comparable among models with different response variables).

Table 5. Results of SIMPER routine for bottom types in the area < 30°N to analysing the contribution (C %; cut off=80%) of typifying species to within-group similarity and showing species that most contribute to dissimilarity. MX, muddy-rocky-cold coral mixed bottoms. R, rocky bottoms. MR, muddy-rocky bottoms. CC, cold coral bottoms. M, muddy bottoms.

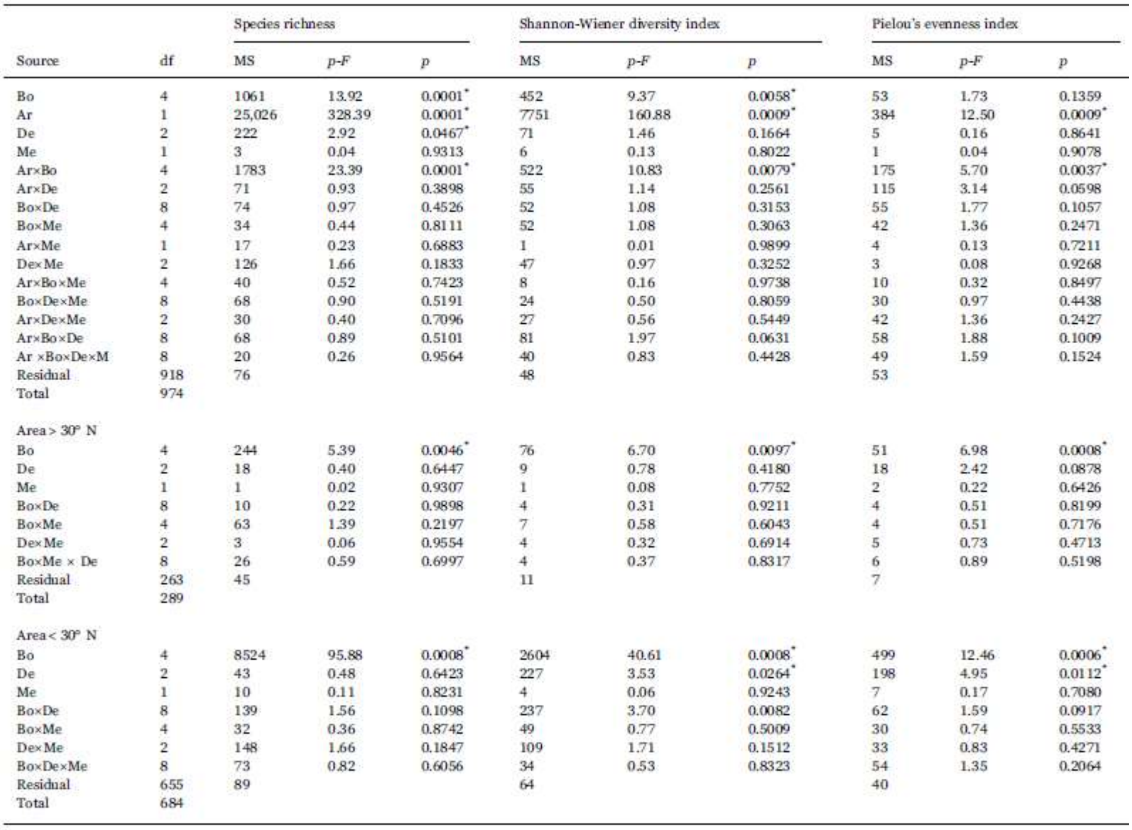
M Average similarity: 66.17		CC Average similarity: 68.00		R Average similarity: 76.93		MX Average similarity: 84.27		MR Average similarity: 60.11	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
T. scabrus	25.4	*A. productus*	37.1	*T. scabrus*	40.8	*T. scabrus*	23.2	*T. scabrus*	63.1
B. melanobranchus	22.8	*M. moro*	32.1	*A. productus*	24.7	*B. favosus*	19.8	*T. cristulata*	10.2
B. favosus	22.4	*A. intermedius*	19.9	*M. moro*	20.0	*B. melanobranchus*	19.6	*M. moro*	9.0
A. bairdii	9.4					*A. productus*	15.9		
						M. moro	13.7		
M and CC Average dissimilarity: 85.7		M and R Average dissimilarity: 66.1		M and MR Average dissimilarity: 61.2		M and MX Average dissimilarity: 40.6		MX and MR Average dissimilarity: 60.0	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
A. productus	13.9	*B. melanobranchus*	15.0	*B. melanobranchus*	16.8	*A. productus*	18.1	*B. favosus*	17.5
T. scabrus	12.7	*B. favosus*	14.8	*B. favosus*	16.6	*A. bairdii*	10.8	*B. melanobranchus*	17.3
B. melanobranchus	11.6	*A. productus*	13.6	*A. bairdii*	7.2	*M. moro*	9.1	*A. productus*	14.3
B. favosus	11.5	*A. bairdii*	7.9	*T. scabrus*	5.9	*A. intermedius*	6.5	*M. moro*	7.9
M. moro	7.6	*M. moro*	6.8	*M. moro*	5.8	*C. zaniophorus*	6.4	*A. bairdii*	6.8
A. intermedius	6.5	*T. cristulata*	5.1	*C. zaniophorus*	5.1	*C. squamosus*	5.7	*A. intermedius*	6.1
A. bairdii	6.2	*A. intermedius*	4.6	*A. intermedius*	5.1	*N. aequalis*	5.6	*T. cristulata*	6.0
C. squamosus	4.4	*C. zaniophorus*	4.5	*T. cristulata*	4.9	*T. scabrus*	4.3	*T. scabrus*	5.2
D. hystricosa	3.6	*T. scabrus*	4.3	*H. mediterraneus*	4.5	*B. favosus*	3.6		
				N. aequalis	4.4	*B. melanobranchus*	3.5		
						T. cristulata	3.5		
						H. ovenii	3.4		
R and MX Average dissimilarity: 51.4		CC and R Average dissimilarity: 58.3		CC and MR Average dissimilarity: 75.6		CC and MX Average dissimilarity: 57.1		R and MR Average dissimilarity: 54.5	
Species	C %	Species	C %	Species	C %	Species	C %	Species	C %
B. favosus	6.7	*T. scabrus*	33.4	*T. scabrus*	23.9	*T. scabrus*	20.4	*A. productus*	24.1
B. melanobranchus	6.6	*A. intermedius*	11.8	*A. productus*	19.3	*B. favosus*	17.6	*M. moro*	13.2
T. cristulata	6.5	*A. productus*	10.3	*M. moro*	11.1	*B. melanobranchus*	17.2	*A. bairdii*	10.3
A. intermedius	6.2	*T. cristulata*	9.8	*A. intermedius*	8.3	*A. productus*	8.0	*A. intermedius*	9.7
C. squamosus	6.2	*C. squamosus*	9.6	*C. squamosus*	6.4	*A. intermedius*	7.9	*T. cristulata*	8.2
M. moro	6.0	*M. moro*	8.2	*T. cristulata*	6.2	*C. squamosus*	6.8	*H. mediterraneus*	6.9
								D. hystricosa	6.3

This model suggested that abundance decreases monotonically with depth in each type of bottom, except in cold-coral and rocky substrata where the relationship is concave-down and thus increases of abundance with depth are predicted in the shallower waters (Table 7, Fig. 4). Abundances were higher in the northern area and on muddy bottoms. The models for the diversity indexes suggested variable relationships with depth. Species richness (S) did not change predictably with depth and was higher in the northern area and on muddy bottoms (Table 8, Fig. 5). The evenness index (J′) related to depth in a way that differed among bottom types (increasing with depth on muddy-rocky and muddy substrata, decreasing on mixed substrate) and was higher in the northern area and on mixed bottoms (Table 8, Fig. 6). The Shannon- Wiener diversity index (H′) changed with depth in a context-dependent way as well (increasing on cold-coral, rocky and muddy-rocky substrata) and was higher in the northern area and on mixed and muddy substrata (Table 8, Fig. 7).

The Center of Gravity (CoG) of the 15 species with the highest standardized abundance in the latitudes above and below 30° N (a total of 26 species for both areas jointly) showed significant differences in latitude (ANOVA, F=78.01 > F0.05,24, > 1000=1.52, p <

0.0001) (Fig. 8). Some species, such as *A. rostratus*, *H. johnsonianus*, *C. labiatus* and *A. cornuta* displayed a very close latitudinal distribution with their CoG located between 30.86° N and 31.04° N. A second group of species, such as *C. opalescens, D. hystricosa, H. mirabilis, B. favosus, A. intermedius*, *S. ringens*, *A. productus*, *B. melanobranchus*, and *N. aequalis*, were distributed in both areas with higher abundance above 30° N and their CoG located between 30.03° N and 30.46° N. A third group of species, such as *T. cristulata*, *N. melanurum*, *A. productus*, *A. laurussonii*, *G. dispar*, *H. ovenii*, *M. moro*, and *H. mediterraneus*, were equitably distributed in both areas, with their CoG located between 29.37° N and 29.82° N. The fourth group was composed of species such as *A. bairdii*, *T. scabrus*, and *C. squamosus*, and distributed in both areas with higher abundance below 30° N and CoG located between 28.11° N and 29.01° N. The fifth group was formed by *M. zugmayeri*, *H. cadenati* and *C. zaniophorus*. The latter group corresponded to species located below 30° N. ANOVA test did not show significant differences in the CoG between the species of each group (F > 17.49 > F0.05, > 2, > 1000 < 3.00, p<0.0001), with the exception of the fourth
group (F=0.87 < F0.05,8, > 1000 < 1.94, p>0.05).

Table 6. Results of the PERMANOVA analysis as a whole and for each area separately for Species richness, Shannon-Wiener diversity index, and Pielou's evenness index. *values indicate significant differences at p < 0.05. df, degrees of freedom; MS, mean squares; p-F, pseudo F value; p, p value. Bo, bottom; Me, mesh size; Ar, Area; De, depth.



		Species richness			Shannon-Wiener diversity index			Pielou's evenness index		
Source	df	MS	*p-F*	*p*	MS	*p-F*	*p*	MS	*p-F*	*p*
Bo	4	1061	13.92	0.0001*	452	9.37	0.0058*	53	1.73	0.1359
Ar	1	25,026	328.39	0.0001*	7751	160.88	0.0009*	384	12.50	0.0009*
De	2	222	2.92	0.0467*	71	1.46	0.1664	5	0.16	0.8641
Me	1	3	0.04	0.9313	6	0.13	0.8022	1	0.04	0.9078
Ar×Bo	4	1783	23.39	0.0001*	522	10.83	0.0079*	175	5.70	0.0037*
Ar×De	2	71	0.93	0.3898	55	1.14	0.2561	115	3.14	0.0598
Bo×De	8	74	0.97	0.4526	52	1.08	0.3153	55	1.77	0.1057
Bo×Me	4	34	0.44	0.8111	52	1.08	0.3063	42	1.36	0.2471
Ar×Me	1	17	0.23	0.6883	1	0.01	0.9899	4	0.13	0.7211
De×Me	2	126	1.66	0.1833	47	0.97	0.3252	3	0.08	0.9268
Ar×Bo×Me	4	40	0.52	0.7423	8	0.16	0.9738	10	0.32	0.8497
Bo×De×Me	8	68	0.90	0.5191	24	0.50	0.8059	30	0.97	0.4438
Ar×De×Me	2	30	0.40	0.7096	27	0.56	0.5449	42	1.36	0.2427
Ar×Bo×De	8	68	0.89	0.5101	81	1.97	0.0631	58	1.88	0.1009
Ar ×Bo×De×M	8	20	0.26	0.9564	40	0.83	0.4428	49	1.59	0.1524
Residual	918	76			48			53		
Total	974									
Area > 30° N										
Bo	4	244	5.39	0.0046*	76	6.70	0.0097*	51	6.98	0.0008*
De	2	18	0.40	0.6447	9	0.78	0.4180	18	2.42	0.0878
Me	1	1	0.02	0.9307	1	0.08	0.7752	2	0.22	0.6426
Bo×De	8	10	0.22	0.9898	4	0.31	0.9211	4	0.51	0.8199
Bo×Me	4	63	1.39	0.2197	7	0.58	0.6043	4	0.51	0.7176
De×Me	2	3	0.06	0.9554	4	0.32	0.6914	5	0.73	0.4713
Bo×Me × De	8	26	0.59	0.6997	4	0.37	0.8317	6	0.89	0.5198
Residual	263	45			11			7		
Total	289									
Area < 30° N										
Bo	4	8524	95.88	0.0008*	2604	40.61	0.0008*	499	12.46	0.0006*
De	2	43	0.48	0.6423	227	3.53	0.0264*	198	4.95	0.0112*
Me	1	10	0.11	0.8231	4	0.06	0.9243	7	0.17	0.7080
Bo×De	8	139	1.56	0.1098	237	3.70	0.0082	62	1.59	0.0917
Bo×Me	4	32	0.36	0.8742	49	0.77	0.5009	30	0.74	0.5533
De×Me	2	148	1.66	0.1847	109	1.71	0.1512	33	0.83	0.4271
Bo×De×Me	8	73	0.82	0.6056	34	0.53	0.8323	54	1.35	0.2064
Residual	655	89			64			40		
Total	684									

