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Thesis of
Elizabeth A. Johnson

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

August 2024

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

A Comparative Analysis of Extant Oceanic Shark Species Using Trait-Based Ecology

Elizabeth A. Johnson

Submitted to the Faculty of
Halmos College of Arts and Sciences
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the degree of Master of Science with a specialty in:

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Abstract

Over the past few decades, scientists have been working together to mitigate human impacts on global shark populations, but deciding which species need the most immediate attention can be difficult. This study uses a newly emerging approach to ecology, trait-based ecology, to identify trends in trait expression with depth and determine which species have the most unique sets of traits. While trait-based ecology has already been applied to numerous fields, a trait-based approach to shark research is still in its infancy. A total of 15 traits across 337 oceanic shark species were examined to identify trends in trait expression and determine which species have the most unique sets of traits. These species are likely invaluable to the proper functioning of their ecosystem. Surprisingly, the trait that caused the most variance between species was not vertical distribution, but the presence or absence of an anal fin. It was discovered that species with an anal fin have higher trait diversity compared to species without an anal fin. More research is needed to understand the function and importance of the anal fin. Of the 33 species with unique sets of traits, one species, *Carcharhinus obscurus*, is Endangered and needs immediate protection to help preserve the species' unique traits and the important role it plays in the functioning of the oceanic ecosystem. Literature analysis revealed a severe lack of available trait data. Additional research on traits across all shark species is vital to identifying and protecting unique species before it is too late.

Keywords: *trait-based analysis; conservation; epipelagic; deep sea; chondrichthyans; elasmobranchs; Selachii; evolution*

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Statement of Significance

To date, there are only a handful of articles that have focused on comparing epipelagic (0-200 m) and deep-sea (200+ m) shark species (Larsen et al., 2020; Litherland et al., 2009; Pimiento et al., 2023a; Treberg et al., 2003). These articles, with the exception of Pimiento et al. (2023a), have only focused on a few species or traits rather than a full comprehensive analysis of multiple species and traits. The study conducted by Pimiento et al. (2023a) examined trends in traits across all elasmobranch species with respect to geographic location. The purpose of the current study is to compare multiple traits across multiple shark species in order to identify any trends in trait expression with depth and determine which oceanic shark species are the most dissimilar. The stark differences between the epipelagic and deep-sea environments noted below point towards the idea that there are likely multiple differences between sharks that reside in the two depth regions. Even within species that reside in the same depth zone, there are a multitude of variations in the traits of sharks. Identifying which species have the most unique sets of traits will reveal which oceanic shark species need the most immediate conservation protection. These species play a role within their ecosystem that cannot be replaced by any other species and therefore must be preserved at all costs. By identifying the species with unique sets of traits and a threatened conservation status, conservationists can use the results from this study to most efficiently protect these exceptional species.

Introduction

The Oceanic Environment

The ocean can be divided into two main environmental zones: the neritic zone and the oceanic zone. The neritic zone is comprised of the coastal environment that rests on the continental shelf, typically above 200 meters (m) (Karleskint et al., 2013). Moving off the continental shelf, the oceanic zone begins. Geologically, the oceanic zone includes the continental slope, the continental rise, and the abyssal plains (Torres & Bailey, 2022). In this study the oceanic zone will include both the pelagic and benthic habitats associated with the waters off the continental shelf. The oceanic zone can be divided into several major regions based on light penetration and will be discussed here with regards to clearest ocean waters. The epipelagic zone spans from the surface down to 200 m where there is enough light to promote photosynthesis (Merrett & Haedrich, 1997; Priede, 2017; Torres & Bailey, 2022). Around 200 m, the amount of light becomes insufficient for photosynthesis, thus marking the transition into the deep sea. The mesopelagic zone, between 200 m and 1000 m, is also referred to as the twilight zone, as there is enough downwelling light for vision but not photosynthesis. Below the mesopelagic zone lies the bathypelagic zone (1000 m to 3000 m), the abyssopelagic zone (3000 m to 6000 m), and the hadopelagic zone (all depths greater than 6000 m). All these zones are characterized by zero solar light penetration.

There are many factors affecting the composition of organisms in the neritic environment, such as coastal runoff, erosion, and geologic features. The oceanic environment is not affected as strongly by coastal processes and contains vastly different geologic features. In order to reduce the number of factors contributing to trait distribution with depth, only shark species within the oceanic zone will be considered in this study.

Conservation Concerns

Sharks are particularly vulnerable to exploitation compared to other marine fishes due to their relatively slow growth, late sexual maturity, and small litter sizes (Office of International Affairs, Trade, and Commerce, 2024). These characteristics make it difficult for shark populations to recover after environmental impacts such as overfishing, pollution, habitat destruction, and climate change.

Fishing

The most immediate threat to oceanic shark populations is unregulated fishing. While anthropogenic impacts such as pollution and global warming still pose a threat to sharks worldwide, unmanaged and inadequately managed fisheries pose the biggest threat by far (Abel & Grubbs, 2020; Ebert et al., 2021). The threats to sharks from fisheries can be broken down into two main categories, targeted shark fisheries and fisheries bycatch.

Sharks have historically been targeted by fisheries for their fins, meat, liver oil, cartilage, and objects that can be used for souvenirs, such as jaws, teeth, sawfish rostra, and neonate and embryonic sharks. Shark fins are one of the most economically valuable and sought-after parts of the shark (Abel & Grubbs, 2020). Shark fining can be both legal and illegal. Illegal shark finning involves the act of removing the fins from the shark at sea, usually while it is still alive, and disposing of the carcass into the ocean. Legal shark finning involves legally catching the shark, bringing the whole shark into port, humanly killing it, and removing the fins. Often times other parts of the shark are used as well. Most targeted species belong to the families Carcharhinidae, Laminidae, Sphyrnidae, and Pristidae (Abel & Grubbs, 2020).

Since the decline of other global fisheries, such as tuna and swordfish, shark meat has become the viable alternative. The shark meat trade has seen an average annual increase of 5.23% since 2000 (Abel & Grubbs, 2020). Most of the targeted species for these fisheries are comprised of deep-sea sharks and rays (Finucci et al., 2024). Compared to the fin and meat trade, fisheries targeting shark liver oil, cartilage and other products are not nearly as large, but they are still worth noting. Shark liver oil and cartilage have long been sought after for their claimed medicinal properties. While many of the medicinal properties derived from sharks can now be manufactured synthetically (Able & Grubbs, 2020), shark liver oil fisheries continue to target deep-sea shark liver oils for other purposes due to their high squalene contents (Finucci et al., 2024). In fact, nearly two-thirds of all threatened deep-sea shark species have been used for their liver oil (Finucci et al., 2024). Shark cartilage is also commonly used as a health supplement, even though its medicinal benefits are not always founded in fact (Abel & Grubbs, 2020). Shark jaws and teeth, sawfish rostra, and shark embryos and neonates can all legally be sold at trade shows, markets, souvenir shops, and online. The only species that are exempt from this are species that are listed on the US Endangered Species list (Abel & Grubbs, 2020; Endangered Species Act, 1973) or listed in Appendix I of CITES (Abel & Grubbs, 2020; Convention on International Trade in Endangered Species or Wild Fauna and Flora, 2024).

Shark bycatch poses by far the biggest threat to shark species worldwide (Abel & Grubbs, 2020). While shark fisheries do threaten shark populations around the world, they are less likely to directly contribute to their extinction purely because lower shark populations would be uneconomical for the fishery (Ebert et al., 2021). On the other hand, other fisheries that often catch sharks as bycatch are not directly affected by global shark population trends. These fisheries often target non-shark species that can reproduce and grow quickly and can therefore withstand high fishing pressures, unlike sharks (Ebert et al., 2021). There are a wide variety of nets used in fishing and each net type affects a different group of shark species.

Pelagic fishing techniques include the use of pelagic trawl nets, gillnets, pelagic longlines, and purse seines. Trawl nets are funnel-shaped nets that are towed behind the boat, collecting everything in their path. Pelagic trawl nets target schooling species, such as squid, pollock, and sardines (Abel & Grubbs, 2020). These fisheries typically have relatively low bycatch rates, but sharks that target these species as a source of food are still susceptible to being caught in these nets. The Sharpnose Sevengill Shark (*Heptranchias perlo*) is known to consume squid and is therefore often caught as bycatch in pelagic trawl net fisheries. This shark species has a relatively long generation length (13.5 years) making it especially vulnerable to population decline (International Union for Conservation of Nature, 2024).

Gillnets pose an even bigger threat to shark populations through their high rates of bycatch (Ebert et al., 2021). Gillnets are often anchored to one spot or left to drift in the water column and rely on fishes swimming directly into the net and becoming entangled. These nets are typically cheap and easily available, making them common in all forms of fishing, from artisanal to commercial (Ebert et al., 2021). Modern gillnets use clear, artificial fibers making them especially hard to see in the water column. Anchored gillnets typically entrap coastal dwelling shark species such as the Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) and the wide-ranging Spiny Dogfish (*Squalus acanthias*). Drift gillnets typically entrap pelagic species such as the Blue Shark (*Prionace glauca*), the Porbeagle Shark (*Lamna nasus*), and the Scalloped Hammerhead (*Sphyrna lewini*).

Longlines use baited hooks and are therefore more selective towards their targeted species. Pelagic longlines typically attract the Blue Shark (*P. glauca*), the Shortfin Mako (*Isurus oxyrinchus*), the Common Thresher (*Alopias vulpinus*), and the Silky Shark (*Carcharhinus falciformis*). While longlines are much cleaner than gillnets or trawls, they do pose a threat to species with slow growth and reproductive trends like sharks since they typically target larger, predatory fish (Abel & Grubbs, 2020).

Compared to trawls and gillnets, longlines and purse seine nets pose a significantly smaller risk to sharks being caught as bycatch. Purse-seine nets are used in almost every major fishery in the world. They currently account for 70% of tuna landings worldwide (Abel & Grubs, 2020). Purse-seines are large nets, typically 1000-2000m (3280-6560 ft) long, 300-650 m (985-2130 ft) in diameter, and up to 200 m (650 ft) deep. They are deployed over deep water and target large schools of fish, which poses a threat to large pelagic predators like sharks. Some of the most common shark species caught as bycatch include the Silky Shark (*C. falciformes*), the Oceanic Whitetip (*Carcharhinus longimanus*), and the Scalloped Hammerhead (*S. lewini*) (Ebert et al., 2021).

Benthic fishing techniques include the use of benthic trawl nets and bottom longlines. According to Abel & Grubs (2020), bottom trawl nets drag along the sea floor bottom, often damaging the surrounding benthic environment and catching excessive amounts of bycatch, making up as much as 90% of the net contents. This form of fishing poses especially high risk to benthic and benthopelagic shark species, such as angelsharks (Squatinidae), dogfish (Squalidae) and catsharks (Scyliorhinidae). Species with slow growing populations, such as deep-sea dogfish and catsharks, are especially at risk.

Bottom or demersal longlines are anchored to the seafloor and species commonly caught in these lines include the Sandbar Shark (*Carcharhinus plumbeus*), the Atlantic Sharpnose Shark (*R. terraenovae*), the Great Lanternshark (*Etmopterus princeps*), and the Dwarf Gulper Shark (*Centrophorus atromarginatus*) (Ebert et al., 2021). The bycatch of bottom longlines can be as much as 50% of the overall catch, which is significantly more than the bycatch rate for pelagic longlines (Abel & Grubbs, 2020). The demersal longline technique is the most used fishing strategy for retrieving deep-sea boney fishes such as the Patagonian Toothfish, or Chilean Sea Bass (Abel & Grubbs, 2020). The mortality rate of deep-sea sharks caught in these lines can be as high as 100%. This is especially problematic since many deep-sea shark species are known to have long generation lengths and low recovery potential (Finucci et al., 2024).

Pollution

There are many forms of pollution affecting global shark populations, but the two main types of pollution impacting oceanic shark species include chemical pollution and plastic pollution.

Chemical pollution can be inorganic or organic. One of the most prominent examples of inorganic chemical pollution is mercury. Since the age of industrialization, mercury in the environment has steadily increased due to the burning of coal and other mercury containing waste (Abel & Grubbs, 2020). Methylmercury can easily accumulate in the body and is slow to breakdown, allowing it to biomagnify up the food chain and become highly concentrated in large organisms such as sharks. Several studies have shown evidence of bioaccumulation of methylmercury to potentially dangerous levels in shark species such as the Shortfin Mako (*Isurus oxyrinchus*), the Blue Shark (*Prionace glauca*), and the Oceanic Whitetip (*Carcharhinus longimanus*) (Kiszka et al., 2015). High levels of mercury can cause changes in cell function, inhibition of protein synthesis, damage to DNA and disrupt cell division, and can interfere with the development of the nervous system and brain function (Abel & Grubbs, 2020).

Organic chemical pollutants in the marine environment include oil and persistent organic pollutants (POPs). Polycyclic aromatic hydrocarbons (PAHs) are the most toxic and commonly studied component of crude oil. Fortunately, sharks are able to metabolize PAH contaminated prey items and dispose of PAHs through the liver (Abel & Grubbs, 2020). However, if the shark is exposed to PAH for a prolonged period, the body's ability for detoxification decreases and this exposure may result in cellular damage, reproductive impairment, mutagenetic effects, or even death (Abel & Grubbs, 2020). Research into the long-term effects of prolonged exposure to PAH is still being conducted.

Unlike PAHs, POPs are often extremely difficult for organisms to metabolize. POPs include synthetic organic chemicals that are persistent in the marine environment and can easily bioaccumulate in the fatty tissues of larger organisms (Abel & Grubbs, 2020). A study by Lyons et al. (2015) found that the liver of an adult female Shortfin Mako (*I. oxyrinchus*) contained nearly one hundred times the human no-consumption level set for one specific type of POP, dichloro-diphenyl-trichloroethane (DDT). The effects of POP exposure include cancer, birth defects, damage to the nervous system, reproductive disorders, endocrine disruption, and even death (Abel & Grubbs, 2020).

As plastic manufacturing continues to increase, the threat plastic pollution poses to the marine environment also increases. It has been estimated that between 1.8% and 10% of annual global plastic production ends up in the marine environment (Abel & Grubbs, 2020). The primary concern for sharks is entanglement or ingestion of these plastics. Fishing nets that have been lost or forgotten become 'ghost nets' and continue to fish unregulated, collecting everything in their path. Sharks and other marine organisms become entangled in these nets and die. While the direct ingestion of smaller macro- and microplastics by sharks is rare, evidence of ingested plastic has been found in several oceanic shark species including *P. glauca* (Bernardini et al., 2018), *Etmopterus spinax* (Cartes et al., 2016), *Squalus acanthias* (Avio et al., 2015), and *Rhincodon typus* (Fossi et al., 2017). Ingestion of plastics can lead to the adsorption of chemical pollutants on the surface of microplastics, such as DDT (Abel & Grubbs, 2020). Research on the effects of plastic pollution on sharks is still very new but with the continuing production and pollution of plastics into the marine environment, it is likely that more studies will be published in the near future.

Habitat Destruction

While destruction of habitats such as mangrove forests pose a threat to coastal shark populations, the most notable source of habitat destruction in the oceanic environment is deep-sea mining. As resources of precious metals and rare earth elements begin to dwindle, industrial mining companies have begun to turn more towards deep-sea mining as a potential solution. Deep-sea mining targets polymetallic nodules, cobalt-rich ferromanganese crusts, and polymetallic sulfides, all of which can be found imbedded in the seafloor (International Union for Conservation of Nature, 2022). In order to extract the desired resources, a deep-sea mining vehicle (DSMV) is used. The DSMV moves along the seafloor, drilling into the seabed to collect the targeted resources. The drilling and mechanical operation of the DSMV creates excessive noise and sends large plumes of sediment into the surrounding water column (Drazen et al., 2020). The noise and sediment have numerous potential impacts for species living around the seafloor and in the water column. Potential impacts on individual species include respiratory distress, auditory distress, reduced feeding, reduced visual communication, buoyancy issues, and toxicity (Drazen et al., 2020). The environment most at risk of being affected by deep-sea mining is the deep pelagic ecosystem which makes up more than 90% of the biosphere. The majority of shark species that have been described so far reside below 200 m. Deep-sea mining is therefore yet another potential danger to global shark populations.

Climate Change

As the evidence for global warming and ocean acidification continues to accumulate (Alfonso et al., 2021; Held & Soden, 2006; Keeling et al., 1976; Manabe & Wetherald, 1967), more research is being conducted on the impacts of climate change on marine ecosystems. While research on the impacts of climate change on sharks is still in its infancy, several studies have already linked changes in shark physiology and behavior to ocean acidification and warming.

To date, all studies on the impacts of ocean acidification on sharks have been conducted on oviparous benthic species like the Small-spotted Catshark (*Syliorhinus canicula*) and the Epaulette Shark (*Hemiscyllium ocellatum*) (Abel & Grubbs, 2020). These studies showed that increased carbon dioxide (CO_2) levels were linked to changes in resting metabolic rate and scope for aerobic activity (e.g., ability to increase swimming speed) in *S. canicular*, along with changes in resting oxygen consumption, hypoxia tolerance and aerobic enzyme activity in *H. ocellatum* (Rosa et al., 2017). More research needs to be conducted on oceanic shark species to determine if these changes in physiology and behavior in response to increased CO_2 are representative of all shark species.

While there have been many studies conducted on increased temperature and its impacts on various shark species, few studies have focused on warming in the range associated with anthropogenic climate change and its impacts on shark physiology and behavior (Abel & Grubbs, 2020). There is, however, plenty of evidence that shark movements are driven by temperature (Schlaff et al., 2014). In response to rising ocean temperatures, it has been predicted that many shark species may resort to moving into cooler waters at higher latitudes (Abel & Grubbs, 2020). This will result in new interactions between species which may lead to changes in species population demographics, ecosystem trophic structure, and behavior. The presence of additional predators could also lead to the depletion of, or even extinction of, native species. To date, the only species with a threatened conservation status that has been directly tied to climate change is the New Caledonia Catshark (*Aulohalaelurus kanakorum*) (Dulvy et al., 2014). It is likely that more species will become listed as threatened due to climate change as ocean temperatures and CO_2 levels continue to rise.

Trait-Based Ecology

The most common method for analyzing a population has been to look at the diversity of species within a specified region. While this taxonomy-based approach to understanding ecosystems is important for taxonomic assessments, it does have its limitations. When using a taxonomic approach, it is difficult to connect the individual to the functions of an ecosystem, such as energy, nutrient, and organic matter fluxes. Understanding the role each individual plays within an ecosystem is vital to understanding how an ecosystem may be affected by the changes of individuals. This can be done using trait-based ecology, which uses the traits of individuals to identify the role each individual plays in ecosystem functioning.

A trait can be defined as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole organism” (Violle et al., 2007, pg. 884). By looking at the traits present within an ecosystem, researchers can infer how changes in trait composition may affect the functions and services of that ecosystem. More researchers are beginning to use analysis of trait diversity to understand ecosystems rather than solely relying on analysis of species diversity (de Bello et al., 2021). Cernansky (2017) deemed this the “the biodiversity revolution.” Biodiversity can be defined as the variety of all life on Earth and the evolutionary mechanisms that help to maintain it (de Bello et al., 2021). In an effort to understand the mechanisms behind ecosystem functioning in the oceanic environment, the diversity of traits in the shallow water environment will be compared to the diversity of traits in the deep sea. As stated above, the two depth zones are characterized by vastly different environmental factors. Therefore, the composition of traits will likely vary between the two depth zones. The infraclass Selachii has members in all major ocean basins and spanning multiple depth zones, making this class the perfect candidate for this trait-based analysis.

Examination of multiple species' attributes, such as life history, anatomical, and physiological traits, provides a clear picture of the diversity in traits within an ecosystem. However, not all species contribute equally to the functional diversity of an ecosystem (Pimiento et al., 2023a). Some species possess sets of traits that are unique and different from other species in the same system. If a species with a highly unique set of traits was removed from an ecosystem, it would reduce the trait diversity in that ecosystem and likely leave important ecological roles unoccupied (Mouillot et al., 2013; Pimiento et al., 2023a). This would ultimately alter the functions and services of the ecosystem and could place the ecosystem at a higher susceptibility to impacts such as overfishing. Therefore, species with unique sets of traits must immediately be identified and become the target of conservation efforts.

Shark Traits Examined

As stated above, it is important to examine a wide variety of traits in order to properly capture the diversity within an ecosystem. This study considers anatomical, physiological, and life history traits. The conservation status of each oceanic shark species was also considered. It is important to note that conservation status itself does not fall into the classic definition of a trait, but it is considered here as a potential proxy for other traits such as population growth rate and mortality rate. Data for all of these traits were recorded to determine any trends in trait expression with depth and used as a way to determine (dis)similarity among oceanic shark species. The full trait selection and data collection process is detailed in the Methods.

Anatomical and Physiological Traits

The general structure of sharks' bodies has gone relatively unchanged since the first modern shark evolved (Ebert et al., 2021). A shark's external anatomy can be split into three regions consisting of the head, the trunk, and the tail. Each of these sections contains specific anatomical features (shown in Figure 1). All of these anatomical structures are present in almost every shark, but the size and shape of each structure can vary depending on the shark's habitat and behavior.

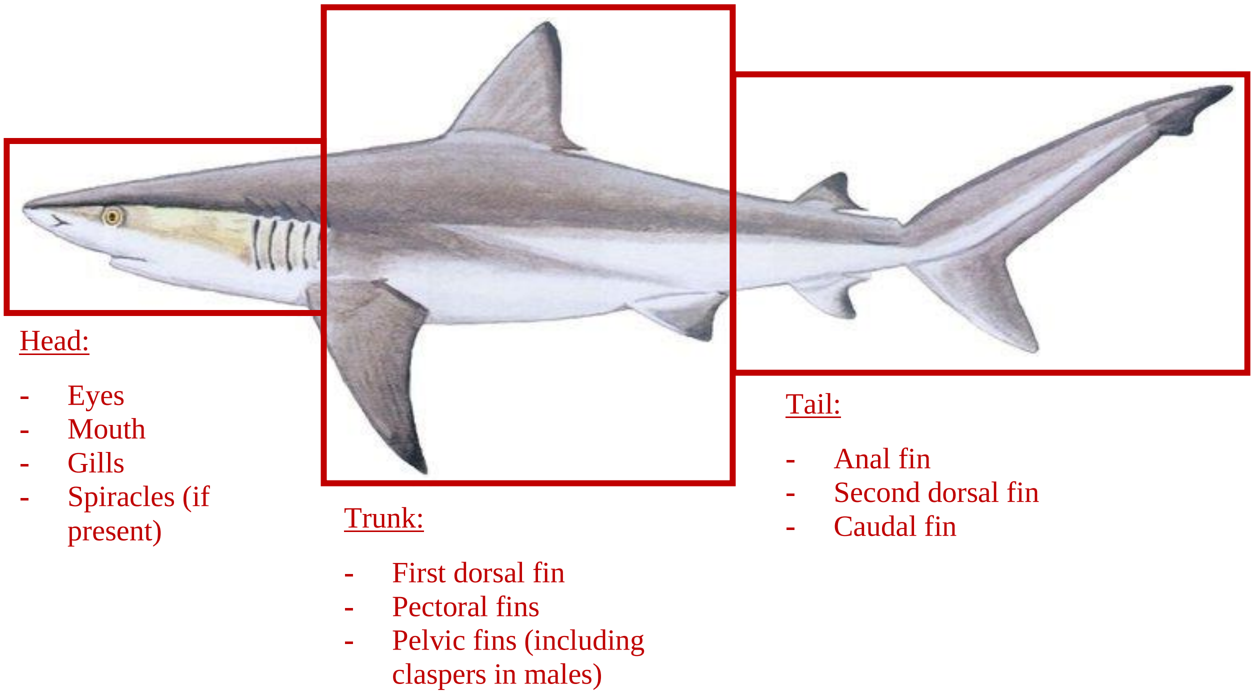

Figure 1 Diagram showing the three main sections of a shark's external anatomy: the head, the trunk, and the tail. Each section consists of specific anatomical features which are listed below the title for each section. The shark used in this diagram is an illustration of *Carcharhinus obscurus* taken from Shark Research Institute (n.d.).