The CoG also revealed a different pattern between the areas located above and below 30° N (Fig. 9). Species such as *H. mirabilis*, *G. dispar*, *N. melanurum*, *H. ovenii*, *C. opalescens*, *A. productus*, *H. mediterraneus*, *A. laurussonii* and *T. cristulata echinata* with a deeper CoG in the area ≥30° N showed, by order, significant differences in depth from 299 to 110 m with respect to the area < 30° N (t-test t > 8.74 > t0.05,1, > 100=1.96, p<0.001). Species such as *T. scabrus, A. cornuta, B. favosus, C. squamosus, B. melanobranchus* and *A. bairdii* showed a similar depth pattern above and below 30° N, with the differences in depths lower than 21 m among the species (t-test t < 1.23 < t0.05,1, > 100=1.96, p>0.05). *N. aequalis* and *D. hystricosa* showed a deeper distribution below 30° N, with differences higher than 65 m (t-test t > 7.49 > t0.05,1, > 100=1.96, p<0.001).

The models obtained with the geostatistic approach showed that the distances of spatial influence (A0) were higher in the area ≥30° N than in the area located southward (Table 9). The low value of the nugget C0 in both areas indicated that the sampling spatial resolution used was appropriate. The spatially structured biomass component (C/[C0+C]) was > 87% in both areas reflecting the same well-defined structures.

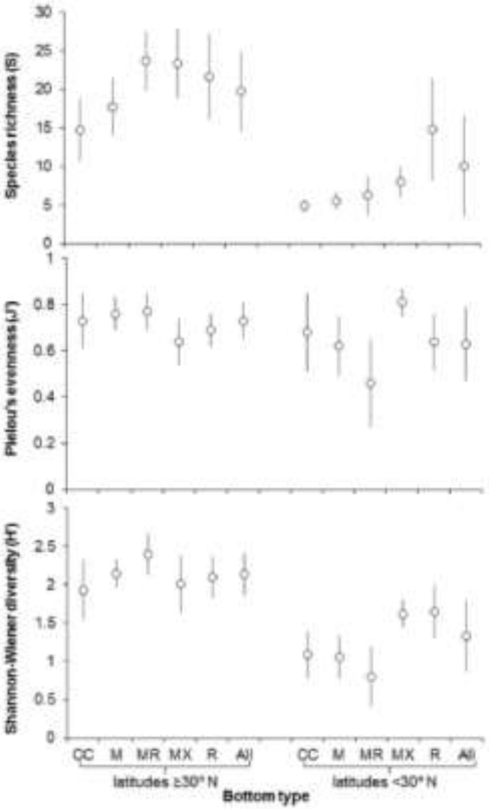


Fig. 3. Estimates of mean (± s.d.) Species richness (S), Pielou's evenness index (J′) and Shannon-Wiener diversity index (H′) for the two studied areas (north and south of parallel 30° N), as well as for the assemblages identified in the present study with respect to bottom type at each area. MX, muddy, rocky, cold coral mixed bottoms; R, rocky bottoms; MR, muddy-rocky bottoms; CC, individual colonies of cold coral bottoms; M, muddy bottoms; All, all bottoms of each area.

An analysis of the goodness of fit showed that the isotropic exponential model for the area ≥30° N and the Gaussian model for the area < 30° N provided the lowest RSS and the highest r^2 (Table 9). Maps of abundance calculated in the area with the obtained models by means of the geostatistical analysis for all species as a whole (Fig. 10) showed the highest abundance values in the area < 30° N. As a whole, these differences in standardized abundance were significant between areas (t-test t=12.36 > t0.05, > 1000=1.96, p < 0.0001).

Table 7. Results of the (a) negative binomial (k=4.372, logarithmic link) generalised additive model for the abundance (individuals/km2) of deep-sea fish species on depth (m) by each of two latitudinal zones (north and south of 30°N) and five bottom substrates in the middle slope off northwest Africa. Values of the parametric coefficient and the corresponding Wald tests (t=estimate/standard error) and p-values and smoothed terms for each substrate and area as the equivalent degrees of freedom as well as an F test and its associated p-value. DE(%) deviance explained.

gam(Abundance~*s*(Depth, by=*f*Substrate)+*f*Substrate+*s* (Depth, by=*f*Area)+*f*Area

Parametric coefficients	Estimate	*t*	Pr (> |t|)	Smoothed terms	EDF	*F*	*p*-value
Intercept (Cold coral, North area)	5.21	70.30	< 0.001	*s*(depth):cold coral substrate	2.69	14.69	< 0.001
Rocky substrate	0.19	2.71	0.007	*s*(depth):rocky substrate	2.77	8.39	< 0.001
Muddy-rocky substrate	0.15	1.88	0.060	*s*(depth):muddy-rocky substrate	1.74	8.23	< 0.001
Mixed substrate	0.44	4.79	< 0.001	*s*(depth):mixed substrate	0.85	2.06	0.185
Muddy substrate	0.91	13.79	< 0.001	*s*(depth):muddy substrate	5.34	5.35	< 0.001
South area	−0.30	−5.67	< 0.001	*s*(depth):north area	0.86	6.05	0.023
DE(%)		54.6					

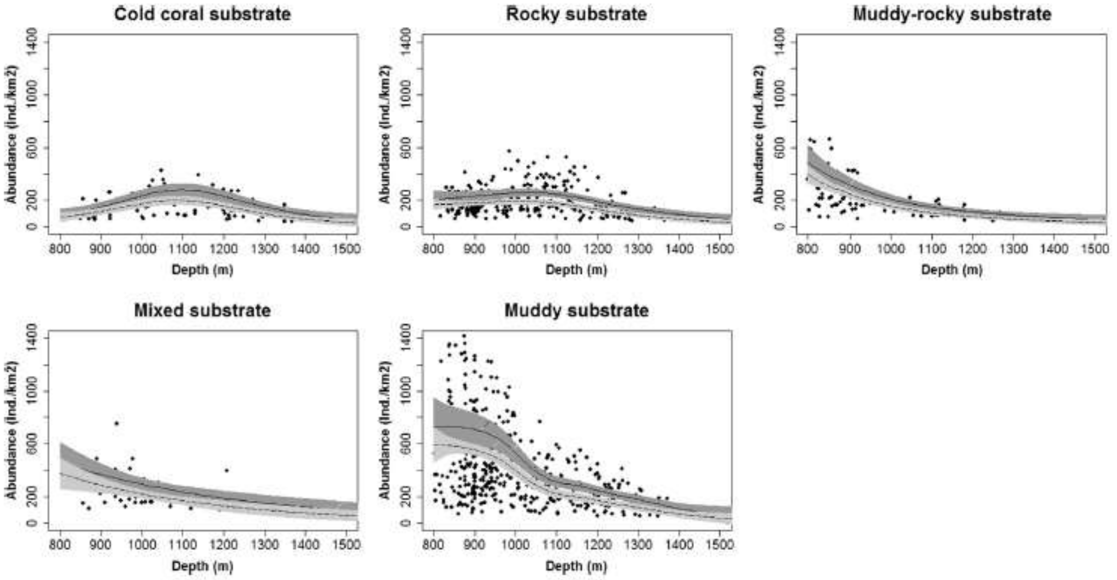


Fig. 4. Scatterplots of the negative binomial generalised additive model for the abundance (individuals/km^2) of deep-sea fish species on depth (m) by each latitudinal zone (north –solid line– and south –dashed line– of 30°N) and five bottom types in the middle slope off northwest Africa. Shaded in grey corresponds with 95% confidence interval.

Table 8. Results of the Gaussian generalised additive model for the (a) species richness (S), (b) Pielou evenness index (J′), and (c) Shannon-Wiener diversity index (H′)) of deep-sea assemblages on depth (m) by each of two latitudinal zones (north and south of 30°N) and five bottom substrates in the middle slope off northwest Africa. Values of the parametric coefficient and the corresponding Wald tests (t=estimate/standard error) and p-values and smoothed terms for each substrate and area as the equivalent degrees of freedom as well as an F test and its associated p-value. DE(%) deviance explained.

Parametric coefficients	Estimate	*t*	Pr(> |t|)	Smoothed terms	EDF	*F*	*p*-value
Species richness (S)							
gam(S~*s*(Depth, by=*f*Substrate)+*f*Substrate+*s* (Depth, by=*f*Area)+*f*Area							
Intercept (cold coral, north area)	17.28	23.72	< 0.001	*s*(depth):cold coral substrate	0.86	0.02	0.907
Rocky substrate	0.60	0.94	0.345	*s*(depth): rocky substrate	0.86	0.34	0.587
Muddy-rocky substrate	2.12	2.89	0.004	*s*(depth):muddy-rocky substrate	2.98	0.56	0.678
Mixed substrate	2.17	2.24	0.025	*s*(depth):mixed substrate	3.44	1.27	0.278
Muddy substrate	5.26	8.61	< 0.001	*s*(depth):muddy substrate	6.07	3.31	0.002
South area	−11.43	−20.45	< 0.001	*s*(depth):north area	7.69	3.15	0.001
DE(%)	54.6			*s*(depth):south area	1.37	0.24	0.749
					0.86	0.02	0.907
Pielou evenness index (J′)							
gam(J′~*s*(Depth, by=*f*Substrate)+*f*Substrate+*s*(Depth, by=*f*Area)+*f*Area							
Intercept (cold coral, north area)	0.75	51.58	< 0.001	*s*(depth):cold coral substrate	2.76	2.40	0.056
Rocky substrate	−0.04	−2.61	0.009	*s*(depth):rocky substrate	0.86	0.001	0.981
Muddy-rocky substrate	−0.07	−4.81	< 0.001	*s*(depth):muddy-rocky substrate	2.00	11.53	< 0.001
Mixed substrate	0.08	4.20	< 0.001	*s*(depth):mixed substrate	0.86	1.02	0.349
Muddy substrate	−0.02	−1.11	0.267	*s*(depth):muddy substrate	1.12	0.45	0.556
South area	−0.07	−7.03	< 0.001	*s*(depth):north area	0.86	0.07	0.802
DE(%)	63.7			*s*(depth):south area	4.68	3.55	0.002
Shannon-Wiener diversity index (H′)							
gam(H′~*s*(Depth, by= *f*Substrate)+*f*Substrate+*s*(Depth, by=*f*Area)+*f*Area							
Intercept (cold coral, north area)	2.03	47.99	< 0.001	*s*(depth):cold coral substrate	2.88	0.98	0.404
Rocky substrate	−0.01	−0.37	0.714	*s*(depth):rocky substrate	4.93	1.79	0.098
Muddy-rocky substrate	0.01	0.348	0.728	*s*(depth):muddy-rocky substrate	4.60	3.36	0.004
Mixed substrate	0.36	6.55	< 0.001	*s*(depth):mixed substrate	1.61	1.39	0.250
Muddy substrate	0.33	8.78	< 0.001	*s*(depth):muddy substrate	2.89	0.83	0.492
South area	−0.88	−28.24	< 0.001	*s*(depth):north area	0.86	0.46	0.529
DE(%)	73.7			*s*(depth):south area	2.46	3.43	0.016

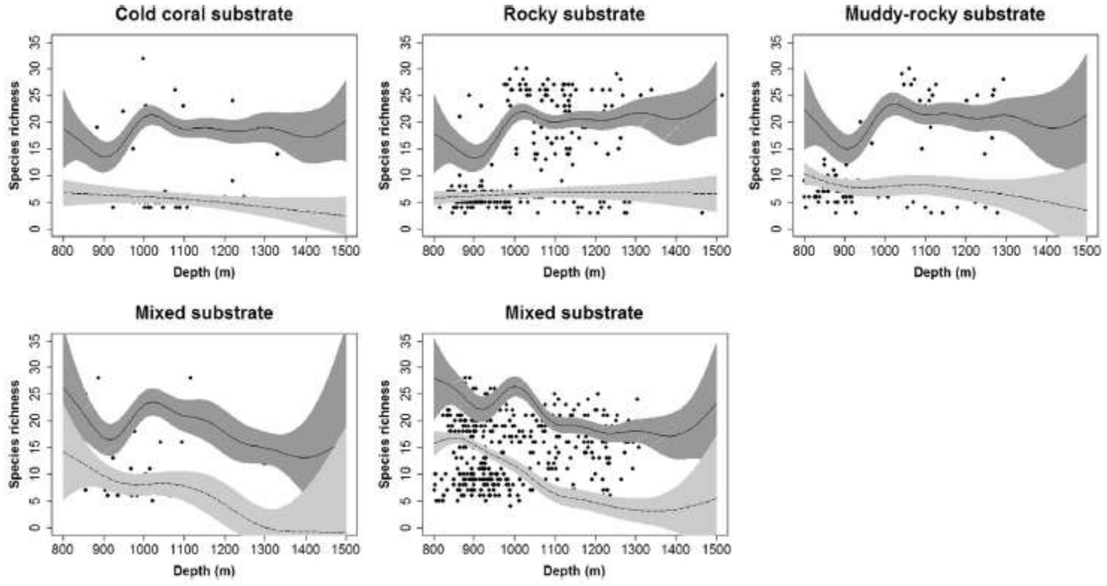


Fig. 5. Scatterplots of the Gaussian generalised additive model for Species richness of deep-sea fish species on depth (m) by each latitudinal zone (north –solid line– and south –dashed line– of 30°N) and five bottom types in the middle slope off northwest Africa. Shaded in grey corresponds with 95% confidence interval.

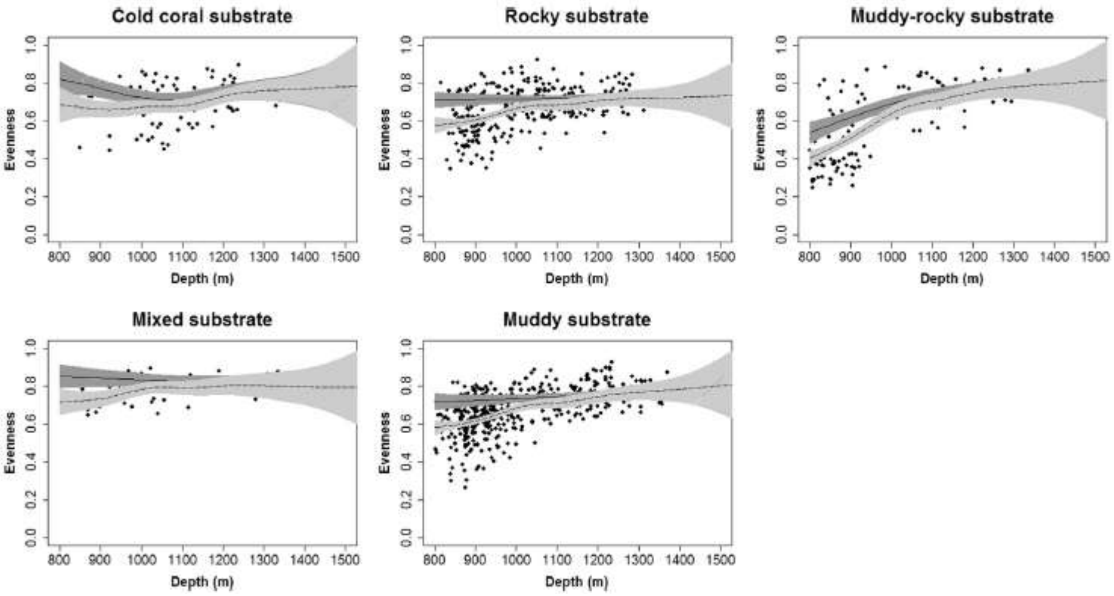


Fig. 6. Scatterplots of the Gaussian generalised additive model for Pielou evenness index (J′) of deep-sea fish species on depth (m) by each latitudinal zone (north –solid line– and south –dashed line– of 30°N) and five bottom types in the middle slope off northwest Africa. Shaded in grey corresponds with 95% confidence interval.

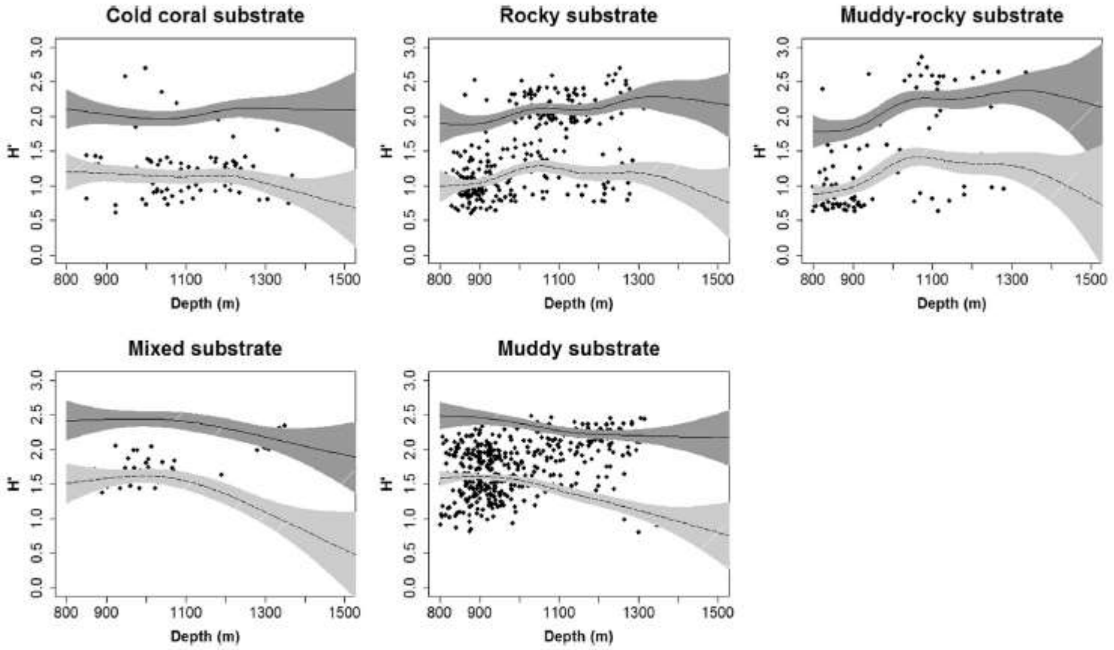


Fig. 7. Scatterplots of the Gaussian generalised additive model for Shannon-Wiener index of diversity (H′) of deep-sea fish species on depth (m) by each latitudinal zone (north –solid line– and south –dashed line– of 30°N) and five bottom types in the middle slope off northwest Africa. Shaded in grey corresponds with 95% confidence interval.

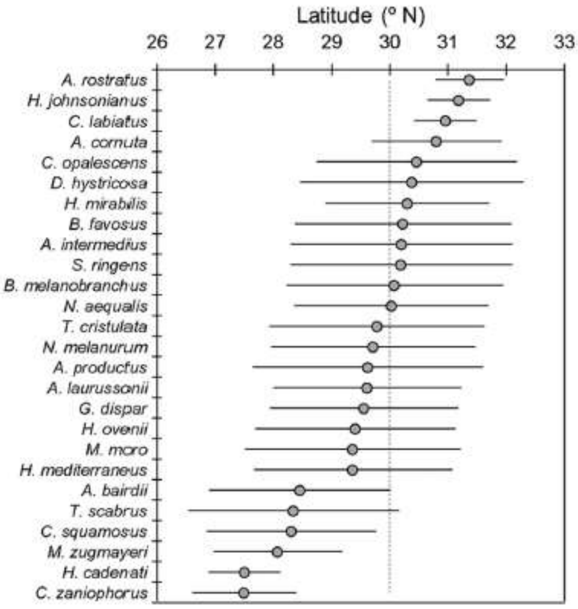


Fig. 8. Center of Gravity (CoG) in latitude for the 15 species with the highest standardized abundance at each area, north and south of parallel 30° N (a total of 26 species for both areas), and their standard deviation. Species are ordered by increasing CoG.

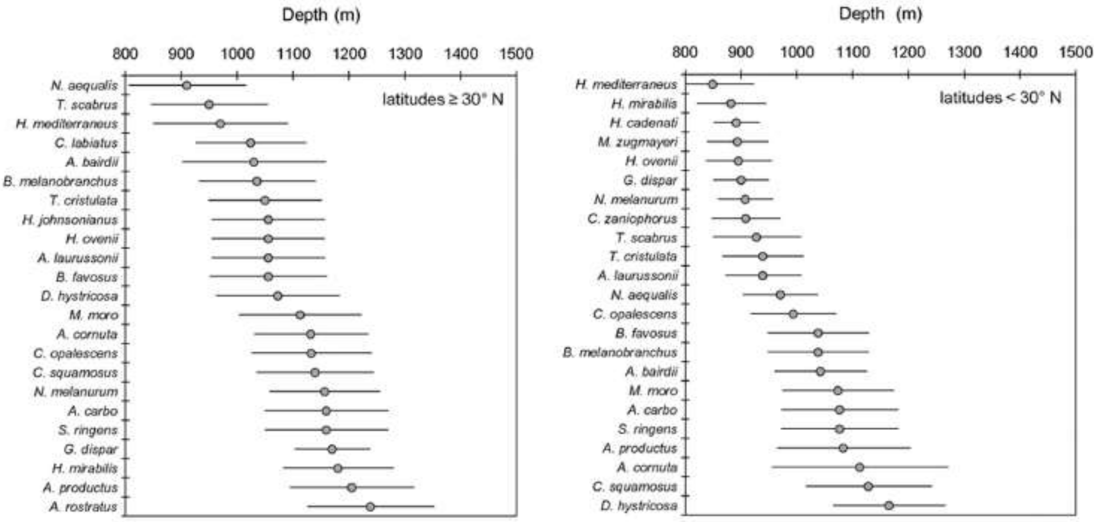


Fig. 9. Center of Gravity (CoG) in depth for the 15 species with the highest standardized abundance at each area, north and south of parallel 30° N (a total of 26 species for both areas), and their standard deviation. Species are ordered by increasing CoG.

Table 9. Parameters of the semivariograms and goodness of fit criteria for variographic analysis based demersal fish abundance (individuals/km2). C0, the nugget effect corresponding with the minimum semivariance; A0, range of the semivariogram; C0+C, sill corresponding with the maximum semivariance; (C/[C0+C]), proportion of variance explained; r^2, coefficient of determination; RSS, residual sum of squares.