Physiology focuses on understanding the mechanisms of an organism. Physiological traits in sharks can include the mode of respiration, metabolic rate, or swimming form. Much like anatomical traits, physiological traits vary between species depending on the shark's habitat and behavior. For example, the anguilliform, or eel-like, swimming pattern is typically observed in slower, more benthic species such as catsharks and frilled sharks (Ebert et al., 2021). The thunniform swimming strategy is far more energy efficient, as the shark only moves its caudal peduncle and caudal fin. This swimming strategy is typically observed in fast-swimming pelagic species like the mako shark.

Life History Traits

Understanding life history can help give insight into how a species and/or population may react to environmental stressors. Typical life history traits include mode of reproduction, growth pattern, size and age of sexual maturity, fecundity, size and sex of offspring, maximum size, gestation period, trophic level, and maximum age. Sharks are characterized by slow growth, late sexual maturity and reproduction, reduced fecundity, a long life, a long gestation period, and a large adult size (Cortés, 2000). While these are the general trends observed across sharks, there is some variation in life history traits between species. For example, the maximum total length of *Rhincodon typus* (an epipelagic species) is estimated to be 2100 cm, while the maximum total length for *Etmopterus carteri* (a deep-sea species) is estimated to be 21 cm (Ebert et al., 2021). Overall, the life history traits observed across most shark species, namely late sexual maturity and a long gestation period, make sharks more susceptible to exploitation (Cortés, 2000). That is why considering life history traits is extremely important for determining which species are at the highest risk for extinction and therefore need the most immediate conservation initiative.

Conservation Status

As the number of threats against the health of our oceans continues to mount, it has become increasingly important to assess the conservation status of marine species. The International Union for Conservation of Nature's (IUCN) Red List of Threatened Species has become the most comprehensive list of species conservation statuses in the world (International Union for Conservation of Nature, 2023). The database acquires information for each species through the help of partnered expert researchers and organizations around the world. Once the species has been assessed, they are given an IUCN Red List Status. The species maybe be classified as Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), or Extinct (EX). These conservation statuses are extremely important for determining which species need the most immediate conservation action and are often used in the development of species protection policies.

Materials & Methods

Data Collection

A comprehensive list of all oceanic shark species, from both pelagic and benthic habitats, was formed through an extensive literature analysis. An oceanic shark species was defined by its daytime distribution patterns. All or most of the shark's daytime distribution must be spent in the oceanic environment (defined above) in order to be considered an oceanic shark species. Only daytime distributions were used to limit the effects of diel vertical migration on shark distribution and trait expression. No neritic species were used in this study. The 'List of Described and Extant Chondrichthyan Species', which was last updated August 2023, (Pollerspöck & Straube, 2023) was used as a full list of all extant shark species. Each of the 559 species was researched individually using the books "Sharks of the World: A Complete Guide" by Ebert et al. (2021) and "Biology of Sharks and Their Relatives – second edition" (Carrier et al., 2012) and the databases shark-references.com (Pollerspöck & Straube, 2023), FishBase (Froese & Pauly, 2024), IUCN Red List (International Union for Conservation of Nature, 2023), and the World Register of Marine Species (WoRMS) (WoRMS Editorial Board, 2024). Any species with 'unknown' depth and distribution ranges were excluded from this study. Any species with distribution ranges in both the oceanic and neritic environment were further researched using various journal articles to determine their primary distribution patterns (Daly-Engel et al., 2019; Juby et al., 2021; Kiraly et al., 2003; Mytilineou et al., 2005; Nakaya et al., 2013; Tagliafico et al., 2019; Viana et al., 2017; Viana & Soares, 2023; White et al., 2021). A total of 337 species were classified as oceanic. Each oceanic species was then further categorized by vertical distribution (shallow-water, deep sea, or wanderer). Oceanic shallow-water species were classified as species that spent all or most of their time between 0 and 200 m during the day. Oceanic deep-sea species were classified as species that spent all or most of their time 200 m and below during the day. Oceanic wanderer species were classified as species that travel between and spend a relatively equal amount of time in shallow and deep water during the day. Each shark was also placed into a habitat category, either benthic, benthopelagic, or pelagic. Benthic species were classified as feeding on or near the seabed. Benthopelagic species were classified as species that feed both on the seabed and in the water column. Pelagic species were classified as species that feed mainly in the water column. Definitions for all habitats were taken from Pimiento et al. (2023a). The same resources detailed above, as well as some additional resources, (Carrier et al., 2004; Carrier et al., 2012; Carrier et al., 2022; Compagno, 2003; Ebert et al., 2021; Froese & Pauly, 2024; International Union for Conservation of Nature, 2023; Pollerspöck & Straube, 2023; WoRMS Editorial Board, 2024) were used to place each species into the vertical distribution and habitat categories.

An extensive literature review was conducted to gather data on the traits detailed below. Any anatomical or physiological characteristics of a shark as well as any life history characteristics were considered to be potential traits. A comprehensive list of potential anatomical and physiological traits was created using the book "Sharks of the World: A Complete Guide" by Ebert et al. (2021) while a list of potential life history traits was created using the databases 'sharkipedia.org' (Mull et al., 2022) and AnAge (Tacutu et al., 2018). A total of 38 potential anatomical traits (Table 1) and 45 potential life history traits (Table 2) were identified. Once a comprehensive list of traits was developed, each trait was researched individually, and all available information was gathered using various journal articles and databases. All trait data were recorded but only traits with data available for the majority (above 50%) of species from each oceanic depth (shallow-water, wanderer, and deep sea) were used for statistical analysis. This was done to ensure adequate representation of the traits displayed in species for each depth zone. Traits without data for over 50% of species from each oceanic habitat were excluded from statistical analysis.

Anatomical and Physiological Traits Used in This Study

The anatomical and physiological traits with data available for over 50% of the species from each oceanic depth zone were the presence or absence of an anal fin, the presence or absence of bioluminescence, caudal fin shape, the presence or absence of dorsal spines, eye position, feeding mechanism, the presence or absence of a lateral keel, the number of dorsal fins, the number of gill slits, and thermoregulation strategy.

The anal fin, when present, is the most posterior fin on the dorsal side, before the caudal fin. It is separate from the pelvic fin which is present in all shark species and is associated with the claspers in males. In fast-swimming species the anal fin is significantly reduced in size which is thought to help reduce drag (Ebert et al., 2021). Several orders of sharks, including Squaliformes, Echinorhiniformes, Squatiniformes, and Pristiophoroformes, do not have an anal fin at all. The anal fin is not thought to provide the shark with any form of maneuverability or stability that is not already provided by the dorsal fin, so the loss of the anal fin in some species is thought to be insignificant (Ebert et al., 2021). The presence or absence of an anal fin was recorded to determine any trends in trait expression with depth and used to identify species with dissimilar trait combinations.

Bioluminescent light is produced as a release of energy during a chemical reaction involving the oxidation of luciferin (a light emitting molecule) utilizing either a luciferase or a photoprotein to catalyze the reaction (Haddock et al., 2010). Organisms can control emission of light to send specific signals such as warning messages, alerting a potential mate, or helping the organism blend in with the surrounding environmental light. The color of this light is typically blue because blue light penetrates the furthest in clear oceanic waters (Archer et al., 1999). Bioluminescence in deep-sea sharks is present in several families within the Squaliformes order and is thought to play important roles in specific behaviors, such as hunting or finding a potential mate. The three families that contain sharks with the ability to luminesce, are Etmopteridae, Dalatiidae, and Somniosidae (Duchatelet et al., 2021). Within these families, there are 62 species of sharks known to produce bioluminescence. The use of bioluminescence by sharks in the deep sea is significant for several reasons. Counterillumination, in which the organism emits light on their ventral side to replace the downwelling light that is blocked by their body, is the most common illumination pattern seen in these sharks. This illumination pattern makes the shark virtually invisible to potential prey items swimming below them, allowing them to strategically hunt and capture prey. Bioluminescent patterns are also species specific, allowing sharks in the deep to decipher whether another shark is of the same species, and therefore a potential mate. Sharks also have a unique method for controlling their luminescence. Most bony fishes use neurological control to emit light, but studies on bioluminescent sharks have hypothesized that they use hormonal control instead (Claes & Mallefet, 2009; Duchatelet et al., 2021). Bioluminescent light organs have been reported around the dorsal spines of at least one species of deep-sea shark, the velvet belly lanternshark (*E. spinax*) (Claes et al., 2013). It is thought that the localized bioluminescence helps illuminate the dorsal spines and alerts potential predators of their presence. The topic of bioluminescence in sharks is relatively new to the field of marine science and requires more research before there is a true understanding of how and why sharks luminesce. The presence or absence of bioluminescence was assessed in this study to identify any trends in trait expression with depth and used as a factor in identifying any species with dissimilarities trait combinations.

The primary function of the caudal fin is to generate thrust while swimming and the shape of the caudal fin changes considerably between species. Pelagic species, such as the shortfin mako (*Isurus oxyrinchus*), have a nearly symmetrical, lunate caudal fin (meaning the upper and lower lobe of the fin are approximately equal in size). The lunate shape allows the shark to generate and maintain speed while chasing after fast moving pelagic prey (Brylske et al., 2022; Giammona, 2021). Benthopelagic and benthic species, such as the spiny dogfish (*Squalus acanthias*), have an asymmetrical, heterocercal caudal fin (meaning one lobe is larger than the other; typically, the upper lobe is larger than the lower lobe). The heterocercal fin shape is better for swimming at a cruising pace with quick and sudden bursts of speed (Brylske et al., 2022; Giammona, 2021). Species with this caudal shape typically feed on slower moving and/or benthic prey items. The shape of the caudal fin, either lunate or heterocercal, was recorded for all species in this study to identify any trends in trait expression with depth and to identify any species with dissimilar sets of traits.

While all sharks have two eyes that are positioned on opposite sides of the head, the exact position of the eyes varies among species. The opposing eye position observed in all species allows the shark to have a nearly 360° visual field, especially while swimming (Hueter et al., 2004). Most shark eyes are positioned more laterally, but some species have more dorso-laterally positioned eyes. This means that the eyes rest slightly closer to the top or dorsal side of the shark. The only sharks with a dorso-lateral eye position are species in the families Orectolobidae and Squatinidae (Hueter et al., 2004). Both of these families are comprised of benthic dwellers. The eye position of each species, either lateral or dorso-lateral, was recorded to determine any trends in traits expression with depth and to identify species with dissimilar sets of traits.

A shark's diet can provide important insights into the role the shark plays within its ecosystem and how the shark may be affected by ecosystem changes. The primary diet-related trait considered in this study was feeding mechanism, as this can be used to infer the diet for species in which the main prey is unknown. There are two primary feeding strategies in sharks: filter feeding and macropredation. Filter feeding involves using the shark's gill rakers to extract food particles that are suspended in the water column (Ebert et al., 2021). The only shark species currently known to filter feed are the Whale Shark (*R. typus*), the Basking Shark (*Cetorhinus maximus*), and the Megamouth Shark (*Megachasma pelagios*). The typical prey of filter feeders includes zooplankton and small fish and crustaceans (Ebert et al., 2021). While each of these species have the same feeding mechanism, each shark has its own individual method for filter feeding making each species uniquely important to the functioning of its ecosystem (Ebert et al., 2021). All other shark species are classified as macropredators. Macropredators are species that actively hunt or catch relatively large prey items (defined in Pimiento et al., 2023b.). These prey items include large fish, crustaceans, squid, marine mammals, turtles, and birds (Ebert et al., 2021). The feeding mechanism of each species, either filter feeder or macropredator, was recorded in order to determine any trends in trait expression with depth and identify species with dissimilar trait combinations.

The lateral keel is located just before the caudal fin, at the caudal peduncle, and its primary function is thought to be stabilization while swimming. It is formed by the dorso-ventral flattening and the lateral widening of the precaudal tail (Ebert et al., 2021). Not all shark species have a lateral keel. Lateral keels are present in fast-swimming pelagic species such as the Mako shark (*I. oxyrinchus*), but they can also be present in benthopelagic and benthic dwellers such as the species in the families Squalidae and Squatinidae. Sharks with lateral keels typically have a large, deep body with large pectoral fins, a narrow caudal peduncle, a conical head, and a relatively symmetrical or lunate caudal fin (Maia et al., 2012). The presence or absence of a lateral keel was noted in this study to help identify any trends in trait expression with depth and species with dissimilar sets of traits.

Shark dorsal fins play a significant role in the maneuverability and stability of the shark while it is swimming. The dorsal fin acts like a keel on a sailboat, allowing the shark to make quick turns and preventing role-over while swimming (Ebert et al., 2021). Dorsal fins can also be used to conserve energy. Great hammerhead sharks (*Sphyrna mokarran*) have even been observed swimming on their side and hydrodynamic modeling suggests this creates lift on the dorsal fin, making for a more efficient way of swimming (Payne et al., 2016). Fast-swimming pelagic species, such as mako sharks, have a first dorsal fin that is significantly larger than the second dorsal fin. It is likely that the second dorsal fin has been reduced in size over time to help reduce drag (Ebert et al., 2021). Some shark species, such as the lemon shark (*Negaprion* *brevirostris*), have a second dorsal fin that is almost the same size as the first dorsal and some species do not have a second dorsal fin at all. Hexanchiformes, which includes cow and frilled sharks, only have one dorsal fin that is located much further back than the first dorsal in most species. These species have been observed rolling while using their saw-like teeth to devour prey and it is likely that the more posterior position of the dorsal fin assists in this process (Ebert et al., 2021). The number of dorsal fins, either one or two, was recorded in order to identify any trends in trait expression with depth and any species with dissimilar trait combinations.

Gills play the important role of exchanging oxygen and carbon dioxide between the body and environment in all fishes. In sharks, the size and number of gill slits varies from species to species. The majority of sharks have a total of five gill slits, but a few species have six or seven. Species in the order Hexanchiformes have six or seven pairs of gill slits and a few species in the order Pristiophoriformes also have six gill slits. Despite the fact that Hexanchiformes are one of the oldest lineages of sharks, the presence of six or more gill slits is not thought to be a basal characteristic of all elasmobranchs (Wegner, 2015). Instead, it is hypothesized that the additional pairs of gill slits evolved independently in Hexanchiformes and again in Pristiophoriformes. The evolution of these additional gill slits is likely an adaptation to low-oxygen habitats, such as the deep sea, but more evidence is needed to support this (Wegner, 2015). The number of gill slits, either five, six, or seven, was recorded to help identify any trends in trait expression with depth and to identify any species with dissimilar sets of traits.

The temperature of the water plays an important role in the distribution of sharks. Most shark species are cold-blooded or ectothermic, meaning their internal body temperature is controlled by the temperature of the surrounding water (Ebert et al., 2021). Ectothermic shark species lose 20 to 40% of the heat produced by their muscles to the surrounding environment through their gills during respiration (Ebert et al., 2021). Shark species that reside strictly in warm water environments require a warm external temperature to function properly; these species may seasonally migrate in order to stay within their preferred temperature zone (Ebert et al., 2021). Ectothermic deep-sea sharks have adapted to their cold-water environments and cannot survive in warm water environments. The lower internal body temperature due to the surrounding cold water causes these sharks to have lower metabolic rates which in-turn causes most deep-sea shark species to be smaller and have slower growth rates when compared to shallow-water shark species (Ebert et al., 2021).

A small number of shark species have the ability to maintain certain organs at higher temperatures than that of the surrounding water. (Bernal et al., 2012; Ebert et al., 2021). This is called regional endothermy and these species will be classified as mesothermic in this study following the classification in Pimiento et al. (2023a). Regional endothermy has been documented in all lamnid sharks. This includes the Porbeagle (*Lamna nasus*), the Salmon Shark (*Lamna ditropis*), the Shortfin Mako (*I. oxyrinchus*), the Longfin Mako (*Isurus paucus*), the White Shark (*Carcharodon carcharias*) and one species of thresher shark, the Common Thresher (*Alopias vulpinas*) (Bernal et al., 2012). All lamnids are able to regulate the heat of their aerobic swimming muscles, their eyes and brains, and their viscera (i.e., the stomach, liver, and spiral valve) (Bernal et al., 2012). Regional endothermy has only been confirmed in the aerobic swimming muscles of the Common Thresher, but it is suspected to also be able to maintain higher temperatures within its eyes, brain, and viscera (Bernal et al., 2012). These sharks are able to keep these select organs at a higher temperature by retaining the metabolic heat that is produced via the aerobic swimming muscles during continuous swimming and through constant digestion and assimilation (Bernal et al., 2012). Mesothermic shark species are able to maintain heat around these organs through a network of paired arteries and veins that branch into what is called a ‘rete mirabile’ which consists of tightly packed capillaries working together in a contraflow heat exchange system (Bernal et al., 2012; Ebert et al., 2021). The capillaries carrying cold blood from the outer blood vessels at the gills run parallel to, but in the opposite direction of the capillaries carrying warm blood from the muscles (Bernal et al., 2012; Ebert et al., 2021). The heat is exchanged between the capillaries so that the blood returning back into the body is always warm when needed. The rete mirabile is located closer to the spine in mesothermic species compared to the blood vessels in ectotherms which also aids in maintaining heat (Bernal et al., 2012; Ebert et al., 2021). Whether or not a species is ectothermic or mesothermic was recorded in this study to determine any trends in trait expression with depth and to identify any species with dissimilar sets of traits.

Life History Traits Used in This Study

The life history traits with enough data for at least 50% of the species from each depth zone were mode of reproduction and trophic level.

There are two main modes of reproduction in sharks: oviparity (egg-laying) and viviparity (live birth) (Ebert et al., 2021). Oviparity can be further split into two types: single oviparity and multiple oviparity (Musick et al., 2005). For both of these, the entire development cycle of the embryo occurs in and is supported by the yolk (Musick et al., 2005). In single oviparity, only one egg is deposited from each oviduct (typically two eggs are deposited at a time, one from each oviduct), the eggs are retained for only a short period of time in the oviduct, and the female can produce several sets of eggs per spawning season (Ebert et al., 2021; Musick et al., 2005; Nakaya et al., 2020). In multiple oviparity, multiple egg cases are deposited in the oviduct and are retained for a substantial period of time, until the embryo is fully developed (Ebert et al., 2021; Musick et al., 2005; Nakaya et al., 2020). Nakaya et al. (2020) describes a new form of oviparity in which the shark lays a single egg in the oviduct, but it is retained for a much longer time than what is seen in normal single oviparity.

The reproductive method used by most extant sharks is viviparity (Ebert et al., 2021). In yolk-sac viviparity, the shark is provided with a single egg yolk as its only source of food during development (Blackburn, 1999; Ebert et al., 2021). Consequently, the juvenile shark weighs only a fraction of the weight of the provided egg yolk; the weight percentage of the juvenile shark varies between species (Ebert et al., 2021). Oophagy is another form of viviparity in which the female releases one or several fertilized eggs (depending on the species) from her ovaries and then continues to produce a steady flow of unfertilized eggs which the juvenile sharks use for food while developing inside of the female (Ebert et al., 2021). In placental viviparity the embryo gets its nutrition from the yolk-sac until that resource is exhausted (Ebert et al., 2021). The yolk-sac then becomes attached to the uterine wall, forming a placenta, and the juvenile shark obtains its nutrition through uterine secretions via the placental cord (Blackburn, 1999; Ebert et al., 2021). The last form of viviparity is embryotrophy and has only been found thus far in tiger sharks (*Galeocerdo cuvier*) (Ebert et al., 2021). In embryotrophy, the juvenile shark is enclosed within a sac, or embryotroph, and is supplied with enough nutrients that it can drastically increase its weight during gestation. Another form of reproduction in sharks is parthenogenesis (or virgin birth, meaning an unfertilized egg develops into an offspring), but so far, this behavior has only been observed in sharks in captivity. The mode of reproduction (viviparity or oviparity) was examined in this study to determine any trends in trait expression with depth and to identify species with dissimilar combinations of traits.

Any missing mode of reproduction data were imputed by gathering information from the species' closest relative which was determined using the WoRMS database (WoRMS Editorial Board, 2024), FishBase (Froese & Pauly, 2024) and Ebert et al. (2021). The reproductive data for five species from the *Bythaelurus* genus (*B. giddingsi*, *B. immaculatus*, *B. incanus*, *B. tenuicephalus*, and *B. vivaldii*) were unavailable and could not be inferred using the closest species relative as reproductive habits vary widely between species within this genus. The handling of these data is detailed in the 'Statistical Tests' section below.

A species' trophic level is a way to rank a species within a food web. The trophic level of a species can be defined as "1 + a weighted average of the lengths of all food chains linking that species to basal species" (Yodzis, 2001). This essentially means that a species' trophic level represents the distance of that species from the primary producers in a food chain. Trophic level 1 is typically composed of autotrophs or primary producers (e.g., algae), trophic level 2 is composed of herbivores (e.g., zooplankton), trophic level 3 is composed of primary carnivores (e.g., small fish), and trophic levels 4 and 5 are composed of secondary and tertiary carnivores (e.g., large fish and marine mammals) (Trujillo & Thurman, 2020). Sharks are carnivores and therefore fall into trophic levels 3 through 5. Species in high trophic levels help to control the populations of their prey and keep the ecosystem balanced. Removing these species from their ecosystem allows for what is known as a mesopredator release, in which the mid-size predator population flourishes (Ripple et al., 2016). This can cause the depletion of primary producers and negatively disrupts the flow of energy within that ecosystem (Ripple et al., 2016). The trophic level of oceanic shark species is therefore an important factor to take into account when considering ecosystem health. Trophic levels were recorded for all oceanic species in order to determine any trends in trait expression with depth and to identify which species have dissimilar sets of traits.

Conservation Status

The conservation status of each oceanic shark species was retrieved from the International Union for Conservation of Nature (IUCN) Red List (International Union for Conservation of Nature, 2023). For this study, shark species were either classified as non-threatened or threatened as used by Pimiento et al. (2023a). Non-threatened statuses include LC and NT. Threatened statuses include VU, EN, and CR. As of the release of this study, there are no shark species listed as EW or EX. Species with NE and DD statuses were not used in this study due to missing data.

Table 1 List of all potential anatomical and physiological traits considered in this study (a total of 38 traits – listed in alphabetical order). All traits that were used for statistical analysis and had data for at least 50% of the species from each habitat are in ***bold italics***. All traits that had data available for at least one species in every habitat but not 50% of the species from each habitat are in *italics*. Traits that are not in *italics* did not have enough data available for at least one species from every depth zone. The data source for each trait is provided when available. If the source is listed as 'N/A', there were no trait data available for oceanic species.