Area	Model	Parameters			Goodness of fit		
		C_0	C_0+C	A_0	(C/[C_0+C])	r^2	RSS
≥30°N	Exponential	2.36	24.38	0.159	90.3	0.803	57.92
<30° N	Gaussian	0.13	0.97	0.057	87.1	0.770	0.33

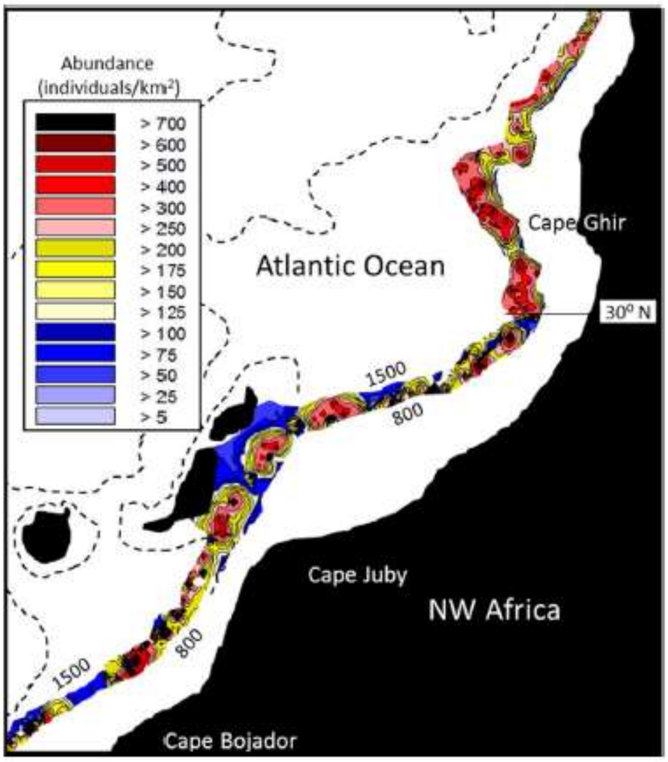


Fig. 10. Map of standardized abundance (individuals/km2) in areas (north and south of parallel 30° N) off the northwestern coast of Africa estimated by using geostatistical analysis.

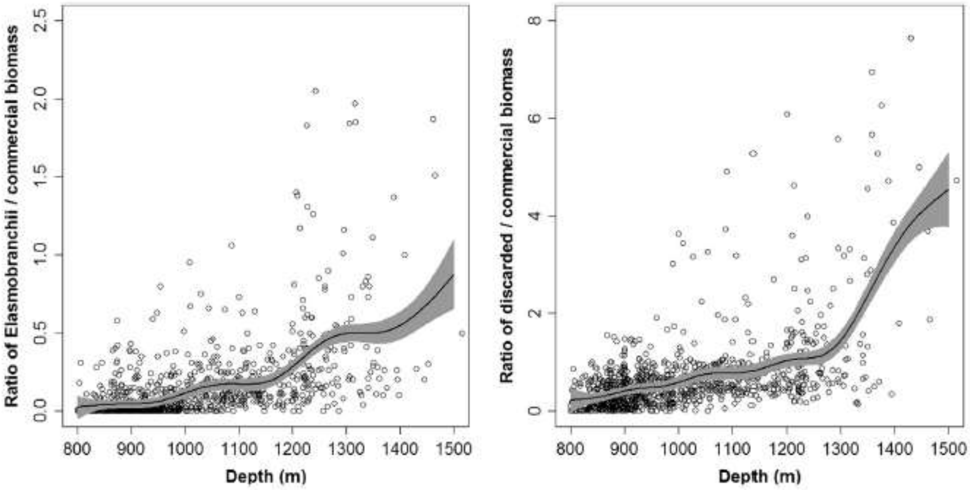


Fig. 11. Scatterplots of the Gaussian generalised additive model with an identity link function for the ratios of Elasmobranchii to commercial biomass (left) and discarded to commercial biomass (right), on depth (m) included as a smoother term. The black line correspond with the fitted values, and shaded in grey with 95%

confidence interval. Model validation was made by examination of plots of the residuals versus the fitted values.

Discussion

The influence of depth, being the primary environmental factor, on the benthic fish communities on the continental shelf and slope has been established in many cases (Haedrich et al., 1975, 1980; Markle et al., 1988; Bianchi, 1992a, 1992b; Koslow, 1993; Moranta et al., 1998, 2008; Massutí et al., 2004). The influence of depth on fish communities are usually linked to abiotic factors that change with depth, such as the temperature, the salinity or the pressure (Markle et al., 1988; Cartes and Sardà, 1993; Maynou and Cartes, 2000; Follesa et al., 2009; Pajuelo et al., 2015). In the present study the most influential factors observed were the latitude followed by the bottom type and depth in the third place. This finding could be explained by the fact that the depth range studied is narrow and entirely occupied by the Mediterranean Water Mass that can be found from approximately 700 to 1600 m of depth. This water mass, which flows southward, shows small changes in temperature and salinity, with values ranging 7–10 °C and 35.3–35.5 psu (Hernández-Guerra et al., 2001; Knoll et al., 2002; Pelegrí et al., 2005a), respectively. However, other abiotic conditions in the upwelling area of study, such as the presence of a wide submarine canyon in the Agadir region, the fluctuation of the upwelling system under variable wind pulses during the year (Arístegui et al., 2004), the formation of a filament structure in Cape Ghir from the coastal upwelling systems (García- Muñoz et al., 2004; Arístegui et al., 2009), and the reduction of the upwelling event from Cape Ghir to Cape Juby (Pelegrí et al., 2005a), could be especially relevant to the existence of boundaries in the area.

The boundary observed at latitudes above and below 30°N can be explained by the existence of topographic and oceanographic factors. Approximately at 30°N, the continental slope is cut by the Agadir Canyon, which collects and channels the sediments of the Souss River, the main river of the Atlas Mountains, along the slope until reaching a depth of 4000 m, where the Agadir Canyon is constrained by two seamounts (Bozzano and Alonso, 2009). In the area above 30°N, a strong upwelling event occurs (Pelegrí et al., 2005a, 2005b) and the Cape Ghir filament drives the transfer of organic matter from the coastal upwelling to the slope by sedimentation (Neuer et al., 2002; García-Muñoz et al., 2005). Additionally, in the north area the shelf is narrower than in the south area, with an average width of 25–30 km.

This narrower shelf has less ability to retain particulate material by deposition and accumulation on the plateau (Bozzano and Alonso, 2009), and more material can reach the middle slope. The absence of clear boundaries based on the different types of bottoms in the area above 30°N, mainly in the first studied stratum, can be linked to the effects of the strong upwelling with higher levels of primary and secondary production; these increased levels of production and the steepness of the slope might reduce the pressure that induces resource partitioning in the deep demersal fish assemblages and therefore might blur the boundaries (Merrett and Marshall, 1981; Merrett and Domanski, 1985a).

In the south region located below 30° N, the reduction of the upwelling event occurs primarily from Cape Ghir to Cape Juby (Pelegrí et al., 2005b). Eberwein and Mackensen (2006) indicated that the area between Cape Ghir and Cape Juby is characterized by lower trophic conditions, with a more seasonal signal in primary productivity. This trophic condition, with lower levels (being high) of primary and secondary production and a steep slope, may increase the pressure on the resources and induce resource partitioning in the deep demersal fish community and therefore may clearly mark the boundaries among the substrata and their corresponding trophic nets as a consequence of the topographic heterogeneity of the study area. Additionally, Merrett and Domanski (1985a) indicated that for this area the substrata could be an important feature affecting the establishment of assemblages.

Other studies have also reported the substratum and productivity or the biological requirements as the main factors defining demersal fish assemblages (Merrett and Marshall, 1981; Snelgrove and Haedrich, 1985; Merrett et al., 1991a; Koslow, 1993; Stefanescu et al., 1993). Although the type of sampling net is one of the main factors that affects the composition and distribution of benthic species linked to selectivity among bottom trawls, which depends on many factors, such as the mesh size, mouth area and towing speed (Merrett et al., 1991a, 1991b; Gordon and Bergstad, 1992; Cartes et al., 2009), the results obtained did not show evidence of the influence of the meshes used on the species composition or assemblage.

The observed reduction in the abundance with depth is linked to the general pattern of the decrease in the flux of organic matter from the coastal area to the lower slope, which produces a depth-related decrease in productivity (Rowe et al., 1991). A similar pattern of decrease, with low values of abundances recorded with depth, has been described in the Atlantic (Haedrich et al., 1975; Wenner and Boesch, 1979; Markle et al., 1988; Cartes et al., 2007), as well as in the Mediterranean (Follesa et al., 2009; Fanelli et al., 2013).

The greatest mean species richness and diversity (also in abundance) were located at latitudes higher than 30° N. This spatial pattern can be linked with the productivity gradient described, which has a direct influence on species diversity (Waide et al., 1999), which is higher in the north area. Paterson and Lambshead (1995) and Rex et al. (2005) suggested that a reduction in species richness is linked to a reduction in food availability, as it takes place in the studied area. South of Cape Ghir, with a general reduction in food availability, other factors linked to the heterogeneity of the habitat and the food availability in each habitat could be responsible for the different values observed in species richness and diversity among the substrata. In both areas, the lowest values of diversity were observed on cold coral bottoms and these low values can be due to the vulnerability of cold coral bottoms to fishing activity (Pham et al., 2015), mainly to bottom trawl fishing. The trawl activity in the study area has affected these biological structures formed by individual colonies of cold corals, and as a result, broken coral parts are hauled with the catches, which explains why trawl activity results in a loss of these slow-growing organisms and thus could eventually reduce the abundance and diversity of related species.

In previous pioneering studies in the area in 1976, Merrett and Domanski (1985a, 1985b) found that of the 60 species recorded at the depth range 800–1500 m and between 27° and 31.26° N (13 hauls), the dominant species, in decreasing order of abundance, were as follows: *Synaphobranchus kaupi* (35% specimens, 990 individuals), *B. melanobranchus*, *H. mediterraneus*, *N. aequalis*, *Gadomus longifilis*, *B. favosus*, *Sphagemacrurus hirundo*, *Rouleina attrita*, *L. macrops*, *H. johnsonianus*, *Halosaurus guentheri* and *Alepocephalus rostratus*. These dominant species are quite different from the main species found in the present work, which are as follows: *T. scabrus*, *B. favosus*, *M. moro*, *A. productus*, *N. aequalis*, *B. melanobranchus*, *H. mediterraneus*, *D. hystricosa*, *A. intermedius*, *A. bairdii* and *A. rostratus*. When comparing three different trawl nets, Merrett et al. (1991a) found similar results and noted that, from the point of view of abundance, the catch from each trawl net was strongly influenced by the respective catching characteristics. Macrouridae, Alepocephalidae and Moridae were found to be the most abundant families caught in large trawl nets, but Synaphobranchidae, followed by Macrouridae and Moridae, were the most abundant in the small nets (Merrett et al., 1991a). Of the 96 species recorded in this study (160% more), 39 were coincident with the species reported by Merrett and Domansky (1985a, b), whereas 21 species reported by Merrett and Domansky (1985a, b) were not recorded in the present study (10 species were represented by only one or two individuals). However, the present study recorded 57 species that were not found by Merrett and Domanski, (1985a, (1985b.

The main difference between the two studies was the low number or absence of individuals of a large size or a high swimming capacity found by Merrett and Domanski (1985a, 1985b), such as for the Elasmobranchii and Holocephali species, which were represented by only 13 individuals (0.44%), as well as the predominance of individuals with a low swimming capacity or low movement behaviour, such as the small-sized species of Synaphobranchidae (cutthroat eels). These differences can be explained by the dissimilarity pattern observed between large and small trawl nets, which are linked to the characteristics of each species (Merrett et al., 1991a). These authors also indicated that species with high fidelity for different size trawl nets corresponded with species of an individual adult size that were sufficient to be retained by the mesh of large nets, but they were not mobile enough to avoid the small nets. The species with high fidelities for large trawl nets, such as *Centroscymnus coelolepis, Deania calcea* or *Aphanophus carbo*, were, as adults, large active fishes that were capable of avoiding the small nets (Merrett et al., 1991a).

The species with high fidelity for small trawl nets were relatively small-sized adults or elongated species with a small cross-sectional area, such as *S. kaupi* or *N. aequalis*. Merrett et al. (1991a) indicated that these species seem to be more frequently retained by small trawl nets as a consequence of their smaller mesh size or because the ground-line operates closer to the bottom due to their smaller-size bobbins. Some authors also indicated that when small nets are used at low speed, large and active fishes are less effectively caught (Day and Pearcy, 1968; Haedrich et al., 1975; Merrett and Marshall, 1981; Pearcy et al., 1982; Merrett and Domanski, 1985a; Merrett et al., 1991a). Results of the present study are similar to those obtained by Golovan (1978) in a southward area (8-27° N) of the African coast who found high incidence of mobile species of large-sized squaloid sharks in samples carried out by a large trawl towed faster. In addition, as occurred in the pioneer works of Merrett and Domanski (1985a, 1985b), a negligible fraction were fishes of the mid-water fauna that could be recorded during the opening/ closing hauls.

In the present work, Macrouridae (grenadiers or rattails) were the most abundant and most diverse fish family, followed by the Centrophoridae (gulper sharks) and Alepocephalidae (slickheads) families. The main diverse Actinopterigi families observed are coincident with those observed in the study area and southward according to several other authors (Golovan, 1978; Merrett and Marshall, 1981; Merrett and Domanski, 1985a, 1985b) and might constitute a faunal characteristic of this eastern boundary upwelling area. Using small nets, traps, and longlines in a southern area (8-27° N) of the African coast, Golovan (1978) found a dominance of macrourids, with more than twice the number of species as the next diverse family, the Alepocephalidae. Golovan (1978) also found that the species of Alepocephalidae showed high diversity and abundance in the entire area comprised between 0° N and 36° N of the African coast, especially on the slope. Both Merrett and Marshall (1981) from 18° to 27° N and Merrett and Domanski, (1985a, 1985b) from 27° to 34° N also indicated the great dominance and diversity of the Macrouridae species, although the main species reported differed between the two studies. Merrett and Marshall (1981) suggested that this might be attributable to the types and selectivity of gear, as well as to differences in the latitudinal range sampled. These differences are coincident with the observations by Merrett et al. (1991a), who also noted a clear variation in the catch composition associated to the trawl characteristic with high influence of species of Synaphobranchidae in the specific composition obtained from small trawl nets, together with a high influence of the Alepocephalidae, Trachichthyidae, Squalidae and Trichiuridae species obtained with large trawls net in relation to small ones.

Additionally, Merrett and Marshall (1981) and Merrett and Domanski (1985a) suggested that the dominance of macrourids is possible because of the existence of resource partitioning among these species. These authors also suggested a lack of competitive exclusion among these closely related species due to the presence of species of three subfamilies of macrourids in the area with different feeding patterns or strategies. A wide-trophic spectra have been observed in *T. scabrus*, *N. aequalis*, *B. favosus* and *B. melanobranchus,* the main macrourid species found in this study. These fish species feed on different prey, including copepods, mysids, shrimps, cephalopods and fishes, among others (Geistdoerfer, 1986,1990; Cohen et al., 1990).

This suggests that more than resource partitioning takes place among these species; it might be that the effects of upwelling, with high level of primary and secondary productivity, could reduce the pressure for resource partitioning among them. Other factors, such as the presence of these species on diverse types of substrata, as has been observed in this study, also contribute to avoid exclusion among these species.

Perhaps the relatively high abundance of the small-sized species of other families, such as *M. moro*, *A. productus*, *H. mediterraneus*, *A bairdii* and *A. rostratus*, as has also been observed by Merrett and Domanski (1985a), could be the result of a lack of competitive exclusion among these species with macrourid species because they also feed on fishes, molluscs, shrimps and mysids, among other prey (Coleman and Mobley, 1984; Markle and Quéro, 1984; Macpherson and Roel, 1987; Pais, 2002). As sampling was restricted to the middle slope, the relative abundance of some species on each substrate may be underrepresented due to incomplete sampling of the depth range that those species commonly occupy. However, a clear dominance in the abundance of *T. scabrus* has been observed, with abundance values five times higher than the rest of the species. This change in the pattern of this macrourid with respect to the pioneer studies in the area in 1976 could be due to changes in the ecosystem caused by more than thirty years of fishing activity.

The deep-sea trawl fishery produces a significant impact on the bathyal ecosystem, primarily on the deep-sea shark species. In the previous study of Merrett and Domanski (1985b), the elasmobranchs recorded were only 0.275% of the total number of specimens collected in the area, giving an indication of low abundance. In the present study, the presence of the deep-sea sharks in the area is also low. However, its importance can be emphasized by their contribution in the total biomass hauled, reaching approximately one-quarter by weight of the total catch. The present data indicated that deep-sea sharks suffer severe impacts from this fishery with approximately 50 deep-sea sharks caught in each haul in the area. Although individuals could be returned live to sea, the rapid changes in temperature and pressure during the hoist of the trawl from the bottom likely affect their survival (Pajuelo et al., 2010). This is aggravated by the vulnerability of elasmobranch populations to fishing activity. Such vulnerability is due to their life strategies, such as late sexual maturity, low fecundity and growth, and in many cases their viviparity (Stevens et al., 2000; Figueiredo et al., 2008; Pajuelo et al., 2010). On the basis of these and other characteristics, the ICES working group on the biology and assessment of deepsea fisheries resources graded some of these deep-sea shark species, such as *C. squamosus* or *C. coelolepis*, with a value of 1.5 on a scale of one to five in terms of vulnerability (one being the most vulnerable) (ICES, 2001). Therefore, an intensive exploitation of this deep taxonomic group, which was found to be characterized by a ratio of one deep-sea shark caught for each nine *T. scabrus* (the most abundant species), result in the overfishing and collapse of deep-sea shark populations before the overfishing of the dominant species.

In the northeast Atlantic the abundance of deep-sea species has declined during the last decades being many of them unsustainable (Devine et al., 2006; Bailey et al., 2009; Clarke et al., 2015). The management based in total allowable catch and effort restrictions has not been a solution for this problem with high levels of bycatch of vulnerable species (Allain et al., 2003; Villasante et al., 2012; Clarke et al., 2015). The introduction by European Union of a depth limit to bottom trawling is considered as a good measure to manage deep-sea fisheries. Clarke et al. (2015) proposed the ratio of discarded to commercial biomass, and the ratio of Elasmobranchii to commercial biomass as good indicators to impose an appropriate depth limit to trawl activity. Using generalised additive models, the same authors determined the relationship between each ratio and depth in the North Atlantic. They found that the ratio of discarded to commercial biomass and the ratio of Elasmobranchii to commercial biomass increases with depth at 600–800 m depth. Clarke et al. (2015) suggested the imposition of a maximum fishing depth limit and the prohibition of bottom trawling at depths > 600 m as a management strategy from an ecosystem approach. That limit reflects the depth at which the commercial fishing has negative consequences for the preservation of the biodiversity and for ecosystem health (Clarke et al., 2015).

Following that criteria and methodology, in the north west coast of Africa the proportion of discarded non-target species increased in all range of depths studied, showing an inflection in the pattern from a depth of 1250 m as well as in the ratio of Elasmobranchii to commercial biomass from a depth of 1150 m (Fig. 11); both indices suggesting that the deepest trawls have greater impact on biodiversity in depths > 1150 m, with high levels of catches that were discarded, mainly shark species with low productivity. As an attempt of having a measure to avoid these discards and reduce the exposure of vulnerable fish species and habitats to deep-sea trawl activity in the north west coast of Africa, a management measure based on a ban on trawling at depths greater than 1100 m, at least, could be considered.

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Chapter 14

Deep-sea sharks as by-catch of an experimental fishing survey for black scabbardfishes (*Aphanopus* spp.) off the Canary Islands (NE Atlantic)

CHAPTER 14 - Deep-sea sharks as by-catch of an experimental fishing survey for black scabbardfishes (Aphanopus spp.) off the Canary Islands (NE Atlantic)

Abstract

The deep-sea sharks associated as by-catch of the Madeiran midwater drifting longline fishery for scabbardfishes (*Aphanopus* spp.) were investigated by means of an experimental survey at 800-1200 m depth within the Canary Islands Exclusive Economic Zone, whose fishing grounds have been exploited during the past 15 years. Nine species of chondrichthyans were identified, belonging to five families: Pseudotriakidae, Centrophoridae, Etmopteridae, Somniosidae and Chimaeridae. Data on length, weight and sex ratio for the 436 chondrichthyan individuals caught in the March 2009 survey are given. Several voucher specimens of each species caught were deposited in the collections of the Natural History Museum of Funchal.

Keywords

By-catch, deep-sea Chondrichthyes, midwater drifting longline, NE Atlantic.

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Introduction

The deep-sea fishery of the bathypelagic black scabbardfishes, Aphanopus carbo and A. intermedius, has a long tradition off the Portuguese mainland and around the Madeira archipelago, representing one of the world's longest standing exploitations of meso- and bathypelagic fishes (Delgado et al. 2013, 2018). Off Madeira this fishery is performed with midwater drifting longlines set between 800 and 1200 m depth over the continental slope and nearby seamounts. This is one of the oldest known fisheries in the world targeting a deep-water resource (Leite 1988).

A preliminary study on the by-catch and incidental catch of a potential black scabbardfish (*Aphanopus* spp.) fishery off the Canary Islands, based on a few experimental surveys on board research vessels, was published by Pajuelo et al. (2010).

Ten years ago, Portugal and Spain signed an agreement to study the impact of the black scabbardfish fishery off the Canary Islands, using commercial fishery vessels from Madeira in an experimental survey. The main objectives were i) to study deep-sea sharks as a by-catch of this Madeiran fishery off the Canary Islands, and ii) to compare this by-catch with the bycatch off Madeira and the Portuguese mainland with the same fishing system. The results of this survey are now presented on this short paper.

Materials and methods

In March 2009 an experimental fishing survey was carried out off the Canary Islands between 800 and 1200 m depth using black scabbardfish midwater drifting longlines of the Madeiran type. This fishing gear has 5000 hooks (type 6) (Martins and Ferreira 1995) and is usually set well above the bottom in the water column between 700 and 1300 m depth, without contacting the seafloor (Delgado et al. 2018). Fishing operations were carried out by two Madeiran professional vessels, F/V Pico Dourado and F/V Pico Alto, with scientific observers on board. In accordance with Canary Islands legislation restrictions (no more than 500 hooks per longline are permitted), both vessels used two separate longlines, one much longer than the other: a professional one with around 5000 hooks and an experimental one with around 500 hooks. The neon flying squid Ommastrephes bartramii was used as bait in all longlines. Twenty hauls were carried out off the islands of Tenerife, La Gomera, La Palma, Fuerteventura and El Hierro (Fig. 1). The sampled areas were not randomly selected, but based on the captains' experience from the fishery grounds, as well as on the target species' vertical distribution in the area (Pajuelo et al. 2008).

Shark individuals caught were identified following Compagno et al. (2005) and then counted and weighed by species on board. Catches of chondrichthyans and CPUE values by fishing operation (location) were calculated, as well as an average CPUE per island. CPUE values were expressed in kg (total weight) per 1000 valid hooks. For each species caught, all individuals or well-representative subsamples were selected and preserved on board and then measured (total length TL, in mm), weighed (total weight TW, in g), and sexed at the laboratory.