List of Potential Anatomical & Physiological Traits Considered in This Study

Trait	Source(s)
Anal Fin – Presence/Absence	Ebert et al. (2021); Fricke et al. (2023); Froese & Pauly (2024); Pollerspöck & Straube (2023)
Bioluminescence – Presence/Absence	Claes et al. (2020); Claes & Mallefet (2009); Duchatelet et al. (2021); Mallefet et al. (2021)
Body Shape	Ebert et al. (2021)
Caudal Fin Shape	Ebert et al. (2021)
Complexity of Nares	N/A
Composition of Buoyancy Lipids in Liver	Bakes & Nichols (1995); Hayashi (1983); Hayashi & Takagi (1981); Jayasinghe et al. (2003a); Jayasinghe et al. (2003b); Jayasinghe et al. (2012); Navarro-Garcia et al. (2000); Nichols et al. (2001); Pethybridge et al. (2010); Phleger (1998); Pinte et al. (2019); Wetherbee & Nichols (2000)
Composition of Muscle Tissue	Perry et al. (2007); Pinte et al. (2021); Sepulveda et al. (2005)
Composition of Photoreceptors in Eye	Bozanno et al. (2001); Claes et al. (2014); Gruber et al. (1975); Hart et al. (2006); Newman et al. (2013)
Counter-Shading – Presence/Absence	N/A
Dermal Denticle Shape & Structure	N/A
Discard/Replacement Rate of Teeth	N/A
Distribution of Electroreceptive Pores	Kempster et al. (2012)

Table 1 (continued)

Trait	**Source(s)**
Estimated Gill Surface Area	N/A
Eye Position	Hueter et al. (2004)
Feeding Mechanism	Pimiento et al. (2023a)
Focal Ratio	N/A
Hunting Strategy	Ebert et al. (2021)
Lateral Keel – Presence/Absence	Ebert et al. (2021); Fricke et al. (2023); Froese & Pauly (2024); Pollerspöck & Straube (2023)
Metabolic Rate	Ste-marie et al. (2020); Weber et al. (2020)
Mode or Respiration	Dapp et al. (2016); Goto et al. (2013)
Nictating Membrane – Presence/Absence	N/A
Number of Dorsal Fins	Ebert et al. (2021); Fricke et al. (2023); Froese & Pauly (2024); Pollerspöck & Straube (2023)
Number of Dorsal Spines	Ebert et al. (2021); Fricke et al. (2023); Froese & Pauly (2024); Pollerspöck & Straube (2023)
Number of Gill Slits	Ebert et al. (2021); Fricke et al. (2023); Froese & Pauly (2024); Pollerspöck & Straube (2023)
Number of Longitudinal Rows of Teeth	N/A
Number of Turns Inside Spiral Valve	N/A
Percent Liver Volume	Baldridge (1970); Deprez et al. (1990); Van Vleet et al. (1984)
Photophore Wavelength of Absorption	Bozzano et al. (2001); Claes et al. (2014); Cohen (1990); Collin & Shand (2003); Crescitelli (1991); Denton & Shaw (1963); Hart (2020); Hart et al. (2011)
Relative Brain Size	Lisney & Collin (2007); Yopak et al. (2007)
Relative Eye Size	Lisney & Collin (2007)
Relative Heart Size	Bernal et al. (2003); Brill & Lai (2015); Larsen et al. (2020)
Shape of Teeth	Ebert et al. (2021)
Skeletal Structure	N/A
Spiracles – Presence/Absence	N/A
Stroke Volume	N/A
Swimming Form	N/A
Thermoregulation	Abel & Grubbs (2020); Bernel et al. (2003); Ebert et al. (2021)
Visual Field	Kajiura (2010); McComb et al. (2009)

Table 2 List of all potential life history traits considered in this study (a total of 45 traits – listed in alphabetical order). All traits that were used for statistical analysis and had data for at least 50% of the species from each habitat are in ***bold italics***. All traits that had data available for species in every habitat but not 50% of the species from each habitat are in italics. Traits that are not in *italics* did not have enough data available for at least one species from every depth zone. All definitions were taken from Mull et al. (2022) unless otherwise specified. If the source is listed as 'N/A', there were no trait data available for oceanic species.

List of Potential Life History Traits Considered in This Study

Trait	Definition	Source(s)
Age at 50% of Individuals Mature	Age at which 50% of individuals are mature	Mull et al. (2022)
Age at 95% of Individuals Mature	Age at which 95% of individuals are mature	N/A
Age at First Maturity	Age at first maturity based on gonadal observation or clasper definition	Mull et al. (2022)
Age at Maternity	Age at first observation of pregnancy	N/A
Age of Largest Immature	Age of largest immature individual; typically based on gonadal observation or clasper calcification	N/A
Allometric Growth Pattern	The growth patterns of specific body parts	N/A
Annual Reproductive Output	The annual number of offspring or biomass of offspring a mother produces per year	N/A
Breeding Interval	Interval of female reproduction (biannual, annual, biennial, or triennial)	N/A
Breeding Time	Observed timing (calendar months) of mating	Mull et al. (2022)
Chemical Balance of Development	Ratio of dry mass between unfertilized ovum and full-term embryos or neonates	N/A
Embryonic Sex Ratio	In utero ratio of Males:Females within a liter	Mull et al. (2022)
Fishing Mortality Rate	Mortality of individuals attributed to fishing	Mull et al. (2022)
Generation Length	Mean age at which a cohort of individuals produce offspring; typically based off IUCN calculation	N/A
Gestation Length	The length of gestation in months for live-bearing species	Mull et al. (2022)
Growth Patterns	Growth pattern based off model	Mull et al. (2022)
Incubation Length	The length of incubation in months for egg-laying species	N/A
Length 50% of Individuals Mature	Length at which 50% of individuals are mature	Mull et al. (2022)
Length 95% of Individuals Mature	Length at which 95% of individuals are mature	Mull et al. (2022)
Length at Birth	Length at birth	Mull et al. (2022)
Length at First Maturity	Length of smallest mature individual based on gonadal observation or clasper calcification	Mull et al. (2022)
Length at Largest Immature	Length of largest immature individual based on gonadal observation or clasper calcification	Mull et al. (2022)
Length at Maternity	Length at first observation of pregnancy	Mull et al. (2022)
Litter Size	Number of ova or developing embryos	N/A

Table 2 (continued)

Trait	**Definition**	**Source(s)**
Longevity	Maximum life span (Tacutu et al., 2018)	Tacutu et al. (2018)
Max. Oviducal Width	Maximum width of the oviducal gland during the reproductive cycle	Mull et al. (2022)
Max. Uterine Width	Maximum uterus width during the reproductive cycle	N/A
Max. Age Estimated from Model	Maximum age estimated from model	Mull et al. (2022)
Max. Intrinsic Rate Population Inc.	Maximum intrinsic rate of population increase	N/A
Max. Length Estimated	Maximum length estimated from model	N/A
Max. Observed Age	Maximum observed age	Mull et al. (2022)
Max. Observed Length	Maximum length observed	Ebert et al. (2021); Mull et al. (2022)
Mode of Reproduction	Mode of reproduction; either viviparous or oviparous	Ebert et al. (2021); Mull et al. (2022)
Natural Mortality Rate	Natural mortality rate	Mull et al. (2022)
Number of Uteri	Single or multiple uteri	Mull et al. (2022)
Offspring Mass	The body mass of individual offspring at the time of birth or hatching	Mull et al. (2022)
Ovarian Fecundity	Maximum number of visible ovarian follicles	Mull et al. (2022)
Ovulation	Observed timing of ovulation	Mull et al. (2022)
Ovum Diameter	Maximum observed ova diameter (uterine or recently ovulated)	Mull et al. (2022)
Participation in Seasonal Breeding	Seasonal breeding patterns (yes or no)	N/A
Parturition	Observed timing of parturition	Mull et al. (2022)
Population Growth Rate	Population growth rate	N/A
Total Body Mass	Total body mass directly measured from individuals or estimated from length-weight relationships	Mull et al. (2022)
Total Mortality Rate	Total mortality rate	Mull et al. (2022)
Trophic Level	1 + a weighted average of the lengths of all food chains linking that species to a basal species (Yodzis, 2001)	Froese & Pauly (2024)
Uterine Fecundity	Maximum number of visible ovulated eggs or developing embryos in both embryos	Mull et al. (2022)

Statistical Tests

All trait and species data were first cataloged into Microsoft Excel. In order to prepare the data for statistical tests, all trait data were placed into a 'species x trait matrix' as detailed in de Bello et al. (2021). Multiple matrices were created for each trait and for each sex (male or female) when sex information was available. If no significant difference was observed between traits with male and female data, the data were combined into a single ‘species x trait matrix’ for that trait. Since the traits being examined were both categorical and quantitative, a principal coordinate analysis (PCoA) was used to examine similarities and differences between the groups. The categorical traits were classified as binary and were given a 0 or 1 ranking so that they could be tested alongside the quantitative traits. For example, looking at the mode of reproduction trait, a viviparous species was given a 0 and an oviparous species was given a 1. This was done for all binary traits. The habitat and vertical distribution traits were split into 3 separate columns each. For example, *Rhincodon typus* was classified as shallow-water-pelagic in this study and was given a 1 in the shallow-water column, a 0 in the wanderer column, a 0 in the deep-sea column, a 0 in the benthic column, a 0 in the benthopelagic column, and a 1 in the pelagic column. This was done so that the trait could be weighted evenly among the other traits later. For ‘species x trait matrices’ with any of the five species with unknown mode of reproduction data, two additional datasets were created. One dataset assumed the mode of reproduction was viviparous and the other assumed the mode of reproduction was oviparous. Once the raw data were cataloged for all four matrices, each trait was examined individually to determine any trends in trait expression with depth zone.

Principal Coordinate Analysis (PCoA)

All trait data were converted to text files and imported into R Studio for statistical testing. The methods used for the PCoA tests followed the methods outlined in de Bello et al. (2021). Each trait in the ‘species x trait matrix’ was tested for normality using histogram plots. Only quantitative traits were tested for normality as binary traits (1s and 0s) are not normal and were weighted accordingly later. All quantitative data was normally distributed and therefore did not need to be transformed. Quantitative traits with more than two categorical options, such as vertical distribution and habitat, were treated as “fuzzy” traits even though they are technically binary. This was done to prepare the data for the statistical tests so that these traits would be weighted evenly among the other traits. Once all data were transformed, a new ‘species x trait matrix’ was created in R. A trait dissimilarity matrix was created using the new “gawdis” function of the *gawdis* package. This new function described in de Bello et al. (2021) uses Gower distances and was used in this study as it accounts for multiple data types (quantitative, binary, and fuzzy) as well as any NAs or missing data. The function evenly weights each trait based on the assigned grouping. Each quantitative and binary trait was given its own group. The fuzzy coded traits (habitat and vertical distribution) were grouped together by labeling each individual column the same number for that group. For example, the columns for vertical distribution or depth (epipelagic, wanderer, and deep sea) were all labelled 1 so that the function grouped those columns together and weighed them all as one trait instead of three separate traits. Within the “gawdis” function, “fuzzy” was set to “TRUE” to account for the fuzzy coded traits. The dissimilarity matrix created using the “gawdis” function was then analyzed in a multidimensional Euclidean space using the “dudi.pco” function of the *FD* package and the “scatter” function to graph the PCoA. The square-root of the dissimilarity matrix was used to eliminate any negative eigenvalues and ensure proper plotting of points in the multidimensional space. The eigenvalues and percent variation explained for each axis of the PCoA were analyzed to determine which axes had the highest eigenvalues and therefore captured the most variability. This was done using the function “cor”. Only the first two axes of each PCoA were used to make the PCoA plots, as these axes contain the highest level of variation possible in two dimensions. The final PCoA plots were made using the “ggplot” function of the *tidyverse* package.

Dendrograms

Using the same species dissimilarity matrix created with the “gawdis” function, a dendrogram was produced for each ‘species x trait matrix’. The function “hclust” was used in combination with the “ward.D2” clustering method. The ‘ward.D2” clustering method uses hierarchical clustering and works best with the Gower distance dissimilarity matrices created in this study. The function “NbClust” of the package *NbClust* was used to determine the number of groups that would maximize the difference between species. This function uses hierarchical clustering and the “gawdis” dissimilarity matrix to determine the optimal number of groups for that particular dataset. By overlaying these groupings onto the original dendrogram, the base of the dendrogram can be easily interpreted. Several heights along the y axis of the cluster dendrogram plots were chosen based on the level of branching in order to analyze the grouping of species. The largest branching occurred around heights 2.5 and 1.0. Height 0.0 at the base of the dendrogram was used to analyze the optimal species groupings determined using the “NbClust” function.

Results

Shark Traits in the Literature

Of the 337 species determined to be oceanic, 26 (7% of oceanic species) were classified as shallow-water, 27 (8% of oceanic species) wanderers, and 284 (85% of oceanic species) deep sea (Tables 1A-4A - Appendix). Of the 83 potential traits originally researched, there was information for 11 traits (13%) for all oceanic species considered in this study. The traits were: feeding mechanism, trophic level, caudal fin shape, number of dorsal spines, number of dorsal fins, presence or absence of an anal fin, number of gill slits, presence or absence of lateral keel, ectothermic or mesothermic, presence or absence of bioluminescence, and eye position. Data were available on the mode of reproduction trait for 282 of the 337 oceanic species in this study. Of the 55 species with unknown mode of reproduction (Table 5A - Appendix), the reproductive mode for 50 species could be inferred from the reproductive mode of other species from the same genus or family. Traits can be passed from generation to generation and close relatives are most likely to share similar traits, making it logical to infer reproductive mode when unknown. The mode of reproduction for five species of the *Bythaelurus* genus could not be inferred, due to the variability of reproductive biology within the genus. Of the 55 species with the inferred mode of reproduction data, only two were from the 'wanderer' depth group (*Mollisquama mississippiensis* and *Asymbolus occiduus*), while the other 53 species were from the 'deep sea' depth group. Of the 45 life history traits considered, mode of reproduction and trophic level were the only life history traits with enough data for all, or nearly all, oceanic shark species. The only other trait with enough data for at least 50% of the species from each habitat was IUCN Red List conservation status. Of the 337 species considered in this study, there were conservation status data for 274 (81%) species (Table 6A - Appendix). All other species have a Data Deficient or Not Evaluated conservation status which was classified as missing data.

Statistical Results

A total of four species x trait matrices were created. The 'species x trait matrix' with data available for all species included data for habitat distribution, vertical distribution/depth range, feeding mechanism, trophic level, caudal fin shape, the number of dorsal spines, the number of dorsal fins, the number of gill slits, the presence or absence of an anal fin, the presence or absence of a lateral keel, the presence or absence of bioluminescence, the mode of reproduction, thermoregulation, and eye position. The ‘species x trait matrix’ with conservation status data included the IUCN Red List conservation status data in addition to all of the data recorded in the ‘species x trait matrix’ with all oceanic species. Two matrices were made for each of these two sets of data: one matrix with the mode of reproduction recorded as oviparous for species in the *Bythaelurus* genus without known reproductive methods, and one with the mode of reproduction recorded as viviparous for species in the *Bythaelurus* genus without known reproductive methods.

One seemingly clear explanation for trait variation among oceanic shark species was depth. Each trait was examined individually to identify any trends in trait expression with depth (Table 3). While most of the traits vary with depth, there are a small number of traits that are unique to a specific depth zone. A lunate caudal fin shape, filter feeding, and a mesothermic thermoregulation strategy are all traits that can only be found in shallow-water species. A single dorsal fin, a single dorsal spine, more than five gill slit pairs, and species in trophic level five are all traits that can only be found in deep-sea species. All traits found in wanderer species were also found in shallow-water and deep-sea species. While there are some trends in trait expression with depth, the majority of the traits examined here vary across all three depth zones. This means there is another trait that contributes significantly more to species dissimilarity which can be determined using PCoAs.

Table 3 Trait composition of all oceanic shark species from all three depth zones. The percentages represent the proportion of species with the respective trait within each respective depth zones. For the deep-sea depth zone 'Mode of Reproduction' trait only, the five species from the *Bythaelurus* genus with reproductive strategies that could not be inferred are not included in the trait composition count. All other trait compositions include all species.

Trait	Shallow Water (26 Species)	Wanderer (27 Species)	Deep Sea (284 Species)
Habitat			
Benthic	-	13 (48%)	180 (63%)
Benthopelagic	4 (15%)	8 (30%)	24 (9%)
Pelagic	22 (85%)	6 (22%)	80 (28%)
# of Dorsal Fins			
2 Dorsal Fins	26 (100%)	27 (100%)	278 (98%)
1 Dorsal Fin	-	-	6 (2%)
# of Dorsal Spines			
2 Dorsal Spines	-	6 (22%)	113 (40%)
1 Dorsal Spines	-	-	2 (1%)
0 Dorsal Spines	26 (100%)	21 (78%)	169 (59%)
# of Gill Slits			
5 Gill Slits	26 (100%)	27 (100%)	276 (97%)
6 Gill Slits	-	-	7 (2%)
7 Gill Slits	-	-	1 (1%)
Anal Fin			
Absent	24 (92%)	12 (44%)	143 (50%)
Present	2 (8%)	15 (56%)	141 (50%)
Bioluminescence			
Absent	26 (100%)	24 (89%)	224 (79%)
Present	-	3 (11%)	60 (21%)
Caudal Fin Shape			
Heterocercal	19 (73%)	27 (100%)	284 (100%)
Lunate	7 (27%)	-	-
Conservation Status			
Data Deficient/ Not Evaluated	1 (3%)	5 (18%)	57 (20%)
Non-Threatened	9 (35%)	14 (52%)	190 (67%)
Threatened	16 (62%)	8 (30%)	37 (13%)
Eye Position			
Dorso-Lateral	-	3 (11%)	7 (2%)
Lateral	26 (100%)	24 (89%)	277 (98%)
Feeding Mechanism			
Filter Feeder	3 (12%)	-	-
Macropredator	23 (88%)	27 (100%)	284 (100%)
Lateral Keel			
Absent	17 (65%)	20 (74%)	240 (85%)
Present	9 (35%)	7 (26%)	44 (15%)
Mode of Reproduction			
Oviparous	1 (4%)	8 (30%)	109 (38%)
Viviparous	25 (96%)	19 (70%)	175 (62%)
Thermoregulation			
Ectothermic	20 (77%)	27 (100%)	284 (100%)
Mesothermic	6 (23%)	-	-
Trophic Level (TL)			
TL 3	4 (15%)	8 (30%)	82 (29%)
TL 4	22 (85%)	19 (70%)	201 (70%)
TL 5	-	-	1 (1%)

Principal Coordinate Analysis (PCoA)

A PCoA was conducted for all four matrices: all-species ‘species x trait matrix’ with oviparous data substitutions, all-species ‘species x trait matrix’ with viviparous data substitutions, conservation status ‘species x trait matrix’ with oviparous data substitutions, and conservation status ‘species x trait matrix’ with viviparous data substitutions. The eigen-values of each axis were analyzed to determine which traits contributed the most to species dissimilarity. Only the first four axes were chosen to describe the dissimilarities among species as these axes typically have the highest eigenvalues and explain the most variance. The eigenvalues and percent of variance did not vary significantly between the matrices when the mode of reproduction was changed for the five *Bythaelurus* species. Therefore, only the data for the oviparous datasets are discussed here. For the all-species matrices, the traits that explained the most variance among species in order from highest to lowest were the presence or absence of an anal fin, the presence or absence of a lateral keel, whether or not a species is benthic, and whether or not a species is pelagic (Table 4). For the conservation status matrices, the traits that explained the most variance among species in order from highest to lowest were the presence or absence of an anal fin, conservation status, whether or not a species is pelagic, and the presence or absence of a lateral keel (Table 5).

Table 4 Eigenvalues, percent variance, and trait correlation for the first four axes of the all-species ‘species x trait matrix’ with oviparous data substitutions for the five *Bythaelurus* species without reproductive data.

Axis	Eigenvalue	% of Variance	Cumulative %	Trait
1	6.427	41.974	41.974	Presence/Absence of Anal Fin
2	2.559	14.053	56.027	Presence/Absence of Lateral Keel
3	1.573	10.818	66.845	Benthic Habitat
4	0.929	6.951	73.796	Pelagic Habitat

Table 5 Eigenvalues, percent variance, and trait correlation for the first four axes of the conservation status 'species x trait matrix' with oviparous data substitutions for the five Bythaelurus species without reproductive data.

Axis	Eigenvalue	% of Variance	Cumulative %	Trait
1	4.970	37.328	37.328	Presence/Absence of Anal Fin
2	2.815	16.736	54.064	Conservation Status
3	1.303	9.965	64.029	Pelagic Habitat
4	0.989	7.136	71.165	Presence/Absence of Lateral Keel

The PCoA plots were created using only the first two axes as these explained over half of the variance between species and displayed the highest possible variation in two dimensions. The position of species with specific traits along a given axes can be determined using the correlation values for the traits that correlated the most with PCo1 (axis 1) and PCo2 (axis 2). Only the traits that correlated the most with each axis were analyzed. There were no other traits that showed the same strong correlation across the axes of the PCoA plots. For both of the all-species PCoA plots (Figures 2 & Figure 1A - Appendix), the majority of species on the right side of the graph have an anal fin while species on the left side of the graph do not. The majority of species at the top of the graph do not have a lateral keel, while species at the bottom of the graph do have a lateral keel. For both of the conservation status PCoA plots (Figures 3 & Figure 2A - Appendix), the majority of species on the right side of the graph have an anal fin, while species on the left side of the graph do not. The majority of species at the top of the graph have a non-threatened conservation status, while species at the bottom of the graph have a threatened conservation status.

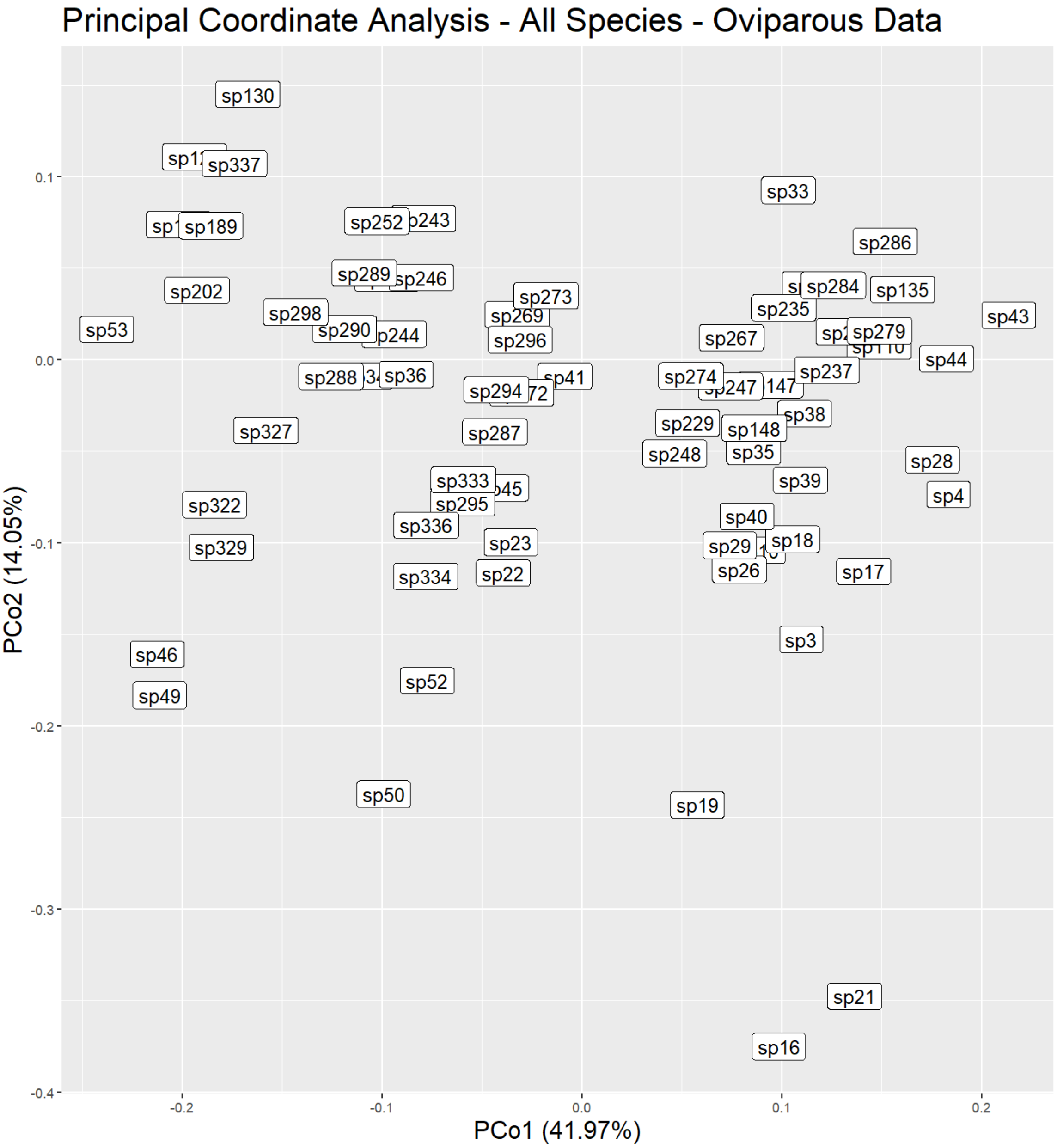

Figure 2 Principal Coordinate Analysis plot of the all-species 'species x trait matrix' with oviparous data substitutions for the five species from the *Bythaelurus* genus without mode of reproduction data. The X-axis and Y-axis represent the two main coordinate axes, and the percentage of variance explained by each axis is in parentheses. A guide for the species labels in this plot is provided in Appendix Table 1A.

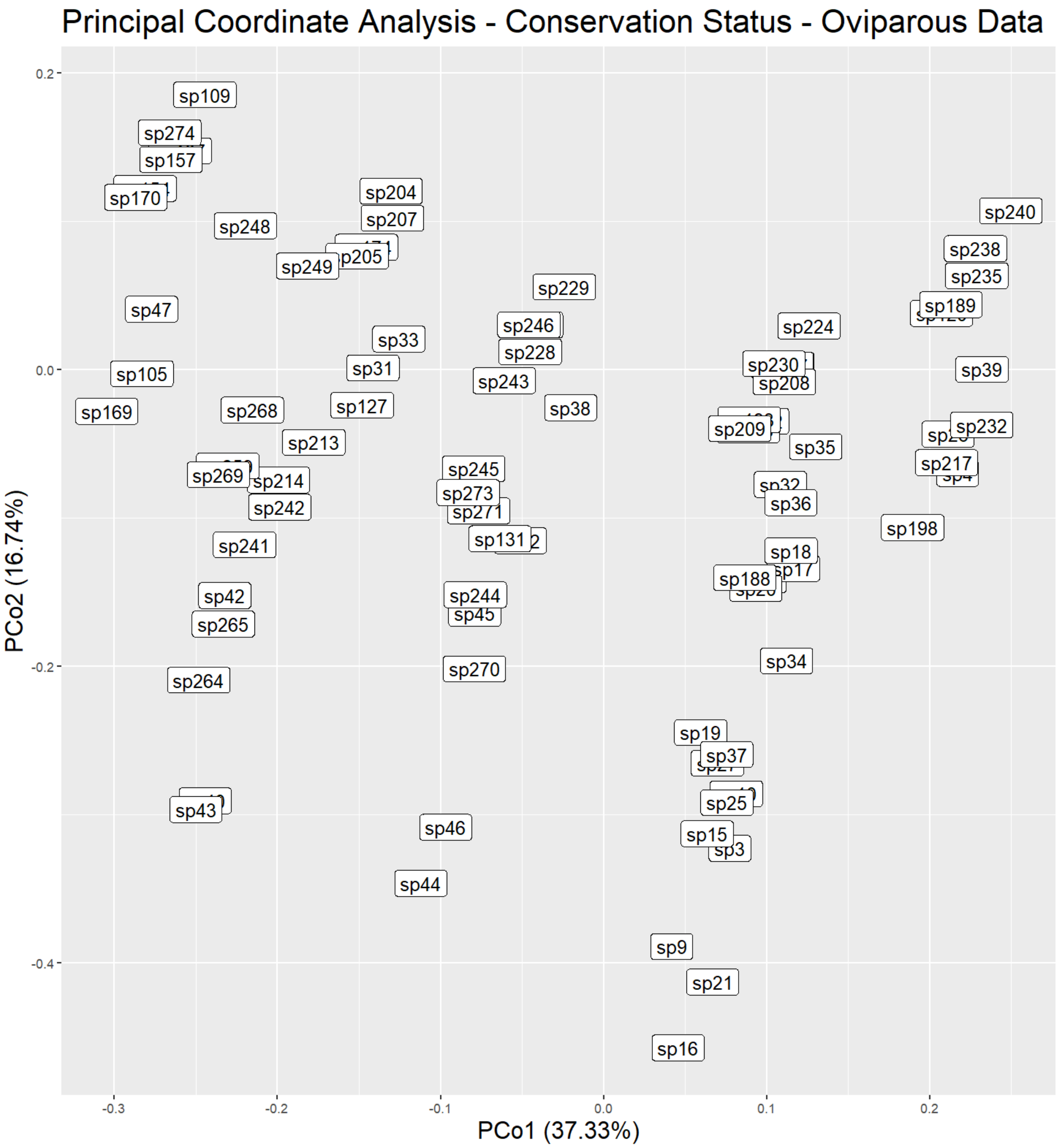

Figure 3 Principal Coordinate Analysis plot of the conservation status 'species x trait matrix' with oviparous data substitutions for the five species from the *Bythaelurus* genus without mode of reproduction data. The X-axis and Y-axis represent the two main coordinate axes, and the percentage of variance explained by each axis is in parentheses. A guide for the species labels in this plot is provided in Appendix Table 6A.

Dendrograms

Dendrograms were created for all four matrices: all-species ‘species x trait matrix’ with oviparous data substitutions, all-species ‘species x trait matrix’ with viviparous data substitutions, conservation status ‘species x trait matrix’ with oviparous data substitutions, and conservation status ‘species x trait matrix’ with viviparous data substitutions. All four plots exhibited a large split into two groups at the beginning of the cluster dendrogram partitioning (around height 2.5 on the Y-axis of the plot) (Figures 4-7). The species composition of each of these groups did not change at this height when the mode of reproduction was altered for the five *Bythaelurus* species without reproduction data. Therefore, only one set of tables for the all-species dataset and one set of tables for the conservation status are used to explain the trait composition of each group at height 2.5. The trait composition of each grouping was studied and for all four plots, one trait seems to be the cause of the first major separation at height 2.5, the presence or absence of an anal fin. Species without an anal fin belong primarily to the superorder Squalomorphi, while species with an anal fin belong primarily to the superorder Galeomorphi. For the purpose of this analysis, the groupings of species in the cluster dendrogram plots will be examined as Squalomorphi species compared to Galeomorphi species.

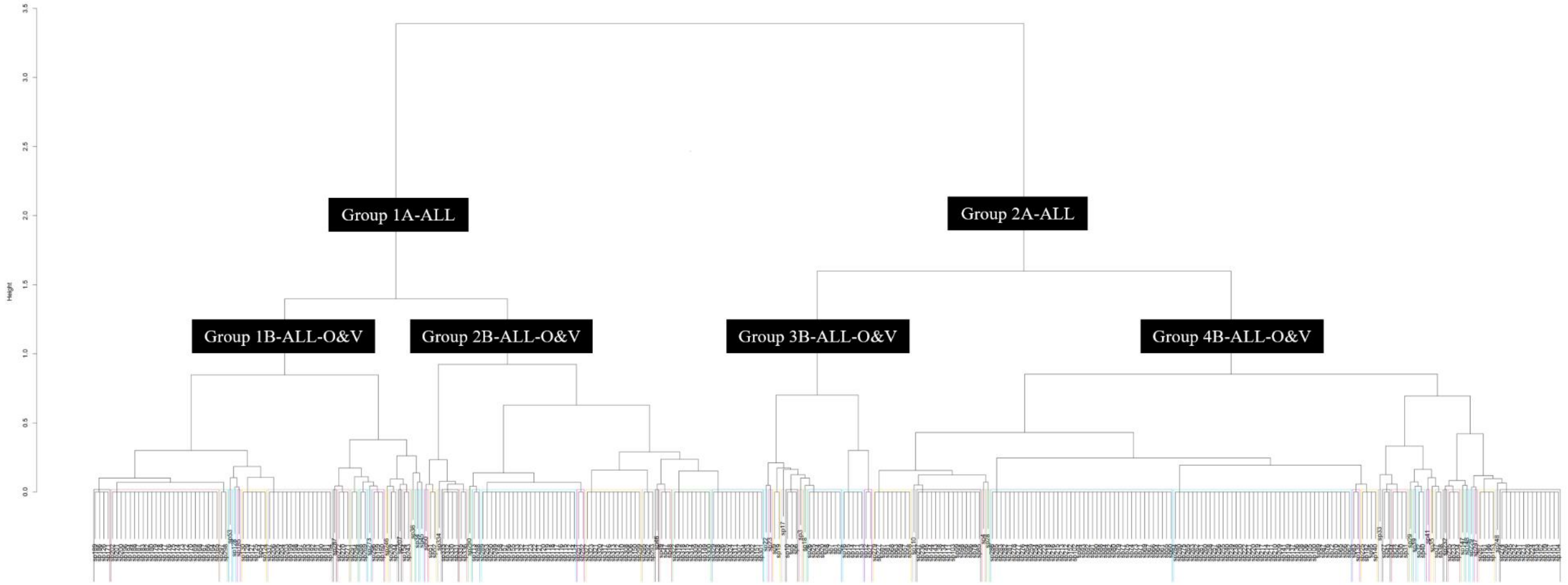

Figure 4 Cluster Dendrogram of all-species ‘ species x trait matrix’ with oviparous data substitutions. Dendrogram shows hierarchical clustering of species within the data set (337 species). The colored boxes show the optimal number of clusters for this data set which was 73. A guide to the species code used in this graph is in Table 1A - Appendix.

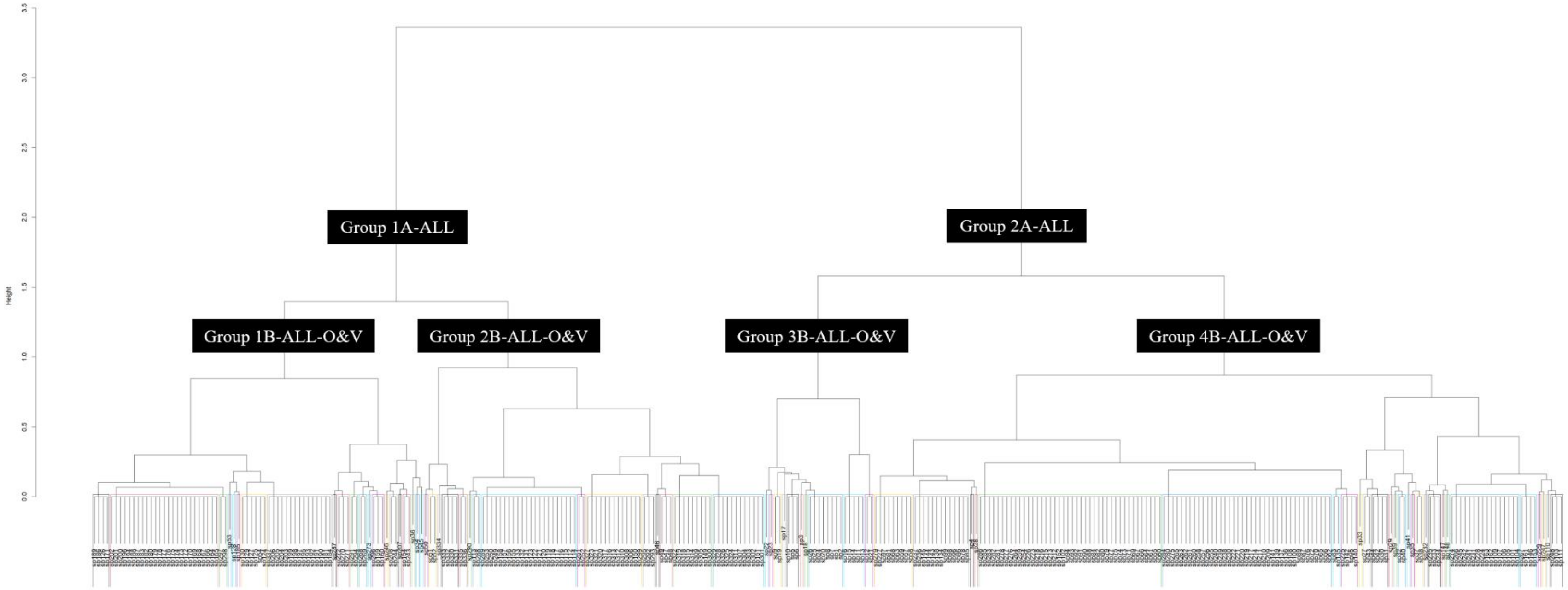

Figure 5 Cluster Dendrogram of all-species ‘ species x trait matrix’ with viviparous data substitutions. Dendrogram shows hierarchical clustering of species within the data set (337 species). The colored boxes show the optimal number of clusters for this data set which was 73. A guide to the species code used in this graph is in Table 1A - Appendix.

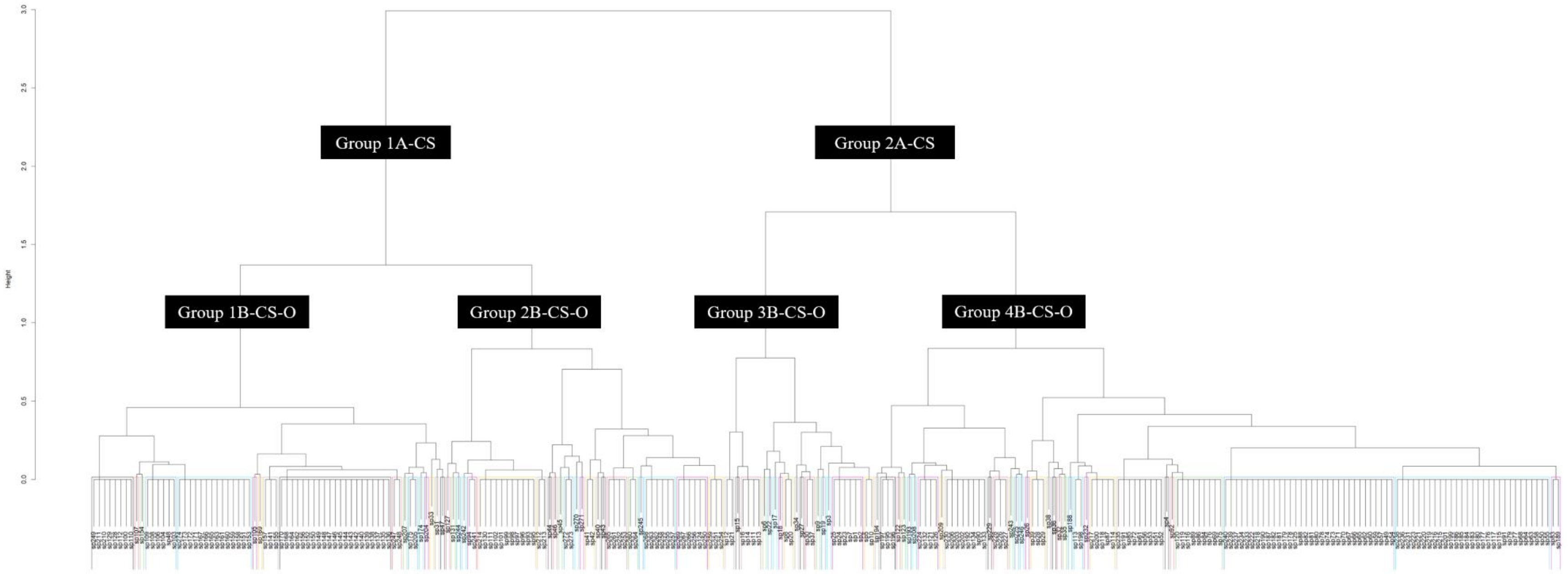

Figure 6 Cluster Dendrogram of conservation status ‘ species x trait matrix’ with oviparous data substitutions. Dendrogram shows hierarchical clustering of species within the data set (274 species). The colored boxes show the optimal number of clusters for this data set which was 86. A guide to the species code used in this graph is in Table 6A - Appendix.

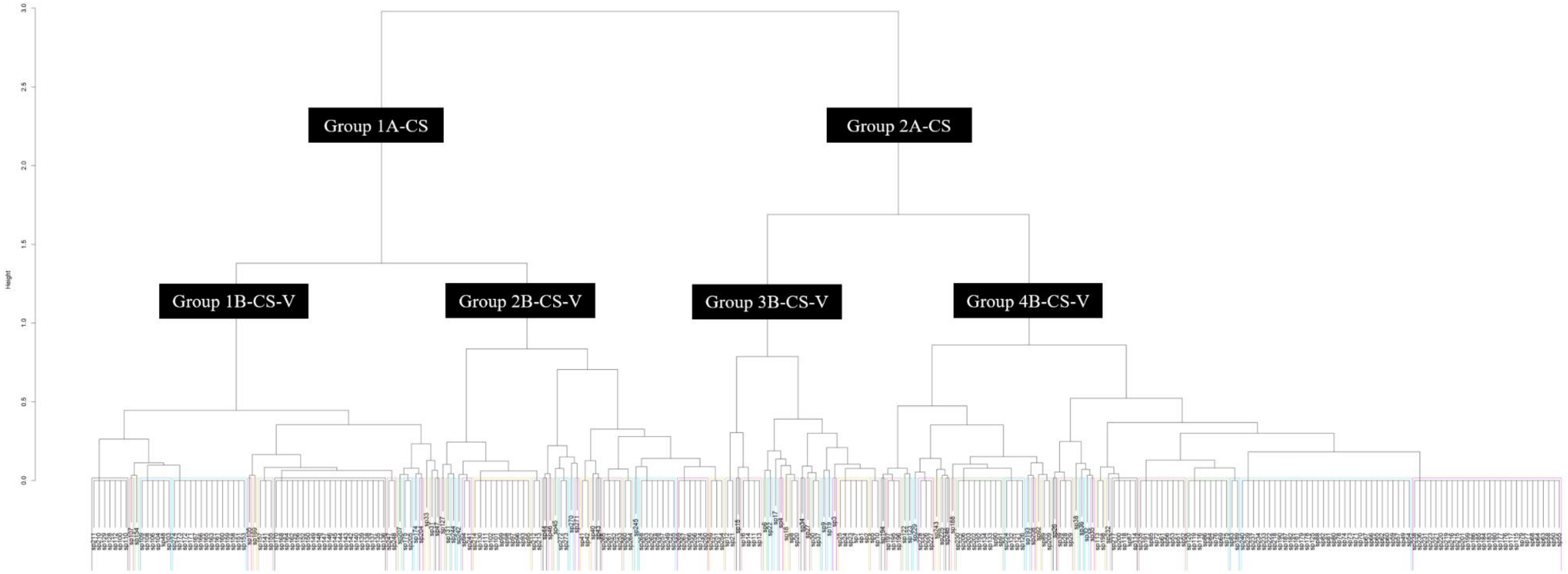

Figure 7 Cluster Dendrogram of conservation status ‘ species x trait matrix’ with viviparous data substitutions. Dendrogram shows hierarchical clustering of species within the data set (274 species). The colored boxes show the optimal number of clusters for this data set which was 86. A guide to the species code used in this graph is in Table 6A - Appendix.

Superorder Squalomorphi Trait Analysis

The dendrogram groups of species with no anal fin that best represent the superorder Squalomorphi included Group 1A-ALL (Table 6) from the all-species matrix and Group 1A-CS (Table 7) from the conservation status matrix. Within Group 1A-ALL, the traits that were consistent for all species within the group were two dorsal spines, heterocercal caudal fin shape, macropredator feeding mechanism, viviparous reproductive strategy, absence of an anal fin, and ectothermic thermoregulation strategy. For Group 1A-CS, the traits that were consistent for all species within the group were two dorsal fins, five gill slits, heterocercal caudal fin shape, macropredator feeding mechanism, viviparous reproductive strategy, absence of an anal fin, and ectothermic thermoregulation strategy. There were several traits that were found exclusively in the groups of species without an anal fin and not in the groups of species with an anal fin. For Group 1A-ALL, these traits included a single dorsal spine, dorso-lateral eye position, and the presence of bioluminescence. Within Group 1A-CS, these traits included the presence of dorsal spines (either one or two spines), dorso-lateral eye position, and the presence of bioluminescence.

Table 6 Composition of traits within Group 1A – ALL taken from the cluster dendrograms of both all-species 'species x trait matrices'. Group 1A – ALL is composed of 154 species. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 1A - ALL (154 total species)
Vertical Distribution	Wanderer (11); Deep Sea (143)
Habitat	Benthic (77); Benthopelagic (20); Pelagic (57)
# of Dorsal Fins	2 Dorsal Fins (154)
# of Dorsal Spines	2 Spines (118); 1 Spine (2); 0 Spines (34)
# of Gill Slits	5 Gill Slits (152); 6 Gill Slits (2)
Caudal Fin Shape	Heterocercal (154)
Eye Position	Dorso-Lateral (10); Lateral (144)
Feeding Mechanism	Macropredator (154)
Mode of Reproduction	Viviparous (154)
Presence/Absence of Anal Fin	Absent (154)
Presence/Absence of Bioluminescence	Present (63); Absent (91)
Presence/Absence of Lateral Keel	Present (51); Absent (103)
Thermoregulation	Ectothermic (154)
Trophic Level	Trophic Level 3 (23); Trophic Level 4 (131)

Table 7 Composition of trait within Group 1A – CS taken from the cluster dendrogram of both conservation status 'species x trait matrices'. Group 1A – CS is composed of 118 species. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 1A - CS (118 total species)
Vertical Distribution	Wanderer (10); Deep Sea (108)
Habitat	Benthic (60); Benthopelagic (14); Pelagic (44)
# of Dorsal Fins	2 Dorsal Fins (118)
# of Dorsal Spines	2 Spines (98); 1 Spine (2); 0 Spines (18)
# of Gill Slits	5 Gill Slits (118)
Caudal Fin Shape	Heterocercal (118)
Conservation Status	Non-Threatened (86); Threatened (32)
Eye Position	Dorso-Lateral (7); Lateral (111)
Feeding Mechanism	Macropredator (118)
Mode of Reproduction	Viviparous (118)
Presence/Absence of Anal Fin	Absent (118)
Presence/Absence of Bioluminescence	Present (59); Absent (59)
Presence/Absence of Lateral Keel	Present (34); Absent (84)
Thermoregulation	Ectothermic (118)
Trophic Level	Trophic Level 3 (18); Trophic Level 4 (100)

The next major split in species occurred at height 1.0, at which point each of the two major groups split into two smaller groups, creating a total of four groups in both the all-species and conservation status matrices. For the all-species matrices, the group that best represented species from the Squalomorphi superorder, Group 1A-ALL, was split into two groups labeled Group 1B-ALL-O&V (Table 8) and Group 2B-ALL-O&V (Table 9). The traits consistent across all species in Group 1B-ALL-O&V that were not consistent in the larger Group 1A-ALL include a lateral eye position and the absence of a lateral keel. For Group 2B-ALL-O&V, the traits consistent across all species in this group that varied in the larger Group 1A-ALL included five gill slits and the absence of bioluminescence.