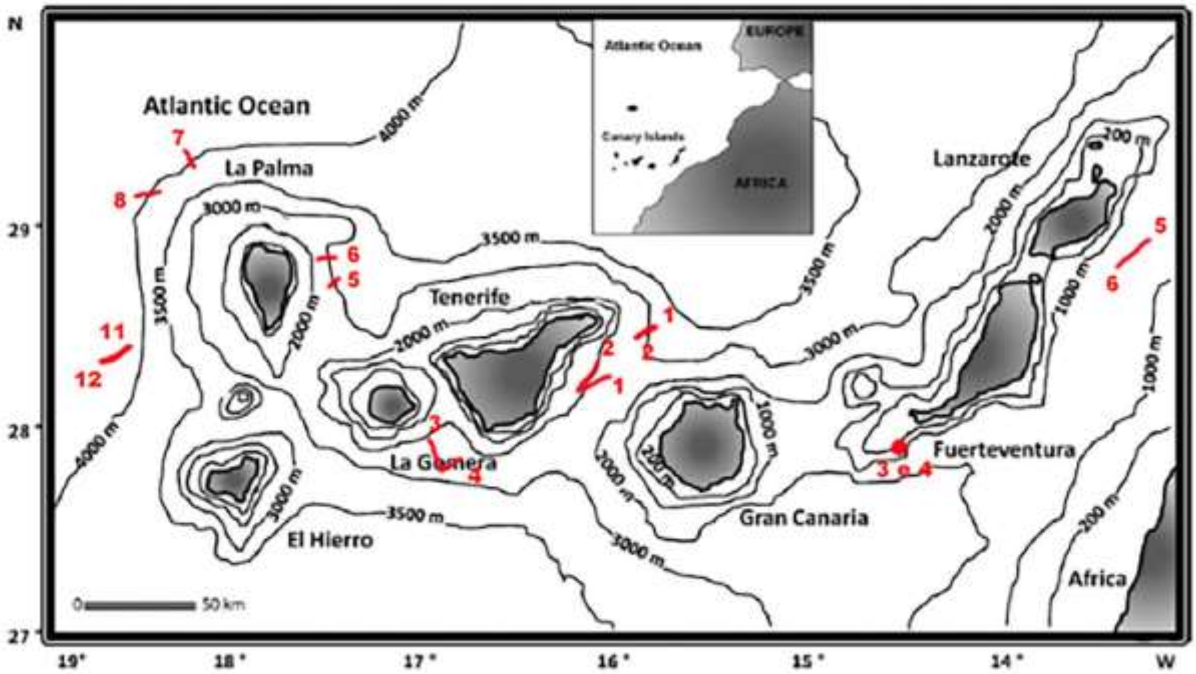


Fig. 1. Map of the Canary Islands showing set locations off the islands of Tenerife, La Gomera, La Palma, Fuerteventura and El Hierro.

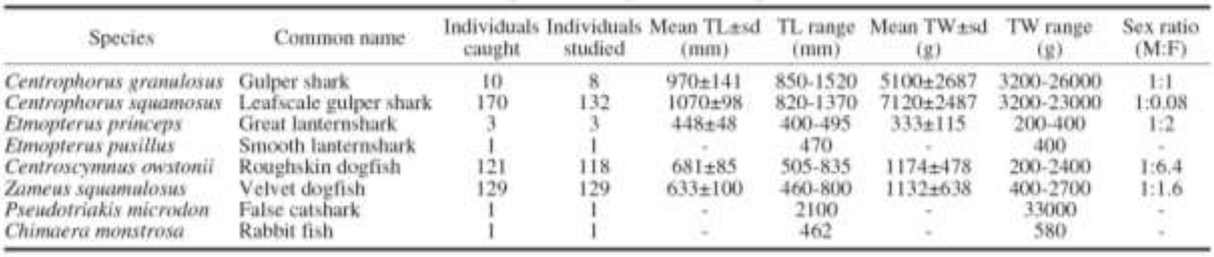
Several voucher specimens of each species caught were deposited in the collections of the Natural History Museum of Funchal (MMF).

Results

A total of 436 individuals of 9 mesopelagic species of Chondrichthyes belonging to 5 families (Pseudotriakidae, Centrophoridae, Etmopteridae, Somniosidae and

Chimaeridae) were captured. The leafscale gulper shark (*Centrophorus squamosus*) (Centrophoridae), represented by 170 individuals, was the most abundant species. The velvet dogfish (*Zameus squamulosus*) (n=129) and the roughskin dogfish (*Centroscymnus owstonii*) (n=121) (both Somniosidae) were well represented in the catches. The capture of the other five chondrichthyans could be considered as incidental (Table 1).

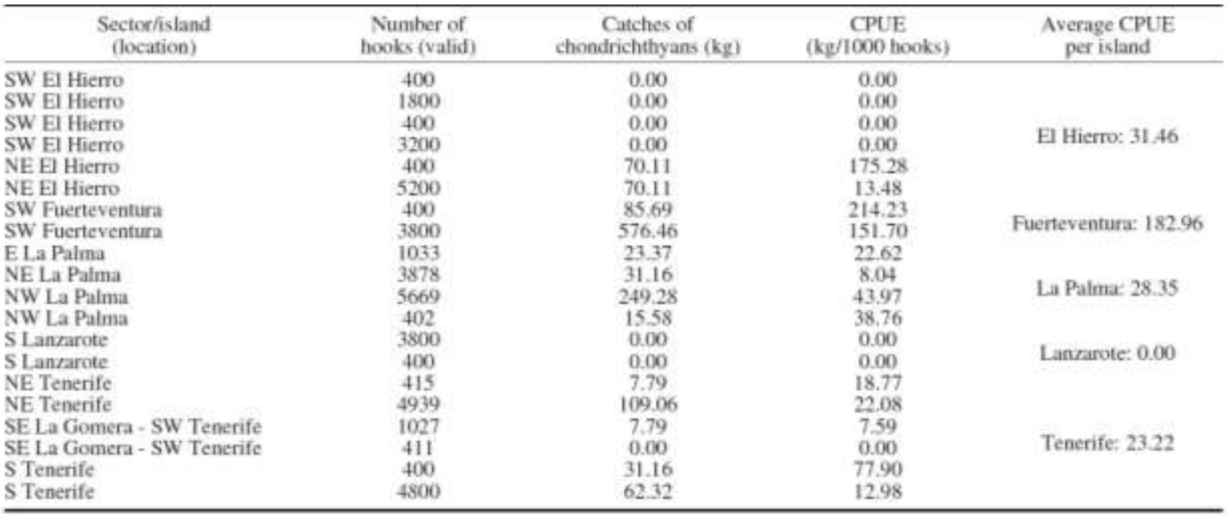
Table 1. Chondrichthyan species caught, with number of individuals, descriptive statistics for size and weight, and sex ratio (males: females). Size as total length (TL); weight as total weight (TW).



Species	Common name	Individuals caught	Individuals studied	Mean TL±sd (mm)	TL range (mm)	Mean TW±sd (g)	TW range (g)	Sex ratio (M:F)
Centrophorus granulosus	Gulper shark	10	8	970±141	850-1520	5100±2687	3200-26000	1:1
Centrophorus squamosus	Leafscale gulper shark	170	132	1070±98	820-1370	7120±2487	3200-23000	1:0.08
Etmopterus princeps	Great lanternshark	3	3	448±48	400-495	333±115	200-400	1:2
Etmopterus pusillus	Smooth lanternshark	1	1	-	470	-	400	-
Centroscymnus owstonii	Roughskin dogfish	121	118	681±85	505-835	1174±478	200-2400	1:6.4
Zameus squamulosus	Velvet dogfish	129	129	633±100	460-800	1132±638	400-2700	1:1.6
Pseudotriakis microdon	False catshark	1	1	-	2100	-	33000	-
Chimaera monstrosa	Rabbit fish	1	1	-	462	-	580	-

Apart from the list of chondrichthyan species caught, Table 1 also indicates the number of individuals captured, the descriptive statistics for size and weight, and the sex ratio (males: females) for each species. Table 2 show catches of chondrichthyans and CPUE values per location. Mean CPUE per island surveyed varied from 0.00 off Lanzarote (no shark was caught) to 182.96 kg/1000 hooks off Fuerteventura, with low CPUE values for the remaining sampled islands.

Table 2. Catches of chondrichthyans and CPUE values per fishing operation (location), with an average CPUE per island. CPUE expressed in kg (total weight) per 1000 hooks.



Sector/island (location)	Number of hooks (valid)	Catches of chondrichthyans (kg)	CPUE (kg/1000 hooks)	Average CPUE per island
SW El Hierro	400	0.00	0.00	El Hierro: 31.46
SW El Hierro	1800	0.00	0.00	
SW El Hierro	400	0.00	0.00	
SW El Hierro	3200	0.00	0.00	
NE El Hierro	400	70.11	175.28	
NE El Hierro	5200	70.11	13.48	
SW Fuerteventura	400	85.69	214.23	Fuerteventura: 182.96
SW Fuerteventura	3800	576.46	151.70	
E La Palma	1033	23.37	22.62	La Palma: 28.35
NE La Palma	3878	31.16	8.04	
NW La Palma	5669	249.28	43.97	
NW La Palma	402	15.58	38.76	
S Lanzarote	3800	0.00	0.00	Lanzarote: 0.00
S Lanzarote	400	0.00	0.00	
NE Tenerife	415	7.79	18.77	Tenerife: 23.22
NE Tenerife	4939	109.06	22.08	
SE La Gomera - SW Tenerife	1027	7.79	7.59	
SE La Gomera - SW Tenerife	411	0.00	0.00	
S Tenerife	400	31.16	77.90	
S Tenerife	4800	62.32	12.98	

Discussion

With regard to the European Red List of Marine Fishes (Nieto et al. 2015), it is important to highlight that the leafscale gulper shark (Centrophorus squamosus), the most captured species in the survey, has been classified as an endangered species. Previously, this shark species was considered as highly vulnerable to depletion and consequently assessed as endangered in the northeast Atlantic (White 2003). Also, this species was included in the OSPAR List of threatened and/ or declining species and habitats (Gibson et al. 2008). Moreover, the gulper shark (Centrophorus granulosus) has been recently catalogued as a critically endangered species (Nieto et al. 2015).

When compared with that of the by-catch identified from the black scabbardfish fishery off Madeira (Bordalo-Machado et al. 2009), chondrichthyan species composition was quite similar to the present results for the Canary Islands waters, except for the absence of the Portuguese dogfish Centroscymnus coelolepis (Somniosidae) and the birdbeak dogfish *Deania calcea* (Centrophoridae) off the Canaries. However, given that the present survey was carried out only in March, any type of seasonal distribution pattern in those species would have been missed.

In the eastern Atlantic, landings of the leafscale gulper shark, *C. squamosus*, the most captured species within the by-catch, over the past decade peaked in 2003 (3042 t) and declined to 243 t in 2009 (Ebert and Stehmann 2013). Based on FAO catch data, in Portugal average landings of this species were 893 t per year from 2000 to 2009. In contrast, short time series of CPUE available for the western coast of Portugal seem to indicate that these landings remain stable (Gibson et al. 2008).

According to the present results and concerns, further studies should be conducted in order to evaluate the real impact of this fishery on the northeastern Atlantic population(s) of the leafscale gulper shark, and should also address technological developments related to the fishing gear tending to minimize its catches.

In order to fully understand the trends of all species caught as by-catch in this fishery, it is important to monitor continuously to obtain representative time series.

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PART V

GENERAL DISCUSSION

Chapter 15

General discussion

GENERAL DISCUSSION

Chondrichthyes as marine predators mediate trophic cascade effects, as top- or mesopredatory species, playing a key role in the ecological balance of the ecosystems (Myers et al., 2007). Nevertheless, they do have not evolved in terms of resistance strategies against rapid fluctuations in mortality caused by anthropogenic pressures and as such proper conservation strategies based on their biology and ecology are essential to maintain their success in the marine ecosystem (Stevens et al., 2000). The European Red List of Marine Fishes consider that in Europe 40.4% of Chondrichthyes are threatened (Nieto et al., 2015). In the archipelago of Madeira, 35.8% of the total reported species are labelled under the same category (Biscoito et al., 2018). Therefore, this group must receive special attention to reverse this trend.