Table 8 Composition of traits within Group 1B-ALL-O&V taken from height 1.0 in the cluster dendrograms of both all-species ‘species x trait matrices’. This group consists of 76 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 1B - ALL - O & V (76 total species)
Vertical Distribution	Wanderer (4); Deep Sea (72)
Habitat	Benthic (29); Benthopelagic (8); Pelagic (39)
# of Dorsal Fins	2 Dorsal Fins (76)
# of Dorsal Spines	2 Spines (53); 1 Spines (2); Spines (10)
# of Gill Slits	5 Gill Slits (74); 6 Gill Slits (2)
Caudal Fin Shape	Heterocercal (76)
Eye Position	Lateral (76)
Feeding Mechanism	Macropredator (76)
Mode of Reproduction	Viviparous (76)
Presence/Absence of Anal Fin	Absent (76)
Presence/Absence of Bioluminescence	Present (63); Absent (13)
Presence/Absence of Lateral Keel	Absent (76)
Thermoregulation	Ectothermic (76)
Trophic Level	Trophic Level 3 (51); Trophic Level 4 (25)

Table 9 Composition of traits within Group 2B-ALL-O&V taken from height 1.0 in the cluster dendrograms of both all-species ‘species x trait matrices’. This group consists of 78 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 2B - ALL - O & V (78 total species)
Vertical Distribution	Wanderer (7); Deep Sea (71)
Habitat	Benthic (48); Benthopelagic (12); Pelagic (18)
# of Dorsal Fins	2 Dorsal Fins (78)
# of Dorsal Spines	2 Spines (65); 0 Spines (13)
# of Gill Slits	5 Gill Slits (78)
Caudal Fin Shape	Heterocercal (78)
Eye Position	Dorso-Lateral (10); Lateral (68)
Feeding Mechanism	Macropredator (78)
Mode of Reproduction	Viviparous (78)
Presence/Absence of Anal Fin	Absent (78)
Presence/Absence of Bioluminescence	Absent (78)
Presence/Absence of Lateral Keel	Present (51); Absent (27)
Thermoregulation	Ectothermic (78)
Trophic Level	Trophic Level 3 (6); Trophic Level 4 (72)

For the conservation status matrices, the species composition of the groups that formed at height 1.0 varied between the oviparous and viviparous datasets. The group that best represented the Squalomorphi superorder for the conservation status datasets, Group 1A-CS, was split into Group 1B-CS-O (Table 10) and Group 2B-CS-O (Table 11) for the dataset with oviparous data substitutions and into Group 1B-CS-V (Table 12) and Group 2B-CS-V (Table 13) for the dataset with viviparous data substitutions. Looking first at the dataset with oviparous data substitutions, the trait that varied in Group 1A-CS but became consistent in Group 1B-CS-O was a lateral eye position. There were no newly consistent traits in Group 2B-CS-O. For the viviparous dataset, the traits that varied in Group 1A-CS but became consistent in Group 1B-CS-V were a lateral eye position and the absence of a lateral keel. There were no newly consistent traits in Group 2B-CS-V.

Table 10 Composition of traits within Group 1B-CS-O taken from height 1.0 in the cluster dendrogram of the conservation status 'species x trait matrix' with oviparous data substitutions. This group consists of 66 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 1B - CS - O (66 total species)
Vertical Distribution	Wanderer (3); Deep Sea (63)
Habitat	Benthic (29); Benthopelagic (5); Pelagic (32)
# of Dorsal Fins	2 Dorsal Fins (56)
# of Dorsal Spines	2 Spines (57); 1 Spine (2); 0 Spines (7)
# of Gill Slits	5 Gill Slits (66)
Caudal Fin Shape	Heterocercal (66)
Conservation Status	Non-Threatened (64); Threatened (2)
Eye Position	Lateral (66)
Feeding Mechanism	Macropredator (66)
Mode of Reproduction	Viviparous (66)
Presence/Absence of Anal Fin	Absent (66)
Presence/Absence of Bioluminescence	Present (58); Absent (8)
Presence/Absence of Lateral Keel	Present (1); Absent (65)
Thermoregulation	Ectothermic (66)
Trophic Level	Trophic Level 3 (39); Trophic Level 4 (27)

Table 11 Composition of traits within Group 2B-CS-O taken from height 1.0 in the cluster dendrograms of the conservation status 'species x trait matrix' with oviparous data substitutions. This group consists of 52 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 2B - CS - O (52 total species)
Vertical Distribution	Wanderer (7); Deep Sea (45)
Habitat	Benthic (31); Benthopelagic (9); Pelagic (12)
# of Dorsal Fins	2 Dorsal Fins (52)
# of Dorsal Spines	2 Spines (41); 0 Spines (11)
# of Gill Slits	5 Gill Slits (52)
Caudal Fin Shape	Heterocercal (52)
Conservation Status	Non-Threatened (22); Threatened (30)
Eye Position	Dorso-Lateral (7); Lateral (45)
Feeding Mechanism	Macropredator (52)
Mode of Reproduction	Viviparous (52)
Presence/Absence of Anal Fin	Absent (52)
Presence/Absence of Bioluminescence	Present (1); Absent (51)
Presence/Absence of Lateral Keel	Present (33); Absent (19)
Thermoregulation	Ectothermic (52)
Trophic Level	Trophic Level 3 (5); Trophic Level 4 (47)

Table 12 Composition of traits within Group 1B-CS-V taken from height 1.0 in the cluster dendrogram of the conservation status 'species x trait matrix' with viviparous data substitutions. This group consists of 65 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 1B - CS - V (65 total species)
Vertical Distribution	Wanderer (3); Deep Sea (62)
Habitat	Benthic (28); Benthopelagic (5); Pelagic (32)
# of Dorsal Fins	2 Dorsal Fins (65)
# of Dorsal Spines	2 Spines (56); 1 Spine (2); 0 Spines (7)
# of Gill Slits	5 Gill Slits (65)
Caudal Fin Shape	Heterocercal (65)
Conservation Status	Non-Threatened (63); Threatened (2)
Eye Position	Lateral (65)
Feeding Mechanism	Macropredator (65)
Mode of Reproduction	Viviparous (65)
Presence/Absence of Anal Fin	Absent (65)
Presence/Absence of Bioluminescence	Present (58); Absent (7)
Presence/Absence of Lateral Keel	Absent (65)
Thermoregulation	Ectothermic (65)
Trophic Level	Trophic Level 3 (13); Trophic Level 4 (52)

Table 13 Composition of traits within Group 2B-CS-V taken from height 1.0 in the cluster dendrograms of the conservation status 'species x trait matrix' with viviparous data substitutions. This group consists of 53 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 2B - CS - V (53 total species)
Vertical Distribution	Wanderer (7); Deep Sea (46)
Habitat	Benthic (32); Benthopelagic (9); Pelagic (12)
# of Dorsal Fins	2 Dorsal Fins (53)
# of Dorsal Spines	2 Spines (42); 0 Spines (11)
# of Gill Slits	5 Gill Slits (53)
Caudal Fin Shape	Heterocercal (53)
Conservation Status	Non-Threatened (23); Threatened (30)
Eye Position	Dorso-Lateral (7); Lateral (46)
Feeding Mechanism	Macropredator (62)
Mode of Reproduction	Viviparous (53)
Presence/Absence of Anal Fin	Absent (53)
Presence/Absence of Bioluminescence	Present (34); Absent (19)
Presence/Absence of Lateral Keel	Present (9); Absent (53)
Thermoregulation	Ectothermic (53)
Trophic Level	Trophic Level 3 (5); Trophic Level 4 (48)

Superorder Galeomorphi Trait Analysis

The groups that consisted of primarily Galeomorphi species (presence of an anal fin) included Group 2A-ALL (Table 14) from the all-species matrix and Group 2A-CS (Table 15) from the conservation status matrix. These groups contained the five species with unknown reproductive methods from the *Bythaelurus* genus and therefore the number of oviparous and viviparous species varied depending on the matrix. Within Group 2A-ALL, there were nine species from the Squalomorphi superorder (*Chlamydoselachus africana*, *Chlamydoselachus anguineus*, *Heptranchias perlo*, *Hexanchus griseus*, *Hexanchus nakamurai*, *Hexanchus vitulus*, *Pristiophorus japonicus*, *Scymnodalatias albicauda*, and *Scymnodalatias oligodon*). There were 15 species from the Squalomorphi superorder found in Group 2A-CS. These included the same Squalomorphs from Group 2A-ALL, minus *S. albicauda* and with the addition of *Pliotrema warreni*, *Pristiophorus delicatus*, *Pristiophorus lanae*, *Pristiophorus nancyae*, *Pristiophorus schroederi*, *Somniosus antarcticus*, and *Somniosus rostratus*. All these species are excluded from the analysis below and discussed later. This was done to target trends in trait expression within the Galeomorphi superorder.

The traits that were consistent for all species within Group 2A-ALL included two dorsal fins, five gill slits, the presence of an anal fin, lateral eye position, and the absence of bioluminescence. The traits that were consistent for all species within Group 2A – CS were two dorsal fins, five gill slits, the presence of an anal fin, no dorsal spines, lateral eye position, and absence of bioluminescence. There were several traits that were found exclusively in the groups of species with an anal fin that were not found in the groups of species without an anal fin. For Group 2A-ALL, these traits included shallow-water depth zone, a lunate caudal fin, filter feeding, mesothermic thermoregulation, and trophic level 5. Within Group 2A-CS, these traits included shallow-water depth zone, a lunate caudal fin shape, filter feeding, mesothermic thermoregulation, and trophic level 5.

Table 14 Composition of trait within Group 2A - ALL taken from the cluster dendrogram of both all-species 'species x trait matrices'. Group 2A - ALL is composed of 174 species. The number of species representing each trait is in parentheses. The mode of reproduction trait is split for the two datasets with the 'O:' data representing the matrix with oviparous data substitutions and the 'V;' data representing the matrix with viviparous data substitutions.

Trait	Trait Composition within Group 2A - ALL (174 total species)
Vertical Distribution	Shallow Water (24); Wanderer (15); Deep Sea (135)
Habitat	Benthic (111); Benthopelagic (14); Pelagic (49)
# of Dorsal Fins	2 Dorsal Fins (174)
# of Dorsal Spines	2 Spine (1); 0 Spines (173)
# of Gill Slits	5 Gill Slits (174)
Caudal Fin Shape	Heterocercal (167); Lunate (7)
Eye Position	Lateral (174)
Feeding Mechanism	Macropredator (171); Filter Feeder (3)
Mode of Reproduction	O: Oviparous (123); Viviparous (51) V: Oviparous (118); Viviparous (56)
Presence/Absence of Anal Fin	Present (174)
Presence/Absence of Bioluminescence	Absent (174)
Presence/Absence of Lateral Keel	Present (9); Absent (165)
Thermoregulation	Ectothermic (166); Mesothermic (8)
Trophic Level	Trophic Level 3 (67); Trophic Level 4 (106); Trophic Level 5 (1)

Table 15 Composition of trait within Group 2A – CS taken from the cluster dendrogram of both conservation status 'species x trait matrices'. Group 2A – CS is composed of 141 species. The number of species representing each trait is in parentheses. The mode of reproduction trait is split for the two datasets with the 'O:' data representing the matrix with oviparous data substitutions and the 'V;' data representing the matrix with viviparous data substitutions.

Trait	Trait Composition within Group 2A - CS (141 total species)
Vertical Distribution	Shallow Water (24); Wanderer (11); Deep Sea (106)
Habitat	Benthic (86); Benthopelagic (10); Pelagic (45)
# of Dorsal Fins	2 Dorsal Fins (141)
# of Dorsal Spines	0 Spines (141)
# of Gill Slits	5 Gill Slits (141)
Caudal Fin Shape	Heterocercal (134); Lunate (7)
Conservation Status	Non-Threatened (112); Threatened (29)
Eye Position	Lateral (141)
Feeding Mechanism	Macropredator (138); Filter Feeder (3)
Mode of Reproduction	O: Oviparous (93); Viviparous (48) V: Oviparous (90); Viviparous (51)
Presence/Absence of Anal Fin	Present (141)
Presence/Absence of Bioluminescence	Absent (141)
Presence/Absence of Lateral Keel	Present (9); Absent (132)
Thermoregulation	Ectothermic (135); Mesothermic (6)
Trophic Level	Trophic Level 3 (54); Trophic Level 4 (86); Trophic Level 5 (1)

At height 1.0, the groups that best represented the Galeomorphi Superorder (presence of an anal fin) split into two smaller groups. For the all-species matrices, Group 2A-ALL split into Group 3B-ALL-O&V (Table 16) and Group 4B-ALL-O&V (Table 17). The species composition of the two groups did not change when the mode of reproduction was adjusted for the five *Bythaelurus* species, therefore both datasets are represented in these tables. The traits that varied in Group 2A-ALL but became consistent across all species in Group 3B-ALL-O&V were a shallow-water vertical distribution, no dorsal spines, and viviparity. For Group 4B-ALL-O&V, the newly consistent traits were a heterocercal caudal fin shape, macropredator feeding mechanism, absence of a lateral keel, and ectothermic thermoregulation.

Table 16 Composition of traits within Group 3B-ALL-O&V taken from height 1.0 in the cluster dendrogram of both all-species ‘species x trait matrices’. This group consists of 23 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 3B - ALL - O & V (23 total species)
Vertical Distribution	Shallow Water (23)
Habitat	Benthopelagic (3); Pelagic (20)
# of Dorsal Fins	2 Dorsal Fins (25)
# of Dorsal Spines	0 Spines (23)
# of Gill Slits	5 Gill Slits (23)
Caudal Fin Shape	Heterocercal (16); Lunate (7)
Eye Position	Lateral (23)
Feeding Mechanism	Macropredator (20); Filter Feeder (3)
Mode of Reproduction	Viviparous (23)
Presence/Absence of Anal Fin	Present (23)
Presence/Absence of Bioluminescence	Absent (23)
Presence/Absence of Lateral Keel	Present (9); Absent (14)
Thermoregulation	Ectothermic (15); Mesothermic (6)
Trophic Level	Trophic Level 3 (4); Trophic Level 4 (19)

Table 17 Composition of traits within Group 4B-ALL-O&V taken from height 1.0 in the cluster dendrogram of both all-species ‘species x trait matrices’. This group consists of 151 species total. The number of species representing each trait is in parentheses. The mode of reproduction trait is split for the two datasets with the ‘O:’ data representing the matrix with oviparous data substitutions and the ‘V;’ data representing the matrix with viviparous data substitutions.

Trait	Trait Composition within Group 4B - ALL - O & V (151 total species)
Vertical Distribution	Shallow Water (1); Wanderer (15); Deep Sea (135)
Habitat	Benthic (111); Benthopelagic (11); Pelagic (29)
# of Dorsal Fins	2 Dorsal Fins (151)
# of Dorsal Spines	2 Spines (1); 0 Spines (150)
# of Gill Slits	5 Gill Slits (151)
Caudal Fin Shape	Heterocercal (151)
Eye Position	Lateral (151)
Feeding Mechanism	Macropredator (151)
Mode of Reproduction	O: Oviparous (123); Viviparous (28) V: Oviparous (118); Viviparous (33)
Presence/Absence of Anal Fin	Present (151)
Presence/Absence of Bioluminescence	Absent (151)
Presence/Absence of Lateral Keel	Absent (151)
Thermoregulation	Ectothermic (151)
Trophic Level	Trophic Level 3 (63); Trophic Level 4 (87); Trophic Level 5 (1)

For the conservation status matrices, Group 2A-CS also split into two smaller groups at height 1.0, but the species composition of these two groups varied when the mode of reproduction was altered for the five *Bythaelurus* species. For the conservation status dataset with oviparous data substitutions, the two smaller groups formed at height 1.0 were Group 3B-CS-O (Table 18) and Group 4B-CS-O (Table 19). The trait that varied in Group 2A-CS but became consistent in Group 3B-CS-O was viviparity. The newly consistent traits in Group 4B-CS-O included a heterocercal caudal fin shape, macropredator feeding mechanism, absence of a lateral keel, and ectothermic thermoregulation. For the dataset with viviparous data substitutions, the two groups were labeled Group 3B-CS-V (Table 20) and Group 4B-CS-V (Table 21). There were no traits that became consistent in Group 3B-CS-V but varied in Group 2A-CS. In Group 4B-CS-V, the newly consistent traits included a heterocercal caudal fin, macropredator feeding mechanism, absence of a lateral keel, and ectothermic thermoregulation.

Table 18 Composition of traits within Group 3B-CS-O taken from height 1.0 in the cluster dendrogram of the conservation status 'species x trait matrix' with oviparous data substitutions. This group consists of 27 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 3B - CS - O (27 total species)
Vertical Distribution	Shallow Water (23); Wanderer (4)
Habitat	Benthic (1); Benthopelagic (5); Pelagic (21)
# of Dorsal Fins	2 Dorsal Fins (27)
# of Dorsal Spines	0 Spines (27)
# of Gill Slits	5 Gill Slits (27)
Caudal Fin Shape	Heterocercal (20); Lunate (7)
Conservation Status	Non-Threatened (7); Threatened (20)
Eye Position	Lateral (27)
Feeding Mechanism	Macropredator (24); Filter Feeder (3)
Mode of Reproduction	Viviparous (27)
Presence/Absence of Anal Fin	Absent (27)
Presence/Absence of Bioluminescence	Absent (27)
Presence/Absence of Lateral Keel	Present (9); Absent (18)
Thermoregulation	Ectothermic (21); Mesothermic (6)
Trophic Level	Trophic Level 3 (5); Trophic Level 4 (22)

Table 19 Composition of traits within Group 4B-CS-O taken from height 1.0 in the cluster dendrogram of the conservation status 'species x trait matrix' with oviparous data substitutions. This group consists of 114 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 4B - CS - O (114 total species)
Vertical Distribution	Shallow Water (1); Wanderer (7); Deep Sea (106)
Habitat	Benthic (85); Benthopelagic (5); Pelagic (24)
# of Dorsal Fins	2 Dorsal Fins (114)
# of Dorsal Spines	0 Spines (114)
# of Gill Slits	5 Gill Slits (114)
Caudal Fin Shape	Heterocercal (114)
Conservation Status	Non-Threatened (105); Threatened (9)
Eye Position	Lateral (114)
Feeding Mechanism	Macropredator (114)
Mode of Reproduction	Oviparous (95); Viviparous (19)
Presence/Absence of Anal Fin	Present (114)
Presence/Absence of Bioluminescence	Absent (114)
Presence/Absence of Lateral Keel	Absent (114)
Thermoregulation	Ectothermic (114)
Trophic Level	Trophic Level 3 (49); Trophic Level 4 (64); Trophic Level 5 (1)

Table 20 Composition of traits within Group 3B-CS-V taken from height 1.0 in the cluster dendrogram of the conservation status 'species x trait matrix' with viviparous data substitutions. This group consists of 28 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 3B - CS - V (28 total species)
Vertical Distribution	Shallow Water (24); Wanderer (4)
Habitat	Benthic (1); Benthopelagic (5); Pelagic (22)
# of Dorsal Fins	2 Dorsal Fins (28)
# of Dorsal Spines	0 Spines (28)
# of Gill Slits	5 Gill Slits (28)
Caudal Fin Shape	Heterocercal (21); Lunate (7)
Conservation Status	Non-Threatened (8); Threatened (20)
Eye Position	Lateral (28)
Feeding Mechanism	Macropredator (25); Filter Feeder (3)
Mode of Reproduction	Oviparous (1); Viviparous (27)
Presence/Absence of Anal Fin	Present (28)
Presence/Absence of Bioluminescence	Absent (28)
Presence/Absence of Lateral Keel	Present (9); Absent (19)
Thermoregulation	Ectothermic (22); Mesothermic (6)
Trophic Level	Trophic Level 3 (5); Trophic Level 4 (23)

Table 21 Composition of traits within Group 4B-CS-V taken from height 1.0 in the cluster dendrogram of the conservation status ‘species x trait matrix’ with viviparous data substitutions. This group consists of 113 species total. The number of species representing each trait is in parentheses.

Trait	Trait Composition within Group 4B - CS - V (113 total species)
Vertical Distribution	Wanderer (7); Deep Sea (106)
Habitat	Benthic (85); Benthopelagic (5); Pelagic (23)
# of Dorsal Fins	2 Dorsal Fins (113)
# of Dorsal Spines	0 Spines (113)
# of Gill Slits	5 Gill Slits (113)
Caudal Fin Shape	Heterocercal (113)
Conservation Status	Non-Threatened (104); Threatened (9)
Eye Position	Lateral (113)
Feeding Mechanism	Macropredator (113)
Mode of Reproduction	Oviparous (91); Viviparous (22)
Presence/Absence of Anal Fin	Present (113)
Presence/Absence of Bioluminescence	Absent (113)
Presence/Absence of Lateral Keel	Absent (113)
Thermoregulation	Ectothermic (113)
Trophic Level	Trophic Level 3 (49); Trophic Level 4 (63); Trophic Level 5 (1)

Oceanic Shark Species with the Most Unique Sets of Traits

Each of the cluster dendrograms for the four matrices examined displayed a specific number of optimal groups. The optimal number of groups for both of the cluster dendrograms for the all-species ‘species x trait matrices’ with oviparous and viviparous data substitutions was 73. In the oviparous data dendrogram, 33 of the 73 groups consisted of a single species, while in the viviparous data dendrogram, 32 groups consisted of a single species. All other groups consisted of two or more species. The individual groups for the all-species ‘species x trait matrix’ with viviparous data substitutions consisted of all the same species as the oviparous data dendrogram except for one species, *O. noronhai*, which was in its own group for the oviparous data dendrogram but was paired in a larger group for the viviparous data dendrogram (Table 22).

Table 22 List of oceanic shark species that are independently grouped in the all-species cluster dendrogram plots (33 species). Shallow-water species are denoted by a ‘*’ symbol. Wanderer species are denoted by a ‘•’ symbol. All other species are deep-sea. The species _Odontaspis noronhai_ (in **_bold italics_**) was independently grouped in the oviparous data cluster dendrogram, but not in the viviparous data cluster dendrogram.

Independently Grouped Oceanic Shark Species in the All-Species Cluster Dendrograms

Alopias vulpinus *
Asymbolus occiduus •
Asymbolus submaculatus *
Bythaelurus tenuicephalus
Carcharhinus obscurus •
Centroscyllium nigrum
Chlamydoselachus africana
Chlamydoselachus anguineus
Etmopterus lucifer
Euprotomicroides zantedeschia
Gollum suluensis
Heptranchias perlo
Heterodontus ramalheira •
Heteroscymnoides marleyi •
Hypogaleus hyugaensis •
Megachasma pelagios *
Mollisquama mississippiensis •
Mollisquama parini
Mustelus albipinnis
Mustelus canis *
Mustelus stevensi •
Odontaspis noronhai
Pristiophorus japonicus •
Pristiophorus schroederi
Scymnodalatias albicauda *
Scymnodalatias garricki
Scymnodalatias oligodon *
Scymnodalatias sherwoodi •
Scymnodon ringens
Squalus acanthias •
Squatina albipunctata •
Squatina pseudocellata
Zameus squamulosus •

The optimal number of groups for both of the cluster dendrograms for the conservation status ‘species x trait matrices’ with oviparous and viviparous data substitutions was 86. In the oviparous data dendrogram, 51 of the 86 groups consisted of a single species, while in the viviparous data dendrogram, 50 groups consisted of a single species. All other groups consisted of two or more species. The individual groups for the conservation status ‘species x trait matrix’ with viviparous data substitutions consisted of the all the same species as the oviparous data dendrogram except for one species, _O. noronhai_, which was in its own group for the oviparous data dendrogram but was paired in a larger group for the viviparous data dendrogram (Table 23).

Table 23 List of oceanic shark species that are independently grouped in the conservation status cluster dendrogram plots (51 species). Shallow-water species are denoted by a '*' symbol. Wanderer species are denoted by a '•' symbol. All other species are deep-sea. The species *Odontaspis noronhai* (in ***bold italics***) was independently grouped in the oviparous data cluster dendrogram, but not in the viviparous data cluster dendrogram.

Independently Grouped Oceanic Shark Species in the Conservation Status Cluster Dendrograms

Alopias vulpinus *
Asymbolus occiduus •
Asymbolus submaculatus *
Bythaelurus tenuicephalus
Carcharhinus altimus *
Carcharhinus longimanus *
Carcharhinus obscurus •
Centroscyllium granulatum
Centroscyllium nigrum
Chlamydoselachus africana
Chlamydoselachus anguineus
Dalatias licha
Echinorhinus brucus
Etmopterus lucifer
Etmopterus spinax
Euprotomicroides zantedeschia
Galeus polli
Gollum suluensis
Heptranchias perlo
Heteroscymnoides marleyi •
Hypogaleus hyugaensis •
Isistius brasiliensis
Lamna ditropis *
Megachasma pelagios *
Mollisquama mississippiensis •
Mollisquama parini
Mustelus albipinnis
Mustelus canis *
Mustelus higmani •
Mustelus lenticulatus •
Mustelus stevensi •
Odontaspis noronhai
Pliotrema warreni
Prionace glauca *
Pristiophorus japonicus •
Pristiophorus schroederi
Schroederichthys saurisqualus
Scymnodalatias oligodon *
Scymnodon ringens
Somniosus antarcticus
Somniosus microcephalus
Somniosus pacificus
Somniosus rostratus
Squalus acanthias •
Squalus formosus •
Squatina albipunctata •
Squatina dumeril •
Squatina formosa
Squatina nebulosa •
Squatina pseudocellata
Zameus squamulosus •

Traits with Limited Data

Several of the potential traits researched during the literature analysis portion of this study did not have enough data for at least 50% of the species from each depth zone but did have at least one representative from each depth. These traits include composition of buoyancy lipids in the liver, composition of muscle tissue, composition of photoreceptors in the eye, distribution of electroreceptive pores across the head, longevity, maximum observed length, relative brain size, and uterine fecundity. The buoyancy lipids with enough data for at least one species from each depth zone included diacyl glyceryl ether (DAGE) (22 species), triacyclglycerols (TAG) (23 species), waxy ethers (33 species), hydrocarbons or squalene (17 species), sterols (13 species), and free fatty acids (13 species). Buoyancy lipids were typically measured in average percentage of all lipids measured within the liver. The average percentage of DAGE, waxy esters, and hydrocarbons in the liver showed a positive relationship with depth. The average percentage of TAG and fatty acids in the liver showed a negative relationship with depth. The average percentage of sterols in the liver showed no relationship with depth. A total of 12 species had enough data for the percentage of red muscle mass within the body and a positive relationship between percentage of red muscle mass and depth was observed. The composition of photoreceptors in the eye was most commonly recorded as a ratio of rod photoreceptors to cone photoreceptors. For this trait, enough data were available for 14 species and showed a higher ratio of rods to cones in deep-sea species compared to shallow-water species. The average percentage of electroreceptive pores across the dorsal and ventral sides of the head was recorded for 34 species and there was no observed trend with depth. Longevity data were available for 28 species and showed a positive relationship with depth. Maximum observed length data were separated between females, males, and ‘unsexed’ (meaning sex was not recorded). Female maximum total length (TL) was recorded for 104 species. Male maximum TL was recorded for 96 species. Unsexed maximum TL was recorded for 197 species. All available TL data (female, male, and unsexed) showed a decrease in average TL with depth. Relative brain size was often recorded as an encephalization quotient and data were available for 18 species. The available data for encephalization quotient showed a decrease in brain size with depth. Uterine fecundity data were available for 89 species. The average minimum uterine fecundity showed an increase with depth.

Discussion

Global oceanic shark populations are threatened by overfishing, pollution, habitat destruction and climate change (Abel & Grubbs, 2020; Drazen et al., 2020; Ebert et al., 2021; Finucci et al., 2024). Oceanic sharks from all trophic levels play an important role as both predators and prey in keeping their respective ecosystems diverse and functional (Heithaus et al., 2022). That is why it is important to protect these species and preserve their ecological roles. By using trait-based analysis it is possible to gain an understanding of the exact role each individual plays within its ecosystem and then use this knowledge to help enact conservation action. This study uses a trait-based approach to understand the role individual sharks play within oceanic ecosystems and how that role may change with depth. Trait-based analysis was also used to identify species with the most unique trait combinations. These species likely play important roles in their respective ecosystems that cannot be filled by any other individual. After analyzing the traits used in this study, the results show that the largest differences between individuals coincided with taxonomy rather than depth. The trait that contributed the most to these differences was the presence or absence of an anal fin. Of the 337 oceanic shark species originally examined, 33 species have trait combinations that cannot be found in any other species. Four of these 33 species have threatened conservation statuses. Lastly, this study revealed a severe lack in available trait data, specifically life-history trait data. This data is vital to our understanding of oceanic shark species and their importance in oceanic ecosystems.

Trends in Trait Expression with Depth

The total number of extant shark species originally pulled from Pollerspöck & Straube (2023) was 559 and of those, 337 were identified as oceanic shark species. Oceanic species in this study included sharks feeding in both the pelagic and benthic habitats. In total, approximately 60% of known species as of August 2023 are oceanic. As more research is conducted in the deep sea and more species are discovered, it is likely that the number of oceanic species will only increase (Randhawa et al., 2015). The large proportion of shark species occupying oceanic ecosystems further emphasizes the importance of this environment.

The vast majority of oceanic shark species were found to reside mostly or entirely in the deep sea. This confirms the previously stated idea that the majority of shark species are deep sea (Ebert et al., 2021). The deep sea is the largest biome on Earth (Drazen et al., 2020; Ramirez-Llorda et al., 2010), and while sharks are only known to occupy a small portion of this depth zone (Priede et al., 2006), the vastness of the deep sea compared to the epipelagic environment is one potential explanation for the large presence of sharks in the deep sea.

Looking at the distribution of species across the three habitats zones, all shallow-water species feed either partially or entirely in the pelagic habitat. Many of the species in this depth zone are migrators, such as the Oceanic Whitetip (*Carcharhinus longimanus*), and travel large distances over open ocean for food and reproduction (Howey-Jordan et al., 2013). The oceanic environment is also defined by its lack of a continental shelf (Torres & Bailey, 2022). The lack of a benthic environment and the migratory behavior of many shallow-water oceanic species is directly related to the pelagic habitat preference of all species found in this depth zone.

The majority of shark species in the wanderer and deep-sea depth zones are benthic, meaning they feed on or near the seabed. The distribution of food in the deep sea may be the factor contributing the most to the distribution of species in the wanderer and deep-sea depth zones. One of the main sources of food in the deep sea comes from food falls. The biggest of these food falls comes from megacarrion (organisms that are at least 100,000 kg) like blue whales that have died and fallen to the bottom (Britton & Morton, 1994; Priede, 2017). These whale falls showcase a full ecological succession and are large enough to supply a distinctive ecosystem that can persist for many years (Priede, 2017; Smith & Baco, 2003). Sharks from all depth zones are known to be scavengers (Auster et al., 2020; Tucker et al., 2019), and the higher concentration of large food items on the sea floor may be the reason so many wanderer and deep-sea shark species spend the majority of their time in the benthic environment. The concentration of deep-sea shark species living in and around the benthic environment also poses concerns about the impacts of deep-sea mining on deep-sea shark populations. The impacts of deep-sea mining include respiratory distress, auditory distress, reduced feeding, reduced visual communication, buoyancy issues, and toxicity (Drazen et al., 2020). All of these effects have the potential to impact a shark’s ability to find prey and potential mates, both of which are essential to the survival of a species. While the true long-term impacts are currently unknown, it is likely that deep-sea mining could be detrimental to deep-sea shark populations.

Surprisingly, the vertical distribution of oceanic shark species did not have a significant impact on trait expression. There was, however, one trend observed between trait expression and depth. Several traits were found to be unique to specific depth zones. The traits unique to the shallow-water depth zone were a lunate caudal fin shape, filter feeding, and mesothermic thermoregulation. The traits unique to the deep sea were a single dorsal fin, a single dorsal spine, six or more gill slit pairs, and a species representative of trophic level 5. There were no traits unique to the wanderer depth zone. This is likely directly related to the fact that these species must be adapted to survive in both the shallow-water and deep-sea depth zones. Each of these traits are analyzed below to understand why they are unique to their respective depth zone.

All seven of the species with a lunate caudal fin (Table 7A - Appendix) are epipelagic and are known to swim long distances offshore in the open ocean. A hydrodynamics study on the lunate caudal fin shape of *Carcharodon carcharias* found that the crescent caudal fin shape resulted in a lower lift to drag ratio and a lower aspect ratio, allowing the shark to make quick turns and produce bursts of speed (Lingham-Soliar, 2005). Maneuverability and quick acceleration are both essential for hunting fast-swimming fish species which are the typical prey items of many oceanic epipelagic-pelagic shark species. *Cetorhinus maximus* and *Rhincodon typus* are both filter feeders. While these species do not need to quickly accelerate to catch their prey, the increased maneuverability and decreased drag provided by the lunate caudal fin shape may still be beneficial when chasing plankton patches and swimming long distances. The exclusive presence of the lunate caudal fin trait in epipelagic shark species is likely a direct result of the niche requirements of an apex predator in this environment.

There are only three oceanic sharks that filter feed as their primary feeding mechanism. These species include *C. maximus, Megachasma pelagios,* and *R. typus*. All three of these species are epipelagic. Filter feeding sharks extract food particles suspended in the water column with their gill rakers as they swim through patches of high productivity at the surface (Ebert et al., 2021). The typical prey items of these species include zooplankton, small fish, and small crustaceans. The distribution of these species in the epipelagic zone is directly related to the concentration of their main prey item, plankton, at the surface of the ocean (Trujillo & Thurman, 2020). These species are unique in their ability to filter feed and, as a result, have been called evolutionary specialists (Wilga et al., 2007).

All the oceanic species with mesothermic thermoregulation strategies are epipelagic. There are six species with mesothermic thermoregulation strategies and all of them belong to the order Lamniformes (Table 8A - Appendix). These sharks are able to retain heat in several of their internal organs by using the heat produced from the muscles used in continuous swimming and through constant digestion and assimilation (Bernal et al., 2012). One major advantage this trait gives these shark species is the ability to occupy a wide range of water temperatures (Ebert et al., 2021). This range expansion allows the sharks to access prey items in areas such as the deep sea and higher latitudes that would otherwise be inaccessible (Bernal et al., 2012). While an increased range for hunting is a major advantage to being mesothermic, maintaining the temperature of specific organs is quite energetically costly (Dickson & Graham, 2004). In order to survive in the deep sea, organisms must conserve their energy (Herring, 2002) and a process such as endothermy is likely too energetically costly to be advantageous. This is likely why mesothermic species can only be found in the epipelagic environment. The unique contraflow heat exchange system these six species use to maintain a constant temperature for specific organs has not been observed in any other species of sharks.

Of all oceanic species considered in this study, only six species have one dorsal fin while the rest have two. All six of these species (Table 9A - Appendix) reside in the deep sea. As stated above, the dorsal fin acts like a boat keel, allowing the shark to make sharp turns and preventing roll-over while swimming (Ebert et al., 2021). The positioning of the single dorsal fin closer to the tail is thought to be related to the feeding strategy of these Hexanchiformes. The lower dorsal fin may aid in stability while the shark rolls and uses its saw-like teeth to devour its prey (Ebert et al., 2021). Hexanchiformes are also one of the oldest lineages of sharks (Barnett et al., 2012; Ebert et al., 2021; Royer & Coffey, 2017). This suggests that the presence of a single dorsal fin is a primitive trait. It is possible that this trait has only persisted in these six species while evolution has favored a second dorsal fin for additional stability in all other shark species, but more research on the evolutionary history of these species is needed to confirm this.

Dorsal spines are only present in species that spend some or all of their time in the deep-sea (Table 10A - Appendix). There are several possible reasons for this. The first is self-defense.

The dorsal spine acts as a defense mechanism against predators, injuring the soft inside of the mouth upon consumption (Claes et al., 2013). Deep-sea sharks are typically smaller than their epipelagic counterparts (Kyne & Simpfendorfer, 2012) and having a dorsal spine may provide an additional layer of protection against predation. A species of lanternshark (*Etmopterus spinax*) has been reported to have bioluminescent dorsal spines, alerting potential predators of their presence (Claes et al., 2013). The second potential reason shallow-water species do not have dorsal spines is because the spines can cause drag (Ebert et al., 2021). Dorsal spines produce drag while the shark is swimming and are therefore entirely absent or extremely small in fast swimming species (Ebert et al., 2021). Epipelagic sharks must be able to swim fast enough to catch their fast-swimming oceanic prey, such as tuna, therefore it is possible these species evolved without dorsal spines to ensure optimal hydrodynamics while swimming. Of all the species with dorsal spines (121 species), only two species have one dorsal spine while the rest have two. These two species *Squaliolus aliae* and *Squaliolus laticaudus* are the only representatives of the genus *Squaliolus*. The evolutionary history of these two species is relatively understudied. Therefore, the reason the species of this genus only have one dorsal spine is unknown.

A total of eight deep-sea species have more than five gill slit pairs (Table 11A - Appendix). Seven of these species have six gill slit pairs, while one species (*Heptranchias perlo*) has seven gill slit pairs. All of these species belong to the orders Hexanchiformes and Pristiophoriformes. As stated above, the Hexanchiformes order contains one of the oldest lineages of shark species These sharks have a body similar to that of prehistoric shark fossils from around 201 to 145 million years ago (mya) (Barnett et al., 2012; Ebert et al., 2021; Royer & Coffey, 2017). The presence of six or seven gill slits in this order is likely a trait that has remained in this species since its early ancestors in the Jurassic period (Royer & Coffey, 2017). The two species from the Pristiophoriformes order (*P. kajae* and *P. warreni*) are the only deep-sea species of that order with more than five gills. Another species from this order, *Pliotrema annae*, also has six gill slits but was not considered in this study because it is a neritic species. The genus *Pliotrema* is thought to have evolved around 66 to 56 mya, long after the suggested evolution of Hexanchiformes (Nevatte & Williamson, 2020). The higher order relationships of the Pristiophoriformes order are still debated, but it is currently placed in the superorder Squalomorphii which also includes the order Hexanchiformes (Nevatte & Williamson, 2020;

WoRMS Editorial Board, 2024). The relationship of the two orders, Pristiophoriformes and Hexanchiformes, may be the reason the six-gill slit trait appears in the genus *Pliotrema*, but this has never been confirmed.

Trophic level did not appear to vary significantly with depth. The average trophic level of species from the shallow-water depth zone was 4, while the average trophic level of the wanderer and deep-sea species was 3.7. Each depth zone contained a wide range of species from different trophic levels, but there was only one species from trophic level 5, *Bythaelurus tenuicephalus*. It is possible that the true trophic level of this species is 5, but it is also likely that assumptions about the prey items for this species were made that led to a higher trophic level. This species was only recently described by Kaschner et al. (2015) and very little is known about its diet. According to FishBase, the trophic level for this species was calculated based on its body size and the trophic levels of its closest relatives (Froese & Pauly, 2024). It is very likely that as more research is conducted on the diet of *B. tenuicephalus*, the trophic level will change.

Trait (Dis)Similarities Between Oceanic Shark Species

The one trait that caused the most dissimilarities between species was the presence or absence of an anal fin. This trend was observed in all four PCoA plots and all four dendrograms. After analyzing the species composition of clusters in the dendrograms, it became clear that the presence or absence of an anal fin was distinctly split along taxonomic lines. The majority of species without an anal fin belonged to the Squalomorphi superorder, while the majority of species with an anal fin belonged to the Galeomorphi superorder. Shark anal fins are relatively understudied compared to other shark fins. Currently, the primary function of the anal fin is thought to be stability while swimming, especially at high speeds (Ebert et al., 2021). One possible explanation for the lack of an anal fin in Squalomorphs is energy conservation. The majority of species from the Squalomorphi superorder are deep sea and in order to survive in this extreme environment organisms must learn to conserve their energy (Herring, 2002). Deep-sea sharks are generally slower swimmers compared to their epipelagic counterparts (Ebert et al., 2021) and therefore the additional stability provided by the anal fin may be unnecessary. It is possible that Squalomorphs have evolved without an anal fin simply because the absence of this additional fin became more cost effective, but more research is needed to confirm this. The taxonomic split observed in species with and without an anal fin suggests that there is a linkage between the evolution of sharks and the evolution of this fin.

While the taxonomic split between species with an anal fin and species without an anal fin held true for almost all sharks, there were some exceptions. There were several Squalomorphi species in the dendrogram group that best represented the Galeomorphs. Like most Squalomorphs, the anal fin in many of these species was absent. The expression of specific traits, such as the presence or absence of a lateral keel or conservation status, likely caused these species to be placed in the dendrogram groups that best represented the Galeomorphi superorder. These two traits played a more secondary role in the dissimilarities observed between species which will be discussed later. A small number of the Squalomorphs placed in the Galeomorphi groups did have an anal fin. All six of these species belonged to the order Hexanchiformes. The anatomical characteristics of species in this order are extremely similar to sharks present in the fossil record from close to 200 million years ago (Royer & Coffey, 2017). The presence of an anal fin in these species but not in other oceanic Squalomorphs could provide insights into the evolutionary history of species in this superorder. The taxonomic classification of the species within the Hexanchiformes order has been highly debated in the past (De Carvalho, 1996) and it is possible that more research on these species may cause their taxonomy to change.

After analyzing the dendrogram groups that represented the Squalomorphi and Galeomorphi superorders, several trends in trait composition emerged. Species from the Squalomorphi group had six traits consistent across all species in the all-species dataset and seven traits consistent across all species in the conservation status dataset. For the Galeomorphi group, there were between five and six traits consistent across all species depending on the dataset. There were also several traits found only in species in one superorder but not found at all in species from the other superorder. The Squalomorphi superorder had a total of three unique traits, while the Galeomorphi superorder had a total of five unique traits. Together these findings show that Galeomorphs have an overall higher number of traits compared to Squalomorphs and therefore display slightly higher trait diversity. The lower trait diversity and lower number of unique traits compared to Galeomorphs may be related to the fact that the majority of Squalomorphs are deep sea. The lack of sunlight, higher pressures, colder temperatures, and scarcity of food compared to the shallow-water environment make the deep sea a relatively extreme environment (Trujillo & Thurman, 2020). Species that live in these deep ecosystems have evolved specific sets of traits to help them thrive in this environment, such as the ability to bioluminesce. It is possible that the low trait diversity and trait uniqueness observed in Squalomorphs is a result of deep-sea sharks evolving a specialized set of traits in order to succeed in such a niche environment. While these trends in diversity hold true for the traits considered in this study, as more trait data becomes available these trends may change.

There were several traits that played a smaller, but still notable, role in the discrimination of species groups. These traits varied among species in the higher hierarchical dendrogram groupings identified at height 2.5 but became consistent among all species in the groups identified at height 1.0. There were four traits that played a more secondary role in contributing to the dissimilarities in trait composition observed between Squalomorphs. These traits were eye position, the presence or absence of a lateral keel, the number of gill slits, and the presence or absence of bioluminescence. For Galeomorphs, there were seven traits contributing to the dissimilarities in trait composition observed at this level. These traits included vertical distribution, the number of dorsal spines, caudal fin shape, feeding mechanism, mode of reproduction, the presence or absence of a lateral keel, and thermoregulation. The larger number of traits affecting the dissimilarities in trait composition observed in Galeomorph species is directly related to the higher trait diversity observed in Galeomorphs compared to Squalomorphs in this study.

The traits that explained the second highest variability observed between species in the PCoA plots were the presence or absence of a lateral keel and conservation status. The exact influence of these traits on the level of dissimilarity observed between species is hard to determine from the PCoA plots used in this study, but future research utilizing functional diversity indices as described in Pimiento et al. (2023a) will help illustrate the role these traits play in making a species unique.

Species with Unique Trait Combinations

The optimal grouping tool used in the dendrogram analysis placed several species in their own groups. Of the traits considered here, these species likely have unique combinations of traits that cannot be found in any other species. The exact number of species that made up their own group varied between all four of the cluster dendrograms. This highlights the impact changing individual trait data and adding additional traits has on species dissimilarity.

Even though conservation status is not considered a trait on its own, it is possible that it is acting as a proxy for life history traits that did not have enough data to be considered in this study, such as mortality rate and population growth rate. After analyzing the trait composition of species placed in their own groups in the conservation status dendrograms, it became clear that several of the species had the exact same anatomical, physiological, and life history traits but different conservation statuses. The addition of the specific life history traits that contribute to each species' conservation status could make the trait combinations of these species unique, but without those data, a difference in conservation status is not enough to consider a species unique. Therefore, only the species placed in their own groups in the all-species datasets will be considered below as the most dissimilar and the most likely to play a unique role in their ecosystem based on the traits studied here.

The all-species dataset with oviparous data substitutions had 33 single species groups, while the dataset with viviparous data substitutions had 32 single species groups. The one species that varied between the two datasets was *Odontaspis noronhai*. This species had nearly the exact same set of traits as two of the species from the *Bythaelurus* genus, *Bythaelurus giddingsi* and *Bythaelurus vivaldii*. The only difference between these three species was their mode of reproduction. When the mode of reproduction for the *Bythaelurus* species was assumed to be viviparous, all three of these species were grouped together. When the mode of reproduction for the *Bythaelurus* species was changed from oviparous, *O. noronhai* was placed in its own group. All three of these species are pelagic and resided mostly or entirely in the deep sea. The absence of reproductive data for the *Bythaelurus* species makes it difficult to determine if *O. noronhai* plays a role in the pelagic deep-sea environment that is different from the two *Bythaelurus* species. More research must be conducted on *B. giddingsi* and *B. vivaldii* to determine their mode of reproduction so that the ecological significance of *O. noronhai* can be identified and any conservation action to preserve the role of this species can be taken.

Of the 33 total species placed in their own groups, the vast majority have non-threatened conservation statuses. There were, however, four species listed as Data Deficient and four species with threatened statuses. The four Data Deficient species spanned all three depth zones and all three habitats. These species were *Heterodontus ramalheira*, *Scymnodalatias albicauda*, *Scymnodalatias garricki*, and *Scymnodalatias sherwoodi*. The epipelagic species *S. albicauda* is unique in that it is the only epipelagic species without an anal fin. Compared to other benthic wanderers, *H. ramalheira* is the only species with dorsal spines. The traits that make S. sherwoodi unique from other benthopelagic wanderers are its lack of dorsal spines and lack of a lateral keel. Lastly, the trait that separated *S. garricki* from other deep-sea pelagic species was its lack of an anal fin. All these species are rare, only known from a few specimens, and have unknown population sizes (Froese & Pauly, 2024; International Union for Conservation of Nature, 2023). While it is possible that the depth range and habitat of these species may change, with the available data and traits considered in this study it is possible that these four species play an important role in their respective ecosystems. Therefore, it is vital that more research be conducted on these species so that their conservation status can be properly evaluated.