A complete updated species checklist, new records, taxonomic annotations, and clarification as well as filling the gaps on life history of Chondrichthyes in the archipelago of Madeira are mandatory to assess the geographic distribution and depth of the species and to evaluate the fisheries impact on the biology and population dynamics of this group.

Systematics and distribution

Chondrichthyes arose at least 420 million years ago and represent approximately 3.5 % of the modern fish fauna (Nelson, 2006; Kriwet et al., 2008; Ebert *et al*., 2021). The checklist of Chondrichthyes in the waters of the archipelago of Madeira (Biscoito *et al.*, 2018) confirmed the presence of 67 species which represents 5 % of the total valid chondrichthyan species described globally (Weigmann, 2016). Of the species reported 24 are in the list of threatened species as Vulnerable (8), Endangered (9) and Critically

Endangered (7) according to the IUCN European Red List of marine fishes (Nieto *et al.*, 2015).

The checklist of Chondrichthyes of the archipelago of Madeira fills the information gaps on species richness of this important group of fishes, representing an increase of 21 % on the total number of cartilaginous species previously referred to Madeira. Additionally, it includes three species, *Odontaspis noronhai* (Maul, 1955), *Mitsukurina owstoni* Jordan, 1898 and *Chimaera opalescens* (Luchetti *et al.*, 2011), that have not been recorded from the remaining Macaronesian archipelagos.

The checklist of cartilaginous fish of the archipelago of Madeira allowed to verify a latitudinal diversity gradient between the Macaronesian archipelagos of the Canary Islands, Madeira, and the Azores. It was observed that, as latitude increases species richness decreases. The archipelago of Azores located at higher latitudes has the lowest number of species (Santos *et al.*, 1997; Porteiro *et al.*, 2010), while the archipelago of the Canary Islands situated at lower latitudes, has the highest number of species (86 species) (Brito Hernández and Sancho Rafael 2003). This is in accordance with Willig *et al.* (2003) and Hillebrand (2004) that stated that species richness increases from polar to tropical regions for most taxonomic groups.

The deep-water holocephalans *Hydrolagus affinis* (de Brito Capello, 1868) and *C. opalescens* were recorded for the first time for the archipelago of Madeira during this study. Interesting to notice that the results herein presented confirm that *H. affinis* also inhabits oceanic islands and seamounts although it commonly occurs on continental slopes and deep-sea plains. This record not only increases the known area of distribution of this species but also confirms its depth distribution down to 2500 m (Ebert *et al.*, 2021). Concerning *C. opalescens* the first report resulted from the re-examination of a specimen from the Natural History Museum of Funchal (MMF). This specimen was originally identified as *C. monstrosa*, however it was concluded that the specimen was misidentified and that it corresponded to *C. opalescens*. Since no specimens of *C. monstrosa* were located from Madeira in museum collections and Maul's (1948) reference is older than the oldest specimen in MMF, the occurrence of *C. monstrosa* in Madeira remains dubious. As such, for the archipelago of Madeira there are only two valid reports of species of the family Chimaeridae, namely *H. affinis* and *C. opalescens.*

Taxonomic issues including nomenclature, species identification, and determination of taxonomic relationships (Vecchione *et al.*, 2000) are often described for marine identification of closely related species. To clarify and avoid dubious identifications, morphometric and meristic studies are frequently complemented with genetic analyses. One of these cases was the taxonomic uncertainty in the species of the genus *Deania*, mainly between *D. hystricosa* and *D. calcea* that are potentially sympatric species in the archipelago of Madeira and their identification relying on the morphological inspection of skin denticles and skin roughness.

Since the revision of the genus *Deania* in 1984 (Compagno, 1984), the size of the dermal denticles has been adopted as a discriminator between *D. calcea* and *D. hystricosa* (Ebert and Stehmann, 2013). Taxonomic identification mistakes are frequent when the morphological characters used can be affected by factors such as the size of the specimen, state of maturity or area of the body measured, what seems to be the case of these two species (Stefanni *et al.,* 2021; Marrero *et al.,* submitted). In fact, denticle crown length increased accordingly to the size of the specimen and crown length was correlated with sex. In general, for specimens with the same size, females had slightly bigger crown sizes compared to males. Moreover, denticle size differs within specimens according to the region of the body, indicating that this is not a good identification character for discerning between *D. calcea* and *D. hystricosa* (Rodríguez-Cabello *et al.*, 2020; Stefanni *et al.*, 2021).

In this context, two morphological and molecular studies were conducted in order to clarify the uncertainties over identification of these species. The first study considered visual identification of specimens with laboratory inspection of skin denticles and two molecular markers (Stefanni et al., 2021) and the second was performed for dermal denticles, for the mitochondrial genes 16S ribosomal RNA (16S rRNA) and cytochrome oxidase subunit I (COI) (Marrero *et al*., submitted 1).

Genetic analysis did not support the morphological identification relying on the skin roughness since all sequences of the specimens classified as *D. hystricosa* or as *D. calcea*/*D. hystricosa* clustered together as *D. calcea* (Stefanni *et al.*, 2021). Moreover, the ABGD analysis provided support for *D. hystricosa* and *D. calcea* to be considered as the same species and *D. profundorum* as distinct (Marrero *et al*., submitted 1).

We concluded that, *D. calcea* and *D. hystricosa* are the same species and it is proposed that *D. hystricosa* should be considered as a synonym for *D. calcea*. Therefore, from now on conservation assessments and fisheries should consider *D. calcea* and *D. hystricosa* as a single species. Furthermore, IUCN red list assessment should equally be reviewed to reflect the fact that these are same species in the Northeast Atlantic.

Deep sea Chondrichthyes from seamounts

Seamounts are underwater volcanoes that host a wide number of species due to their physical and biological characteristics (Kitchingman and Lai, 2004). These areas often play a pivotal role in species biogeography and connectivity among key stone habitats (Koslow *et al.*, 2016).

The exclusive economic zone (EEZ) of Madeira includes a complex of seamounts. Madeira-Tore geological complex is in the North-eastern Atlantic Ocean, enclosing a number of seamounts extending from the Madeira archipelago (33° N latitude) to the Portuguese mainland EEZ (38° N). Portugal has defined the area as a potentially critical under the Marine Strategy Framework Directive (MSFD), aiming to create new large-scale Marine Protected Areas (MPAs) in the North Atlantic (Biscoito *et al*., 2017).The deep-sea fish fauna of the archipelago of Madeira has been studied over the last 150 years, mostly based on specimens caught by drifting longlines during the artisanal scabbardfish fishery (*A. carbo* and *A. intermedius*) between 800 and 1300 m deep (Bowdich, 1825, Lowe 1834, 1838, 1839, Maul 1948, 1955, 1976, Noronha, 1926, Noronha and Sarmento,1934, 1948, Nunes, 1953, Merrett and Haedrich, 1997; Silva and Menezes, 1921). However, the three Chapters (7 to 9) written and published during this thesis contributed to the knowledge of fish diversity of several seamounts belonging to Madeira-Tore complex at different depth strata down to 2500 m (Freitas *et al.*, 2021), bridging the knowledge gap regarding seamount associated elasmobranchs (Menezes *et al*., 2009; Christiansen *et al*., 2015; Vieira *et al*., 2018).

The studies included data from specimens caught in fishing surveys carried out in Lion, Susan, Unicorn and Seine seamounts (Biscoito *et al*., 2017; Delgado *et al.*, 2017; Freitas *et al*., 2021). New information on the relative growth and reproduction of the deep-water elasmobranchs *C. anguineus*, *S. ringens*, *D. licha*, *C. squamosus*, *D. profundorum* and *D. hystricosa* was added to the existent in the literature (Delgado et al., 2017). The contribution to the knowledge of life history of seamount elasmobranchs is particularly important considering that seamount species, and particularly seamount-aggregating species, are more vulnerable to overfishing than other deep-sea species (Morato and Clark 2007). It also made it possible to report on the species recorded in the trawl survey catches, including some species that are rarely caught or whose presence in the area was previously doubtful. (Delgado *et al*., 2017).

The study performed in the Seine and Unicorn seamounts using fish traps, mid-water drifting longlines, and bottom longlines, carried out during BIOMETORE 5 cruise, allowed to perform the characterization of benthopelagic fish species composition and assemblage structure. In the two surveyed seamounts 42 species were collected including the chondrichthyan fish *C. granulosus*, *C. coelolepis*, *C. owstonii*, *Etmopterus* sp., *E. princeps, E. pusillus*, *P. glauca*, *R. maderensis* and *Torpedo* sp. (Biscoito *et al*., 2017).

The fishing cruises carried out in the Seine and Unicorn seamounts allowed to update the checklist of cartilaginous fish species for these seamounts (Freitas et al., 2021). 17 species were confirmed for Seine seamount and 11 to Unicorn seamount corresponding to about 31% of the total valid chondrichthyan species reported for the archipelago of Madeira (Biscoito et al., 2018), and to 2.3% of the total species worldwide (Weigmann, 2016). Interestingly, species were reported for the first time for the Seine (*C. granulosus* and *S. rostratus*) and Unicorn (*C. granulosus*, *C. coelolepis* and *C. crepidater*) seamounts (Freitas *et al*, 2021).

The checklist of sharks, rays and chimaeras of the Seine and Unicorn seamounts also included the frequency of occurrence, the depth range, the maximum size of the specimens and the IUCN Red List status. The most frequent species caught were *D. calcea* and *C. coelolepis* that present a similar depth range to those described in previous works (Menezes et al., 2009). Nevertheless, *E. pusillus, R. maderensis* and *H. affinis* were caught at greater depths than those recorded in the literature (Ebert and Stehmann, 2013). Regarding total length, *D. profundorum* presented a larger size than the maximum length recorded by Ebert and Stehmann (2013) unlike all other species that presented total lengths within their known size range (Freitas et al., 2021).

Deep sea Chondrichthyes fisheries and biology

The studies carried out in the Madeira-Tore geological complex, while providing valuable new information on the diversity of seamount-associated fishes of these seamounts, which may serve as a tool to strengthen a future proposal for the creation of an MPA within this geological complex (Freitas *et al.*, 2021), have also confirmed the need for additional research on these ecosystems and strict conservation and management approaches to deal with anthropogenic activities, such as fishing, in these important and vulnerable areas. (Delgado *et al.*, 2017).

Overfishing is presently the most important and prevalent threat for elasmobranchs worldwide (Dulvy *et al.*, 2014; Davidson *et al.,* 2016). In the North Atlantic, the fisheries management system in force is ineffective for the conservation of elasmobranchs (Clarke, 2009). Several factors such as poor quality of data, unknown discard rates, species misidentification and gaps in the biology and ecology of these species contribute for the unsuccessful management of elasmobranchs.

The conservation of the commercially exploited elasmobranch species in the archipelago of Madeira is worrying. Of the species landed between 1990 and 2020, 2 are classified as Critically Endangered (*C. granulosus, O. ferox*), 2 as Endangered (*C. squamosus* and *D. licha*) and 2 as Vulnerable (*M. mustelus* and *G. galeus* and) according to the European Red List of Marine Fishes (Nieto *et al.*, 2015).

The lack of reliable analysis of elasmobranch landings in the Madeira archipelago is addressed in this study. As such, a long-term overview of elasmobranch fisheries was carried out for the first time in this region. The main results showed that more than 90 % of the total annual elasmobranchs landed in the study period corresponded to deep-water sharks and that they were mainly caught as bycatch species in the mid-water drifting longline scabbardfishes fishery that represents approximately 50 % of the region's total fisheries (Delgado *et al*., 2013).