Of the four individually grouped species with threatened conservation statuses, three are Vulnerable and one is Endangered. The Endangered species, *Carcharhinus obscurus*, or the Dusky Shark, is unique from other pelagic wanderers in that it has a trophic level of 4 and is viviparous. Both traits that make *C. obscurus* unique are life history traits. This differs from other species with unique trait combinations as the traits that typically make those species unique are anatomical. Life history traits, such as the mode of reproduction and a species trophic level, directly relate to the organism's overall fitness and success in its respective ecosystem (Fabian & Flatt, 2012). The unique life history traits of the Dusky Shark show just how specialized this species has become to survive as a pelagic wanderer. Thus, it is highly likely that this shark plays a vital role in the functioning of the pelagic environment as it swims between the epipelagic and deep-sea depth zones. Currently, global populations for *C. obscurus* are in decline due to targeted fisheries and bycatch (International Union for Conservation of Nature, 2023). Upon evaluation, the IUCN estimated that global population reduction over three generations (89.4 to 114 years) was between 50 and 79%. The unique trophic level and mode of reproduction seen in the Dusky Shark compared to other pelagic wanderers suggest that this species plays an important role as a drifter between the epipelagic and pelagic deep-sea environments that cannot be filled by any other species. It is crucial that this species be protected before it is too late.

The three Vulnerable species that were individually grouped are *Squalus acanthias*, *Squatina albipunctata*, and *Scymnodon ringens*. Two of these species, *S. acanthias* and *S. albipunctata*, are benthopelagic wanderers. The traits that separated *S. acanthias* from other benthopelagic wanderers were the presence of two dorsal spines and the presence of a lateral keel. For *S. albipunctata,* the traits that make this species unique from other benthopelagic wanderers are the presence of a lateral keel and a dorso-lateral eye position. The third species, *S. ringens*, is pelagic deep sea and the trait that separated this species from other deep-sea species of the same habitat was the presence of two dorsal spines. All three of these species are frequently targeted by shark fisheries and/or caught as bycatch via longlines or trawling (International Union for Conservation of Nature, 2023). The unique trait combinations of these three species suggest that they play a niche role in their respective ecosystems. Therefore, they must be protected so that this role can be preserved.

The cluster dendrograms also showed which species split into their own groups first. The species that split off the earliest have the highest level of dissimilarity compared to the other oceanic shark species. Looking at the cluster dendrograms for the all-species datasets, the first species to split into its own independent cluster was *Megachasma pelagios,* or the Megamouth Shark. The first species to split into their own groups for the conservation status dendrograms were *Mollisquama mississippiensis,* or the American Pocket Shark, and *M. pelagios*. Looking at the raw data, the reason these species split off early becomes clear. The species *M. pelagios* is one of only three epipelagic species that filter feeds. The trait that separated *M. pelagios* from the other two filter feeders was its lack of a lateral keel. Although direct observation of this species is extremely rare, the lack of a lateral keel along with weak body musculature and soft fins suggests that this species is a slow swimmer compared to other filter feeding sharks (Watanabe & Papastamatiou, 2019). The illusive nature of this species and its tendency to remain in deeper waters during the day (120-166 m) make *M. pelagios* a difficult species to study (Watanabe & Papastamatiou, 2019). It is very likely that this species plays a unique and important role in the epipelagic environment that cannot be fulfilled by other filter feeders. As more research is conducted and more trait data becomes available, this role will become clearer.

For the wanderer species, *M. mississippiensis* is the only wanderer-pelagic species with a trophic level of 3 and the ability to bioluminescence. This species is severely understudied and is only known from two specimens (Claes et al., 2020). All specimens of this shark have been captured via trawling. Therefore, whether this species is primarily epipelagic or deep-sea is unclear. For this study, *M. mississippiensis* was labeled as a wanderer. Compared to *M. mississippiensis*, all other pelagic wanderers have a trophic level of 4. FishBase states that the trophic level for this species was calculated based on its size and the trophic levels of its closest relatives (Froese & Pauly, 2024). It is possible that more research on the diet of this species will alter its exact trophic level. The American Pocket Shark was also the only wanderer species with the ability for bioluminescence. All other bioluminescent species reside mostly or entirely in the deep sea. As more specimens are collected, it is likely that the preferred depth range of this species will become deep sea. The traits of *M. mississippiensis* more closely align with other bioluminescent deep-sea sharks and the only other known species from this genus, *Mollisquama parini*, is deep sea. When considering the traits used in this study and the available depth data, *M. mississippiensis* appears to have a unique set of traits and may play an important role as a pelagic wanderer, but more data is needed to confirm this.

Limitations in Available Trait Data

While conducting the literature analysis portion of this study, the lack of available trait data became abundantly clear. Only 15% of all potential traits considered in this study had enough data available for all 337 oceanic shark species. The majority of these traits were anatomical. Anatomical traits can help provide insights into a species' habitat and behavior without directly observing the habitat or behavior. They can also give insight into a shark's evolutionary history by linking traits of extant species to traits of extinct species (Ebert et al., 2021). The more anatomical traits with data available for all shark species, the more we can learn about a shark's habitat, behavior, and evolutionary history. While anatomical traits are important and can give insights into a shark's habitat and behavior, life history traits are extremely important for determining how a species and/or population may react to environmental stressors (Cortés, 2000). Traits such as maximum total length, growth patterns, size at sexual maturity, length of gestation period, and fecundity are all important indicators for the life history patterns of a species. By having a complete understanding of a species' life history traits, researchers can make population dynamics models which can in turn aid in conservation efforts (Cortés, 2000).

As threats to sharks around the world continue to mount (Abel & Grubs, 2020; Ebert et al., 2021; Finucci et al., 2024), the need for adequate life history trait data is becoming more and more prevalent.

Conservation status from the IUCN Red List of Endangered Species was the only trait that did not have enough information for all species but still had enough data for at least 50% of individuals in each habitat zone. Conservation status plays an important role in establishing policy to help protect the marine environment. Conservation efforts, such as the creation of marine protected areas, are typically targeted at species with threatened conservation statuses (as seen in Pimiento et al., 2023a). The deep-sea depth zone had the highest percentage of species with 'Data Deficient' and 'Not Evaluated' conservation statuses. This is likely directly related to the difficulty in accessing this habitat compared to the epipelagic environment. The lack in conservation evaluation for species in the deep sea is especially concerning as the threat of deep-sea mining continues to increase along with the already detrimental effects of fishing for deep-sea shark liver oil and meat (Finucci et al., 2024).

Of the three depth zones identified in this study, shallow-water shark species had the highest percentage of individuals with a threatened conservation status. It is also possible that the increased accessibility of the epipelagic zone to commercial fishing is causing a higher percentage of species to be listed as threatened compared to other habitats. The majority of target species for the shark fin trade are from families with representatives in the oceanic epipelagic zone (Abel & Grubbs, 2020). Oceanic epipelagic species are also frequently caught as bycatch in pelagic trawl nets, gill nets, longlines, and purse-seine nets (Abel & Grubbs, 2020; Ebert et al., 2021).

The majority of the species from the wanderer and deep-sea depth zones were non-threatened. This could be due to the higher percentage of 'Data Deficient' and 'Not Evaluated' statuses in the wanderer and deep-sea habitats and/or the difficulty in accessing these habitats for exploitation compared to the epipelagic environment. As more research is conducted on the deep-sea habitat and the potential threats to these species, such as the oil and meat trade and deep-sea mining, are evaluated, it is possible that the percentage of threatened species in the deep-sea and wanderer habitats may increase.

Without adequate data for at least 50% of species within each habitat, it is difficult to draw conclusions about trends in trait expression with depth or how a trait contributes to the overall dissimilarity of a particular species. Although the eight traits with adequate information for at least one species from each depth zone (composition of buoyancy lipids in the liver, composition of muscle tissue, composition of photoreceptors in the eye, distribution of electroreceptive pores across the head, longevity, maximum observed length, relative brain size, and uterine fecundity) could not be used in this study, there were some apparent differences in trait expression between species from different depth zones. The average percentage of several liver oils (diacyl glyceryl ether (DAGE), waxy ester, and hydrocarbons), the average percentage of red muscle mass in the body, the ratio of rods photophores to cone photophores, longevity, and minimum uterine fecundity all showed a positive relationship with depth. The average percentage of the liver oils triacylglycerols (TAG) and fatty acids, the maximum total length for females, males, and unsexed individuals, and the average brain size (encephalization quotient) all displayed a negative relationship with depth. The average percentage of sterols in the liver and the distribution of electro-sensory pores across the head both displayed no relationship with depth. More information is needed to ensure an adequate representation of species for each habitat and to verify these trends in trait expression. The trends that could be seen from the available data for all these traits show that each habitat likely holds a unique set of traits, but without all the trait data for each species, it is not possible to solidity any trends in trait expression with depth. This trait data would also help create a more complete picture of each individual species and further our understanding of the role sharks play in their respective ecosystems. This knowledge could in turn be used to ensure adequate protection of species with roles vital to the functioning of their ecosystem.

Conclusion

While vertical distribution did not have as large of an impact on the dissimilarities between oceanic shark species as expected, there were several trends in trait expression observed with depth. A total of three traits were found to be unique to shallow-water species and four traits were found to be unique to deep-sea species. There were no traits unique to wanderer species. Wanderer species have adapted to live in both the shallow and deep-water environments, which is why they display traits seen in both shallow and deep-water species and do not display any unique traits of their own. Looking at conservation status, shallow-water species had the highest percentage of threatened species compared to other depth zones. The large number of threatened species in this depth zone may be due to the accessibility of this environment for commercial fishing and conservation research compared to the deep sea. Looking at the distribution of shark species across the three depth zones, the vast majority of oceanic sharks are deep sea and feed on or around the benthic habitat. The looming threat of deep-sea mining raises concerns over the future of these benthic deep-sea shark populations.

The trait that explained the highest amount of variation among species, and therefore had the largest impact on species dissimilarity, was the presence or absence of an anal fin. The impact this trait had on species dissimilarity is directly related to taxonomy. Most species from the Squalomorphi superorder do not have an anal fin and most species from the Galeomorphi superoder do have an anal fin. In the context of the traits used in this study, it was discovered that Galeomorphs have higher trait diversity and more unique traits compared to Squalomorphs, which have lower trait diversity and fewer unique traits. One potential explanation for this, is the large number of species in the Squalomorphi superorder that are deep sea. It is possible these species have evolved a specialized set of traits in order to succeed in such a niche environment, thus contributing to the low trait diversity and uniqueness observed here. While these trends in trait diversity may change with the addition of more trait data, it is clear that shark anal fins play an important role in species dissimilarity. Anal fins warrant further research, as they may provide taxonomic insights into the evolutionary history of oceanic shark species.

Several oceanic sharks were discovered to have unique combinations of traits that were not observed in any other species in this study. These species are especially important because they likely play a unique role in their ecosystem that cannot be fulfilled by any other species. The extinction of these species could have detrimental effects on the functioning of their respective ecosystem. One species in particular, *Carcharhinus obscurus*, or the Dusky Shark, is already listed as Endangered by the IUCN. The unique trophic level and mode of reproduction seen in the Dusky Shark compared to other pelagic wanderer species suggests that this shark plays an important role as a drifter between the epipelagic and pelagic deep-sea environments. It is therefore crucial that action be taken to protect this species before it is too late.

Many of the traits that were initially examined in this study did not have enough data for even one species from each depth zone. Life history traits such as total length, fecundity, size at sexual maturity, and gestation period are vital to the understanding of a species ability to rebound from environmental stressors. By adding more life history traits, it is very likely that more species will be categorized as dissimilar or unique. Additional research on traits with a limited amount of data would help illuminate more species with unique sets of traits and contribute significantly to our understanding of sharks in oceanic ecosystems.

References

Abel, D. C., & Grubbs, R. D. (2020). *Shark biology and conservation: Essentials for educators, students, and enthusiasts*. Johns Hopkins University Press.

Alfonso, S., Gesto, M., & Sadoul, B. (2021). Temperature increase and its effects on fish stress physiology in the context of global warming. *Journal of Fish Biology*, *98*(6), 1496-1508. https://doi.org/10.1111/jfb.14599

Archer, S. N., Djamgoz, M. B. A., Loew, E. R., Partridge, J. C., & Valerga, S. (1999). *Adaptive Mechanisms in the Ecology of Vision*. Kluwer Academic Publishers.

Auster, P. J., Cantwell, K., Grubbs, R. D., & Hoy, S. (2020). Observations of deep-sea sharks and associated species at a large food fall on the continental margin off South Carolina, USA (NW Atlantic). *Journal of the Ocean Science Foundation*, *35*, 48-53. https://doi.org/10.5281/zenodo.3932138

Avio, C. G., Gorbi, S., & Regoli, F. (2015). Experimental development of a new protocol for extraction and characterization of microplastics in fish tissues: First observations in commercial species from Adriatic Sea. *Marine Environmental Research*, *111*, 18-26. https://doi.org/10.1016/j.marenvres.2015.06.014

Bakes, M. J., & Nichols, P. D. (1995). Lipid, fatty acid and squalene composition of liver oil from six species of deep-sea sharks collected in southern Australian waters. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *110*(1), 267-275.

Baldridge Jr, H. D. (1970). Sinking factors and average densities of Florida sharks as functions of liver buoyancy. *Copeia*, *1970 (4)*, 744-754.

Barnett, A., Braccini, J., Awruch, C. A., & Ebert, D. (2012). An overview on the role of Hexanchiformes in marine ecosystems: Biology, ecology and conservation status of a primitive order of modern sharks. *Journal of Fish Biology*, *80*(5), 966-990. https://doi.org/10.1111/j.1095-8649.2012.03242.x

Bernal, D., Carlson, J. K., Goldman, K. J., & Lowe, C. G. (2012). Energetics, metabolism, and endothermy in sharks and rays. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (2nd ed., pp. 211-237). Taylor & Francis Group.

Bernal, D., Sepulveda, C., Mathieu-Costello, O., & Graham, J. (2003). Comparative studies of high performance swimming in sharks I. Red muscle morphometrics, vascularization and ultrastructure. *Journal of Experimental Biology*, *206*(16), 2831-2843. https://doi.org/10.1242/jeb.00481

Bernardini, I., Garibaldi, F., Canesi, L., Fossi, M. C., & Baini, M. (2018). First data on plastic ingestion by blue sharks (*Prionace glauca*) from the Liguruan Sea (North-Western Mediterranean Sea). *Marine Pollution Bulletin*, 135, 303-310. https://doi.org/10.1016/j.marpolbul.2018.07.022

Blackburn, D. G. (1999). Viviparity and oviparity: Evolution and reproductive strategies. In E. Knobil & J. D. Neill (Eds.), *Encyclopedia of reproduction* (Vol. 4, pp. 994-1003). Academic Press.

Bozzanao, A., Murgia, R., Vallerga, S., Hirano, J., & Archer, S. (2001). The photoreceptor system in the retinae of two dogfishes, *Scyliorhinus canicula* and *Galeus melastomus*: Possible relationship with depth distribution and predatory lifestyle. *Journal of Fish Biology*, *59*(5), 1258-1278. https://doi.org/10.1006/jfbi.2001.1737

Brill, R. W., & Lai, N. C. (2015). Elasmobranch cardiovascular system. In R. E. Shadwick, A. P. Farrell, & C. J. Brauner (Eds.), *Fish physiology* (Vol. 34, Part B, pp. 1-82). Elsevier. https://doi.org/10.1016/B978-0-12-801286-4.00001-0

Britton, J. C., & Morton, B. (1994). Marine carrion and scavengers. In A. D. Ansell, R. N. Gibson, & M. Barnes (Eds.), *Oceanography and marine biology: An annual review* (Vol. 32, pp. 369-434). Aberdeen University.

Brylske, A., Wagner, O., Popple, I., & McDougall, P. (2022). *Beneath the blue planet: A diver's guide to the ocean.* Mango Publishing Group.

Carrier, J. C., Musick, J. A., & Heithaus, M. R. (2004). *Biology of sharks and their relatives*. CRC Press.

Carrier, J. C., Musick, J. A., & Heithaus, M. R. (2012). *Biology of sharks and their relatives* (2nd ed.). Taylor & Francis Group.

Carrier, J. C., Simpfendorfer, C. A., Heithaus, M. R., & Yopak, K. E. (2022). *Biology of sharks and their relatives* (3rd ed.). CRC Press.

Cartes, J. E., Soler-Membrives, A., Stefanescu, C., Lombarte, A., & Carrassón, M. (2016). Contributions of allochthonous inputs of food to the diets of benthopelagic fish over the northwest Mediterranean slope (to 2300m*). Deep Sea Research Part I: Oceanographic Research Papers*, 109, 123-136. https://doi.org/10.1016/j.dsr.2015.11.001

Cernansky, R. (2017). The biodiversity revolution. *Nature*, *546*(14), 22-24. https://doi.org/10.1038/546022a

Claes, J. M., Dean, M. N., Nilsson, D.-E., Hart, N. S., & Mallefet, J. (2013). A deepwater fish with 'lightsabers'–dorsal spine-associated luminescence in a counterilluminating lanternshark. *Scientific Reports*, *3*(1), 1308. https://doi.org/10.1038/srep01308

Claes, J. M., Delroisse, J., Grace, M. A., Doosey, M. H., Duchatelet, L., & Mallefet, J. (2020). Histological evidence for secretory bioluminescence from pectoral pockets of the American Pocket Shark (*Mollisquama mississippiensis*). *Scientific Reports*, 10, 18762. https://doi.org/10.1038/s41598-020-75656-8

Claes, J. M., & Mallefet, J. (2009). Bioluminescence of sharks: First synthesis. In V. B. Meye-Rochow (Ed.), *Bioluminescence in focus: A collection of illuminating essays* (pp. 51-65).

Claes, J. M., Nilsson, D.-E., Straube, N., Collin, S. P., & Mallefet, J. (2014). Iso-luminance counterillumination drove bioluminescent shark radiation. *Scientific Reports*, *4*(1), 4328. https://doi.org/10.1038/srep04328

Cohen, J. L. (1990). Adaptations for scotopic vision in the lemon shark (*Negaprion brevirostris*). *Journal of Experimental Zoology*, *256*(S5), 76-84.

Collin, S. P., & Shand, J. (2003). Retinal sampling and the visual field in fishes. In S. P. Collin, & N. J. Marshall (Eds.), *Sensory processing in aquatic environments* (pp. 139-169). Springer. https://doi.org/10.1007/978-0-387-22628-6_8

Compagno, L. (2003). *Sharks of the order Carcharhiniformes*. Blackburn Press.

Convention on International Trade in Endangered Species of Wild Fauna and Flora. (2024, May 25). *CITES Appendices I, II and III valid from 25.05.2024*. CITES. https://cites.org/sites/default/files/eng/app/2024/E-Appendices-2024-05-25.pdf

Cortés, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science*, *8*(4), 299-344. https://doi.org/10.1080/10408340308951115

Crescitelli, F. (1991). Adaptations of visual pigments to the photic environment of the deep sea. *The Journal of Experimental Zoology*, *256*(S5), 66-75. https://doi.org/10.1002/jez.1402560510

Daly-Engel, T. S., Baremore, I. E., Grubbs, R. D., Gulak, S. J. B., Graham, R. T., & Enzenauer, M. P. (2019). Resurrection of the sixgill shark *Hexanchus vitulus* Springer & Waller, 1969 (Hexanchiformes, Hexanchidae), with comments on its distribution in the northwest Atlantic Ocean. *Marine Biodiversity*, *49*(2), 759-768. https://doi.org/10.1007/s12526-018-0849-x

Dapp, D. R., Walker, T. I., Huveneers, C., & Reina, R. D. (2016). Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality. *Fish and Fisheries*, *17*(2), 507-524. https://doi.org/10.1111/faf.12124

de Bello, F., Carmona, C. P., Dias, A. T., Götzenberger, L., Moretti, M., & Berg, M. P. (2021). *Handbook of trait-based ecology: From theory to R tools*. Cambridge University Press.

De Carvalho, M. R. (1996). Higher-Level Elasmobranch phylogeny, basal squaleans, and paraphyly. In M. L. Stiassny, L. R. Parenti, & G. D. Johnson (Eds.), *Interrelationships of fishes* (pp. 35-62). https://doi.org/10.1016/B978-012670950-6/50004-7

Denton, E., & Shaw, T. (1963). The visual pigments of some deep-sea elasmobranchs. *Journal of the Marine Biological Association of the United Kingdom*, *43*(1), 65-70.

Deprez, P., Volkman, J., & Davenport, S. (1990). Squalene content and neutral lipid composition of Livers from Deep-sea sharks caught in Tasmanian waters. *Marine and Freshwater Research*, *41*(3), 375-387.

Dickson, K. A., & Graham, J. B. (2004). Evolution and consequences of endothermy in fishes. *Physiological and Biochemical Zoology*, *77*(6), 998-1018. https://doi.org/10.1086/423743

Drazen, J. C., Smith, C. R., Gjerde, K. M., Haddock, S. H., Carter, G. S., Choy, C. A., Clark, M. R., Dutrieux, P., Goetze, E., Hauton, C., Hatta, M., Koslow, J. A., Leitner, A. B., Pacini, A., Perelman, J. N., Peacock, T., Sutton, T. T., Watling, L., & Yamamoto, H. (2020). Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *Proceedings of the National Academy of Sciences, 117*(30), 17455-17460. https://www.pnas.org/cgi/doi/10.1073/pnas.2011914117

Duchatelet, L., Claes, J. M., Delroisse, J., Flammang, P., & Mallefet, J. (2021). Glow on sharks: State of the art on bioluminescence research. *Oceans*, *2*(4), 822-842. https://doi.org/10.3390/oceans2040047

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K., Davidson, L. N. K., Fordham, S. V., Francis, M. P., Pollock, C. M., Simpfendorfer, C. A., Burgess, G. H., Carpenter, K. E., Compagno, L. J. V., Ebert, D. A., Gibson, C., Heupel, M. R., Livingstone, S. R., … White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*. https://doi.org/10.7554/eLife.00590

Ebert, D. A., Dando, M., & Fowler, S. (2021). *Sharks of the world: A complete guide* (Vol. 19). Princeton University Press.

Endangered Species Act, 16 U.S.C. 1531-1544. (1973). https://www.fws.gov/media/endangered-species-act.

Fabian, D., & Flatt, T. (2012). *Life history evolution*. Nature Education Knowledge. https://www.nature.com/scitable/knowledge/library/life-history-evolution-68245673/

Finucci, B., Pacoureau, N., Rigby, C. L., Matsushiba, J. H., Faure-Beaulieu, N., Sherman, C. S., VanderWright, W. J., Jabado, R. W., Charvet, P., & Mejía-Falla, P. A. (2024). Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays. *Science*, *383*(6687), 1135-1141. https://doi.org/10.1126/science.ade9121

Fossi, M. C., Baini, M., Panti, C., Galli, M., Jiménez, B., Muñoz-Arnanz, J., Marsili, L., Finoia, M. G., & Ramírez-Macías, D. (2017). Are whale sharks exposed to persistent organic pollutants and plastic pollution in the Gulf of California (Mexico)? First ecotoxicological investigation using skin biopsies. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 199, 48-58. https://doi.org/10.1016/j.cbpc.2017.03.002

Fricke, R., Durville, P., Potin, G., & Mulochau, T. (2023). *Squalus longispinis*, a new species of spurdog (Elasmobranchii: Squalidae) from La Réunion, southwestern Indian Ocean. *TAXA*, 2, 1-21.