The period comprised between 2004 and 2014, was marked by annual landings of deep-water sharks of over 50 t, which is of significance considering the artisanal nature of this fishery in the archipelago of Madeira, mainly for unmanaged elasmobranch species at the time (Freitas *et al*., submitted 2). It was evident that *C. squamosus* was the most representative landed species over the study period, most likely explained by the depth at which the fishing gear is deployed in the scabbardfish fishery, which overlaps with the depth range, between 800 and 1300 m, in which this species is more abundant. The peak in catches of this species occurred in 2008, coinciding with the peak in catches of scabbardfish (3.109 tons), and was due to an increase in fishing effort in terms of the number of vessels and trips (ICES, 2021).

In recent years, i.e. since 2015, the weight landed for deep-sea sharks has not exactly reflected the weight harvested for these species, since their catch has been regulated by TACs imposed by the EU, and any fish caught after the regulatory limits have been reached must be discarded.. This regulation only applies to bycatch in the scabbardfish fishery using longline in EU waters of CECAF regions 34.1.1, 34.1.2 and 34.2.

The imposed regulations aimed to reduce bycatch and to gather information on the species' biology and population dynamics. However, this regulation does not reflect the real weight of unwanted catches of elasmobranchs in the archipelago of Madeira, as the fishing gear remains unchanged. Presently, deep-sea sharks’ landings are strictly forbidden, and all accidental catches are discarded.

The pelagic shark, *P. glauca*, caught by mid-water drifting longlines, also had some expression, between 1990 and 2004, with a landing peak superior to 30 tons in 2003. This event was coincident with data reported by Roxo *et al*. (2017) for Portugal mainland and was explained by the growing market demand for this species. Similarly, shark finning was banned by the EU in 2003 (Council Regulation (EC) Nº 1185/2003 of 26 June 2003), which resulted in a reduction of the landings of *P. glauca* in the archipelago of Madeira from 2004 onwards.

A trend of supply and demand was observed when looking into annual landed tonnage and mean price values analyzed, with a decrease in landings being translated into an increasing market value over time, as previously verified for species with commercial value in other regions.

The implementation of conservation measures aiming to reduce bycatch post-release mortality would benefit from upcoming scientific fishing cruises inferring on species-specific survival rates, as well as fishing gears’ soak time, since, according to fishermen, most individual deep-water sharks do not survive the hauling of the fishing gear. Fluctuations in hydrostatic pressure are highly likely to ensure that discarded individuals do not survive. (Large et al., 2003).

Furthermore, data on both the impact resulting from the selective removal of predator or prey at an ecosystem level, and on the enhancement of food amount through discards is still very rare and should be included in fisheries management and conservation plans. Moreover, and to correctly gather robust data on mortality rates, a fisheries observer program for the archipelago of Madeira should be implemented as soon as possible (Stevens *et al*., 2000; Freitas *et. al*., submitted 2).

The information on the biology of commercial deep-sea species, with slow growth and late maturity, is essential for the development of integrative management actions aiming at a sustainable exploitation. To fill biological information gaps in the most important bycaught species in the archipelago of Madeira, a long-term population analysis of the deep-water shark *C. squamosus* was performed considering two time series, separated by a period of over 20 years. This information is pivotal to assess the scabbardfish fishery impact on the biology and population dynamics of *C. squamosus* and to establish suitable management strategies to preserve this species in the archipelago of Madeira.

The main results showed differences between the frequency distribution by size class and mean length of the specimens between time series, though a similar size range was observed. Sexual dimorphism was confirmed with females achieving larger sizes than males as reported for most deep-sea sharks of the family Squalidae (Aranha *et al*., 2009; Clarke *et al*., 2002; Jakobsdóttir, 2001; Sion *et al.,* 2003). It was also verified that males outnumbered females in both time series which is in accordance with Clarke *et al*. (2001) that observed the same pattern. Since scabbardfish fishery is carried out at depths between 800 and 1300 m, females' bycatch is less probable to occur once they occur at deeper waters (Muñoz-Chápuli and Ramos, 1984; Parker and Francis, 2012)

Segregation by sex and maturity state is well documented in the literature for squalid species, in which pregnant or mature females occur in different depth strata than the rest of the population (Yano and Tanaka, 1988; Yano, 1991; Yano, 1995). In the NE Atlantic this trend was confirmed for species of the genus *Centrophorus* (Muñoz-Chápuli and Ramos, 1984), *Deania* (Sousa *et al*., 2009) and *Etmopterus* (Aranha *et al*., 2009).

Centrophorus squamous is a long-living species that could achieve a longevity of 39 years. Similar longevity was estimated by Parker and Francis (2012) for specimens caught in New Zealand. A trend of higher asymptotic growth in females for both time series was observed in accordance with the length of the largest sampled specimens. However, when comparing groups between time-series a similarity in the estimated rates for females and for males was verified. Similar biological parameters were estimated for this species in Ireland and Scotland (Clarke *et al*., 2001).

Only 10 to 15 % of the total of the individuals analised were immature and juveniles with less than 70 cm being absent from the catches, confirming that scabbardfish fishery depth range seems not to match with any nursery grounds. Possibly juveniles inhabit different depth ranges than the rest of the population (Yano and Tanaka, 1988). Since, adults' specimens of *E. pusillus* (< 40 cm) are simultaneously caught by the Madeiran scabbardfish fishing gears (Severino *et al*., 2009), the selectivity of the hooks could not justify the absence of juveniles of *C. squamosus* in the catches.

The breeding season of *C. squamosus* in the archipelago of Madeira appears to occur between July and December. The size at first maturation showed a similar trend between females and males in both time series, with females achieving larger sizes. Presently, the size at first capture is greater than the size at first maturation for both sexes, suggesting that most of the specimens are caught after achieving sexual maturity. This appears to safeguard reproduction of the species, indicating that at least 50% of the total population reproduces before being caught.

Natural and fishing mortality exert similar pressure on exploited populations, however total mortality is higher in males, since they are more susceptive to be caught by the drifting longline, once they occur in the depth range of the scabbardfish fishery.

The estimation of fishing mortality in the second time series should be wisely analyzed, once the estimation of the mortality was limited by the TAC of 7 tons, imposed by the Council Regulation (EU) 2018/2025 of 17 December 2018. It is also important to emphasize that a small number of females with embryos in the terminal state of development was caught during this study. As such, the fishing pressure on this species does not expressively affect pregnant females neither immature individuals. Probably because females and immatures inhabit other zones or depths which are different from the fishing areas or depths operated by the scabbardfish fishing gear in the archipelago of Madeira.

The study on the biology and population dynamics of *C. squamosus* allowed to verify that the pressure of fishing did not cause critical changes in the life history parameters of the species over 22 years. Additionally, it was concluded that fishing pressure targets mainly adult males, constituting low pressure on immatures and differentiating and expecting females. Furthermore, it became evident that the application of a TAC does not contribute proficiently to the sustainable exploitation of this species. Since no modifications have been made to the fishing gear, similar amounts of sharks are caught. Inversely, with the application of the TAC (0 tons), caught specimens are not landed, making it impossible to quantify the catches and estimate biological parameters, which hinds the scientific knowledge on the species.

New information on the life history of deep-water elasmobranchs in the archipelago of Madeira was made available through the study of the length-weight relationships (LWRs) for eight species. Since, all LWRs obtained were estimated for the first time for the Madeira region. LWRs are essential for the development of comparative life-history studies since they provide crucial data on the growth, fitness, and wellbeing of a population in an ecosystem. Particularly in species susceptible to overexploitation as elasmobranchs (Freitas et al., 2022).

Sexual dimorphism was observed for *C. squamosus, C. crepidater*, *C. coelolepis* and *C. owstonii* with females achieving larges sizes than males, probably related to differential morphological development, reproductive investment, and habitat preference (King, 2007). Additionally, results indicate normal growth dimensions and/or healthy populations since the b values are within the range of 2.5 to 3.5 (Froese, 2006; King, 2007).

The update and clarification of the taxonomy of deep-sea cartilaginous fishes occurring within the 200 nautical miles EEZ was accomplished during this work, with the realization of updated checklists, confirmation of new records and the resolution of uncertainties over the identification of *D. calcea* and *D. hystricosa*. Furthermore, this work contributed to the knowledge of fish communities, fish diversity and occurrence of the seamounts around Madeira and provided the baseline information for sustainable use and management measures of these areas.

A reliable overview of Madeira’s elasmobranch fisheries and their evolution between 1990 and 2020 was provided. Additionally, life history and population dynamics of several chondrichthyan species were estimated and a study on the long-term exploitation of *C. squamosus* through a comparative study over a 20-year period was accomplished, aiming to contribute to the development of suitable management strategies for their preservation.

The information presented herein is helpful for the development of suitable management plans for the fisheries of the archipelago of Madeira in order to mitigate the direct effects of fishing pressure on the exploited populations, since from the 13 Chondrichthyes landed in the archipelago, between 1990 and 2020, two are classified as Critically Endangered (*C. granulosus, O. ferox*), two as Endangered (*C. squamosus* and *D. licha*) and two as Vulnerable (*G. galeus* and *M. mustelus*) on the European Red List of Marine Fishes (Nieto *et al*., 2015).

As such accurate studies, population and/or stock assessment, together with a multinational approach is essential to avoid overexploitation of these resources, especially in the Azores, an ideal habitat, refuge and nursery for some key elasmobranch species and as top-over area for other migratory species.

Implications of this study and concluding remarks.

The scientific information gathered in this thesis has important implications for:

a) The fishing (artisanal and semi-industrial) of deep-water sharks: The results of this study indicate that the population sizes of several species of deep-water sharks in the Madeira archipelago and adjacent seamounts are likely smaller than previously assumed. This suggests that fishing pressures on these populations should be reduced or eliminated to avoid overfishing and potential depletion.

b) The fragility of ecosystems in the Madeira archipelago and adjacent seamounts: The presence of several species of deep-water sharks in the area suggests that these ecosystems are complex and highly interconnected. This highlights the need for comprehensive ecosystem-based management approaches to ensure the sustainable use of these resources and to prevent irreversible damage.

c) The taxonomic and genetic identification of concerned shark species and the assessment of their populations in the region: The taxonomic and genetic identification of deep-water shark species in the Madeira archipelago and adjacent seamounts is essential for their conservation. This study provides important baseline data for future monitoring and conservation efforts.

d) The conservation of these shark species: The results of this study highlight the need for conservation measures to protect deep-water shark populations in the Madeira archipelago and adjacent seamounts. This includes the establishment of marine protected areas and the implementation of sustainable fishing practices, as well as the development of management plans that consider the complex ecosystem dynamics of the region. Conservation efforts must be based on the best available scientific information, and must involve the collaboration of all stakeholders, including fishermen, scientists, and policymakers.

In summary, the scientific information obtained in this thesis has significant implications for the fishing of deep-sea sharks, the fragility of marine ecosystems in the Madeira archipelago and adjacent seamounts, the taxonomic and genetic identification of the species of sharks concerned, the evaluation of their populations in the region, and the conservation of these species. It is important that this information be considered by the responsible authorities for the management and conservation of marine resources in the Region to ensure the sustainability of these ecosystems and ensuring the survival of shark species in the future. Effective conservation and fisheries management policies need to be implemented, and measures taken to reduce the incidental capture of sharks in fisheries targeting other species. Additionally, it is important to promote education and public awareness about the importance of sharks and the need to protect them. The scientific information gathered in this thesis is valuable to inform and support these initiatives, and we hope it can contribute to the conservation of deep-sea sharks in the Madeira archipelago and other parts of the world.

In 2022 the incidental catch monitoring program for mammals, reptiles, seabirds and fish and the stranding net monitoring program was established, under the Marine Strategy Framework Directive (MSFD). The challenge now is to implement an electronic onboard observer program, under the National Data Collection Framework so we hope in the near future to be able to monitor the decrease of bycatch and the accidental captures of deep sea Chondrichthyes in Madeira.

To conclude, **I hope this thesis can contribute to the valorization and suistanibility of deep-sea Chondrichthyes in Madeira archipelago, nearby seamounts and other parts of the world.**

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