Froese, R. & Pauly, D. (Eds.). (2024). *FishBase* (Version 02/2024). World Wide Web electronic publication. www.fishbase.org

Giammona, F. F. (2021). Form and function of the caudal fin throughout the phylogeny of fishes. *Integrative and Comparative Biology*, *61*(2), 550-572. https://doi.org/10.1093/icb/icab127

Goto, T., Shiba, Y., Shibagaki, K., & Nakaya, K. (2013). Morphology and ventilatory function of gills in the carpet shark family Parascylliidae (Elasmobranchii, Orectolobiformes). *Zoological Science*, *30*(6), 461-468. https://doi.org/10.2108/zsj.30.461

Gruber, S. H., Gulley, R. L., & Brandon, J. (1975). Duplex retina in seven elasmobranch species. *Bulletin of Marine Science*, *25*(3), 353-358.

Haddock, S. H., Moline, M. A., & Case, J. F. (2010). Bioluminescence in the sea. *Annual Review of Marine Science*, *2*, 443-493. https://doi.org/10.1146/annurev-marine-120308-081028

Hart, N. S. (2020). Vision in sharks and rays: Opsin diversity and colour vision. *Seminars in Cell & Developmental Biology*, *106*, 12-19. https://doi.org/10.1016/j.semcdb.2020.03.012

Hart, N. S., Lisney, T. J., & Collin, S. P. (2006). Visual communication in Elasmobranchs. In F. Ladich, S. P. Collin, P. Moller, & B. G. Kapoor (Eds.), *Communication in fishes (*Vol. 1, pp. 338-392). Science Publishers.

Hart, N. S., Theiss, S. M., Harahush, B. K., & Collin, S. P. (2011). Microspectrophotometric evidence for cone monochromacy in sharks. *Naturwissenschaften*, *98*, 193-201. https://doi.org/10.1007/s00114-010-0758-8

Hayashi, K. (1983). Component glyceryl ethers in liver lipids of spiny dogfish and Japanese cat shark. *Bulletin from the Faculty of Fishes, Hokkaido University*, *34*(3), 250-259.

Hayashi, K., & Takagi, T. (1981). Distribution of squalene and diacyl glyceryl ethers in the different tissues of deep-sea shark, *Dalatias licha*. *Bulletin of the Japanese Society of Scientific Fisheries*, *47*, 281-288.

Heithaus, M. R, Dunn, R. E., Farabaugh, N. F., Lester, E., Madin, E., Meekan, M. G., Papastamatiou, Y. P., Roff, G., Vaudo, J. J., & Wirsing, A. J. (2022). Advances in our understanding of the ecological importance of sharks and their relatives. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithus, & K. E. Yopak (Eds.), *Biology of sharks and their relatives* (3rd ed., pp. 487-521). CRC Press. https://doi.org/10.1201/9781003262190

Held, I. M., & Soden, B. J. (2006). Robust responses of the hydrological cycle to global warming. *Journal of Climate*, *19*(21), 5686-5699. https://doi.org/10.1175/JCLI3990.1

Herring, P. (2002). On being efficient. *The biology of the deep ocean*. Oxford University Press.

Howey-Jordan, L. A., Brooks, E. J., Abercrombie, D. L., Jordan, L. K., Brooks, A., Williams, S., Gospodarczyk, E., & Chapman, D. D. (2013). Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the western North Atlantic. *PloS One*, *8*(2), e56588. https://doi.org/10.1371/journal.pone.0056588

Hueter, R. E., Mann, D. A., Maruska, K. P., Sisneros, J. A., & Demski, L. S. (2004). Sensory biology of elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.) *Biology of sharks and their relatives* (pp. 325-368).

International Union for Conservation of Nature. (2022). *Deep-Sea mining*. International Union for Conservation of Nature. https://www.iucn.org/sites/default/files/2022-07/iucn-issues-brief_dsm_update_final.pdf

International Union for Conservation of Nature. (2023). *The IUCN red list of threatened species*. International Union for Conservation of Nature. https://www.iucnredlist.org. Accessed on January 23, 2024.

International Union for Conservation of Nature. (2024). *Sharpnose sevengill shark*. International Union for Conservation of Nature. https://www.iucnredlist.org/species/41823/2956343

Jayasinghe, C., Gotoh, N., Tokairin, S., Ehara, H., & Wada, S. (2003a). Inter species changes of lipid compositions in liver of shallowwater sharks from the Indian Ocean. *Fisheries science*, *69*(3), 644-653. https://doi.org/10.1046/j.1444-2906.2003.00668.x

Jayasinghe, C., Gotoh, N., & Wada, S. (2003b). Variation in lipid classes and fatty acid composition of salmon shark (*Lamna ditropis*) liver with season and gender. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *134*(2), 287-295. https://doi.org/10.1016/S1096-4959(02)00268-3

Jayasinghe, C., Gotoh, N., & Wada, S. (2012). Regiospecific analysis of shark liver triacylglycerols. *Journal of the American Oil Chemists' Society*, *89*(10), 1873-1884. https://doi.org/10.1007/s11746-012-2081-3

Juby, R., Bernard, A. T. F., & Götz, A. (2021). Day/night patterns of habitat use by dogfish sharks (Squalidae) at photic and subphotic warm-temperature reefs: Evidence of diel movements and size- and sex-segregation. *African Journal of Marine Science*, *43*(3), 325-336. https://doi.org/10.2989/1814232X.2021.1951839

Kajiura, S. M. (2010). Pupil dilation and visual field in the piked dogfish, *Squalus acanthias*. *Environmental Biology of Fishes*, *88*, 133-141. https://doi.org/10.1007/s10641-010-9623-z

Kaschner, C. J., Weigmann, S., & Thiel, R. (2015). *Bythaelurus tenuicephalus* n. sp., a new deep-water catshark (Carcharhiniformes, Scyliorhinidae) from the western Indian Ocean. *Zootaxa*, *4013*(1), 120-138. http://dx.doi.org/10.11646/zootaxa.4013.1.9

Karleskint, G., Turner, R. L., & Small, J. W. (2013). *Introduction to marine biology* (4th ed.). Brooks/Cole, Cengage Learning.

Keeling, C. D., Bacastow, R. B., Bainbridge, A. E., Ekdahl Jr, C. A., Guenther, P. R., Waterman, L. S., & Chin, J. F. (1976). Atmospheric carbon dioxide variations at Mauna Loa observatory, Hawaii. *Tellus*, *28*(6), 538-551.

Kempster, R. M., McCarthy, I. D., & Collin, S. P. (2012). Phylogenetic and ecological factors influencing the number and distribution of electroreceptors in elasmobranchs. *Journal of Fish Biology*, *80*(5), 2055-2088. https://doi.org/10.1111/j.1095-8649.2011.03214.x

Kiraly, S. J., Moore, J. A., & Jasiniski, P. H. (2003). Deepwater and other sharks of the U.S. Atlantic Ocean Exclusive Economic Zone. *Marine Fisheries Review*, *65*(4), 63.

Kiszka, J. J., Aubail, A., Hussey, N. E., Heithaus, M. R., Caurant, F., & Bustamante, P. (2015). Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses. *Deep-Sea Research I*, 96, 49-58. http://dx.doi.org/10.1016/j.dsr.2014.11.006

Kyne, P. M., & Simpfendorfer, C. A. (2012). Deepwater Chondrichthyans. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation* (pp. 37-113). Taylor & Francis Group.

Larsen, M., Abel, D., Crane, D., & Grubbs, R. (2020). Differences in relative heart mass among deep-sea and coastal sharks with increasing depth. *Marine Biology*, *167*, 1-8. https://doi.org/10.1007/s00227-020-03780-0

Lingham-Soliar, T. (2005). Caudal fin allometry in the white shark *Carcharodon carcharias*: Implications for locomotory performance and ecology. *Naturwissenschaften*, *92*, 231-236. https://doi.org/10.1007/s00114-005-0614-4

Lisney, T. J., & Collin, S. P. (2007). Relative eye size in elasmobranchs. *Brain, Behavior and Evolution*, *69*(4), 266-279. https://doi.org/10.1159/000100036

Litherland, L., Collin, S. P., & Fritsches, K. A. (2009). Visual optics and ecomorphology of the growing shark eye: A comparison between deep and shallow water species. *Journal of Experimental Biology*, *212*(21), 3583-3594. https://doi.org/10.1242/jeb.028589

Lyons, K., Preti, A., Madigan, D. J., Wells, R. J. D., Blasius, M. E., Snodgrass, O. E., Kacev, D., Harris, J. D., Dewar, H., Kohin, S., MacKenzie, K., & Lowe, C. G. (2015). Insights into the life history and ecology of a large shortfin mako shark *Isurus oxyrinchus* captured in southern California. *Journal of Fish Biology, 87*(1), 200-211. https://doi.org/10.1111/jfb.12709

Maia, A. M., Wilga, C. A., & Lauder, G. V. (2012). Biomechanics of locomotion in sharks, rays, and chimaeras. In Carrier, J. C., Musick, J. A., & Heithaus, M. R. (Eds.), *Biology of sharks and their relatives*, 2nd ed., pp. 125-51. https://doi.org/10.1201/b11867-13

Mallefet, J., Stevens, D. W., & Duchatelet, L. (2021). Bioluminescence of the largest luminous vertebrate, the kitefin shark, *Dalatias licha*: First insights and comparative aspects. *Frontiers in Marine Science*, *8*, 633582. https://doi.org/10.3389/fmars.2021.633582

Manabe, S., & Wetherald, R. T. (1967). Thermal equilibrium of the atmosphere with a given distribution of relative humidity. *Journal of the Atmospheric Sciences, 24*(3), 241-259.

McComb, D., Tricas, T., & Kajiura, S. (2009). Enhanced visual fields in hammerhead sharks. *Journal of Experimental Biology*, *212*(24), 4010-4018. https://doi.org/10.1242/jeb.032615

Merrett, N. R., & Haedrich, R. L. (1997). *Deep-sea demersal fish and fisheries* (Vol. 23). Springer Science & Business Media.

Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167-177. https://doi.org/10.1016/j.tree.2012.10.004

Mull, C. G., Pacoureau, N., Pardo, S. A., Ruiz, L. S., García-Rodríguez, E., Finucci, B., Haack, M., Harry, A., Judah, A. B., Vanderwright, W., Yin, J. S., Kindsvater, H. K., & Dulvy, N. K. (2022). Sharkipedia: A curated open access database of shark and ray life history traits and abundance time-series. *Scientific Data*, *9*(1). https://doi.org/10.1038/s41597-022-01655-1

Musick, J. A., Ellis, J. K., & Hamlett, W. (2005). Reproductive evolution of chondrichthyans. In W. C. Hamlett (Eds.), *Reproductive biology and phylogeny of chondrichthyes, sharks, batoids and chimaeras* (Vol. 3, pp. 45-71). CRC Press.

Mytilineou, C., Politou, C., Papaconstantinou, C., Kavadas, S., D onghia, G., & Sion, L. (2005). Deep-water fish fauna in the Eastern Ionian Sea. *Belgian Journal of Zoology*, *135*(2), 229.

Nakaya, K., Inoue, S., & Ho, H. (2013). A review of the genus *Cephaloscyllium* (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from Taiwanese waters. *Zootaxa*, *3752*(1), 29. https://doi.org/http://dx.doi.org/10.11646/zootaxa.3752.1.8

Nakaya, K., White, W. T., & Ho, H.-C. (2020). Discovery of a new mode of oviparous reproduction in sharks and its evolutionary implications. *Scientific Reports*, *10*(1), 12280. https://doi.org/10.1038/s41598-020-68923-1

Navarro-Garcia, G., Pacheco-Aguilar, R., Vallejo-Cordova, B., Ramirez-Suarez, J., & Bolaños, A. (2000). Lipid composition of the liver oil of shark species from the Caribbean and Gulf of California waters. *Journal of Food Composition and Analysis*, *13*(5), 791-798. https://doi.org/10.1006/jfca.2000.0928

Nevatte, R. J., & Williamson, J. E. (2020). The sawshark redemption: Current knowledge and future directions for sawsharks (Pristiophoridae). *Fish and Fisheries*, *21*(6), 1213-1237. https://doi.org/10.1111/faf.12500

Newman, A. S., Marshall, J. N., & Collin, S. P. (2013). Visual eyes: A quantitative analysis of the photoreceptor layer in deep-sea sharks. *Brain Behavior and Evolution*, *82*(4), 237-249. https://doi.org/10.1159/000355370

Nichols, P., Rayner, M., & Stevens, J. D. (2001). *A pilot investigation of Northern Australian shark liver oils: characterization and value-adding*. CSIRO Marine Research Hobart.

Office of International Affairs, Trade, and Commerce. (2024, July 8). *Shark conservation*. NOAA Fisheries. https://www.fisheries.noaa.gov/international-affairs/shark-conservation.

Payne, N. L., Iosilevskii, G., Barnett, A., Fischer, C., Graham, R. T., Gleiss, A. C., & Watanabe, Y. Y. (2016). Great hammerhead sharks swim on their side to reduce transport costs. *Nature Communications*, *7*. https://doi.org/10.1038/ncomms12289

Perry, C. N., Cartamil, D. P., Bernal, D., Sepulveda, C. A., Theilmann, R. J., Graham, J. B., & Frank, L. R. (2007). Quantification of red myotomal muscle volume and geometry in the shortfin mako shark (*Isurus oxyrinchus*) and the salmon shark (*Lamna ditropis*) using T1-weighted magnetic resonance imaging. *Journal of Morphology*, *268*(4), 284-292. https://doi.org/10.1002/jmor.10516

Pethybridge, H., Daley, R., Virtue, P., & Nichols, P. (2010). Lipid composition and partitioning of deepwater chondrichthyans: Inferences of feeding ecology and distribution. *Marine Biology*, 157, 1367-1384. https://doi.org/10.1007/s00227-010-1416-6

Phleger, C. F. (1998). Buoyancy in marine fishes: Direct and indirect role of lipids. *American Zoologist*, *38*(2), 321-330.

Pimiento, C., Albouy, C., Silvestro, D., Mouton, T. L., Velez, L., Mouillot, D., Judah, A. B., Griffin, J. N., & Leprieur, F. (2023a). Functional diversity of sharks and rays is highly vulnerable and supported by unique species and locations worldwide. *Nature Communications*, *14*(1), 7691. https://doi.org/10.1038/s41467-023-43212-3

Pimiento, C., Albouy, C., Silvestro, D., Mouton, T. L., Velez, L., Mouillot, D., Judah, A. B., Griffin, J. N., & Leprieur, F. (2023b). Functional diversity of sharks and rays is highly vulnerable and supported by unique species and locations worldwide [Supplemental material]. *Nature Communications*, *14*(1), 7691. https://doi.org/10.1038/s41467-023-43212-3

Pinte, N., Coubris, C., Jones, E., & Mallefet, J. (2021). Red and white muscle proportions and enzyme activities in mesopelagic sharks. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *256*, 110649. https://doi.org/10.1016/j.cbpb.2021.110649

Pinte, N., Godefroid, M., Abbas, O., Baeten, V., & Mallefet, J. (2019). Deep-sea sharks: Relation between the liver's buoyancy and red aerobic muscle volumes, a new approach. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, *236*. https://doi.org/10.1016/j.cbpa.2019.06.020

Pollerspöck, J. & Straube, N. (Eds). (2023). *Bibliography database of living/fossil sharks, rays, and chimeras* (Version 2023). SharkReferences.com. https://www.shark-references.com/

Priede, I. G. (2017). *Deep-sea fishes: Biology, diversity, ecology and fisheries*. Cambridge University Press.

Priede, I. G., Froese, R., Bailey, D. M., Bergstad, O. A., Collins, M. A., Dyb, J. E., Henriques, C., Jones, E. G., & King, N. (2006). The absence of sharks from abyssal regions of the world's oceans. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1592), 1435-1441. https://doi.org/10.1098/rspb.2005.3461

Randhawa, H. S., Poulin, R., & Krkošek, M. (2015). Increasing rate of species discovery in sharks coincides with sharp population declines: Implications for biodiversity. *Ecography*, *38*(1), 96-107. https://doi.org/10.1111/ecog.00793

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A., & Vecchione, M. (2010). Deep, diverse and definitely different: Unique attributes of the world's largest ecosystem. *Biogeosciences*, *7*(9), 2851-2899. https://doi.org/10.5194/bg-7-2851-2010

Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., Motley, J. L., Self, K. E., Taylor, D. S., & Wolf, C. (2016). What is a trophic cascade? *Trends in Ecology & Evolution*, *31*(11), 842-849. https://doi.org/10.1016/j.tree.2016.08.010

Rosa, R., Rummer, J. L., & Munday, P. L. (2017). Biological responses of sharks to ocean acidification. *Biological Letters*, *13*(3), 1-7. https://doi.org/10.1098/rsbl.2016.0796

Royer, M., & Coffey, D. (2017, March 18). *Getting to know sixgill sharks*. National Ocean and Atmospheric Administration. https://oceanexplorer.noaa.gov/okeanos/explorations/ex1703/logs/mar18/welcome.html

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behavior and habitat use: A review. *Reviews in Fish Biology and Fisheries*, 24, 1089-1103. https://doi.org/10.1007/s11160-014-9364-8

Sepulveda, C. A., Wegner, N. C., Bernal, D., & Graham, J. B. (2005). The red muscle morphology of the thresher sharks (family Alopiidae). *Journal of Experimental Biology*, *208*(22), 4255-4261. https://doi.org/10.1242/jeb.01898

Shark Research Institute. (n.d.). *Dusky shark* – Carcharhinus obscurus. https://www.sharks.org/dusky-shark-carcharhinus-obscurus.

Smith, C. R., & Baco, A. R. (2003). Ecology of whale falls at the deep-sea floor. In R. N. Gibson, & R. J. A. Atkinson (Eds.), *Oceanography and marine biology: An annual review,* (Vol. 41, pp. 319-333). CRC Press.

Ste-Marie, E., Watanabe, Y. Y., Semmens, J. M., Marcoux, M., & Hussey, N. E. (2020). A first look at the metabolic rate of Greenland sharks (Somniosus microcephalus) in the Canadian Arctic. *Scientific Reports, 10,* 19297. https://doi.org/10.1038/s41598-020-76371-0

Tacutu, R., Thornton, D., Johnson, E., Budovsky, A., Barardo, D., Craig, T., Diana, E., Lehmann, G., Toren, D., Wang, J., Fraifeld, V. E., & de Magalhães, J. P. (2018). Human ageing genomic resources: New and updated databases. *Nucleic Acids Research*, *46*(D1), D1083–D1090. https://doi.org/10.1093/nar/gkx1042

Tagliafico, A., Rangel, S., & Broadhurst, M. K. (2019). Maturation and reproduction of *Squalus cubensis* and *Squalus cf. quasimodo* (Squalidae, Squaliformes) in the southern Caribbean Sea. *Ichthyological Research*, *66*(1), 1-8. https://doi.org/10.1007/s10228-018-0640-9

Torres, J. J. & Bailey, T. G. (2022). *Life in the open ocean: The biology of pelagic species*. John Wiley & Sons.

Treberg, J. R., Martin, R. A., & Driedzic, W. R. (2003). Muscle enzyme activities in a deep-sea squaloid shark, *Centroscyllium fabricii*, compared with its shallow-living relative, *Squalus acanthias*. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*, *300*(2), 133-139. https://doi.org/10.1002/jez.a.10318

Trujillo, A. P., & Thurman, H. V. (2020). *Essentials of oceanography* (13th ed.). Pearson.

Tucker, J. P., Vercoe, B., Santos, I. R., Dujmovic, M., & Butcher, P. A. (2019). Whale carcass scavenging by sharks. *Global Ecology and Conservation*, *19*, e00655. https://doi.org/10.1016/j.gecco.2019.e00655

Van Vleet, E. S., Candileri, S., McNeillie, J., Reinhardt, S. B., Conkright, M. E., & Zwissler, A. (1984). Neutral lipid components of eleven species of Caribbean sharks. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, *79*(4), 549-554. https://doi.org/10.1016/0305-0491(84)90364-X

Viana, S. T. de F. L., de Carvalho, M. R. & Ebert, D. A. (2017). *Squalus bassi* sp. nov., a new long-snouted spurdog (Chondrichthyes: Squaliformes: Squalidae) from the Agulhas Bank. *Journal of Fish Biology*, *91*(4), 1178-1207. https://doi.org/http://dx.doi.org/10.1111/jfb.13448

Viana, S., & Soares, A. D. K. (2023). Untangling the systematic dilemma behind the roughskin spurdog *Cirrhigaleus asper* (Merrett, 1973) (Chondrichthyes: Squaliformes), with phylogeny of Squalidae and a key to *Cirrhigaleus* species. *PloS One*, *18*(3), 71. https://doi.org/10.1371/journal.pone.0282597

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882-892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Watanabe, Y. Y., & Papastamatiou, Y. P. (2019). Distribution, body size and biology of the megamouth shark *Megachasma pelagios*. *Journal of Fish Biology*, *95*(4), 992-998. https://doi.org/10.1111/jfb.14007

Weber, J. A., Park, S. G., Luria, V., Jeon, S., Kim, H., Jeon, Y., Bhak, Y., Jun, J. H., Kim, S. W., Hong, W. H., Lee, S., Cho, Y. S., Karger, A., Cain, J. W., Manica, A., Kim, S., Kim, J., Edwards, J. S., Bhak, J., & Church, G. M. (2020). The whale shark genome reveals how genomic and physiological properties scale with body size. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(34), 20662-20671. https://doi.org/10.1073/pnas.1922576117

Wegner, N. C. (2015). Elasmobranch gill structure. *Fish Physiology*, *34*(Part A), 101-151. https://doi.org/10.1016/B978-0-12-801289-5.00003-1

Wetherbee, B. M., & Nichols, P. D. (2000). Lipid composition of the liver oil of deep-sea sharks from the Chatham Rise, New Zealand. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *125*(4), 511-521. https://doi.org/10.1016/S0305-0491(00)00154-1

White, W. T., Arunrugstichai, S., & Naylor, G. J. (2021). Revision of the genus *Mustelus* (Carcharhiniformes: Triakidae) in the northern Indian Ocean, with description of a new species and a discussion on the validity of M. walkeri and M. ravidus. *Marine Biodiversity*, *51*, 1-24. https://doi.org/10.1007/s12526-021-01161-4

Wilga, C. D., Motta, P. J., & Sanford, C. P. (2007). Evolution and ecology of feeding in elasmobranchs. *Integrative and Comparative Biology*, *47*(1), 55-69. https://doi.org/10.1093/icb/icm029

WoRMS Editorial Board (2024). *World register of marine species*. https://www.marinespecies.org. Accessed 2024-01-23.

Yodzis, P. (2001). Trophic levels. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (Vol. 5, pp. 695-700). Academic Press. https://doi.org/10.1016/B0-12-226865-2/00274-1

Yopak, K. E., Lisney, T. J., Collin, S. P., & Montgomery, J. C. (2007). Variation in brain organization and cerebellar foliation in chondrichthyans: Sharks and holocephalans. *Brain, Behavior and Evolution*, *69*(4), 280-300. https://doi.org/10.1159/000100037

Appendix A. Figures

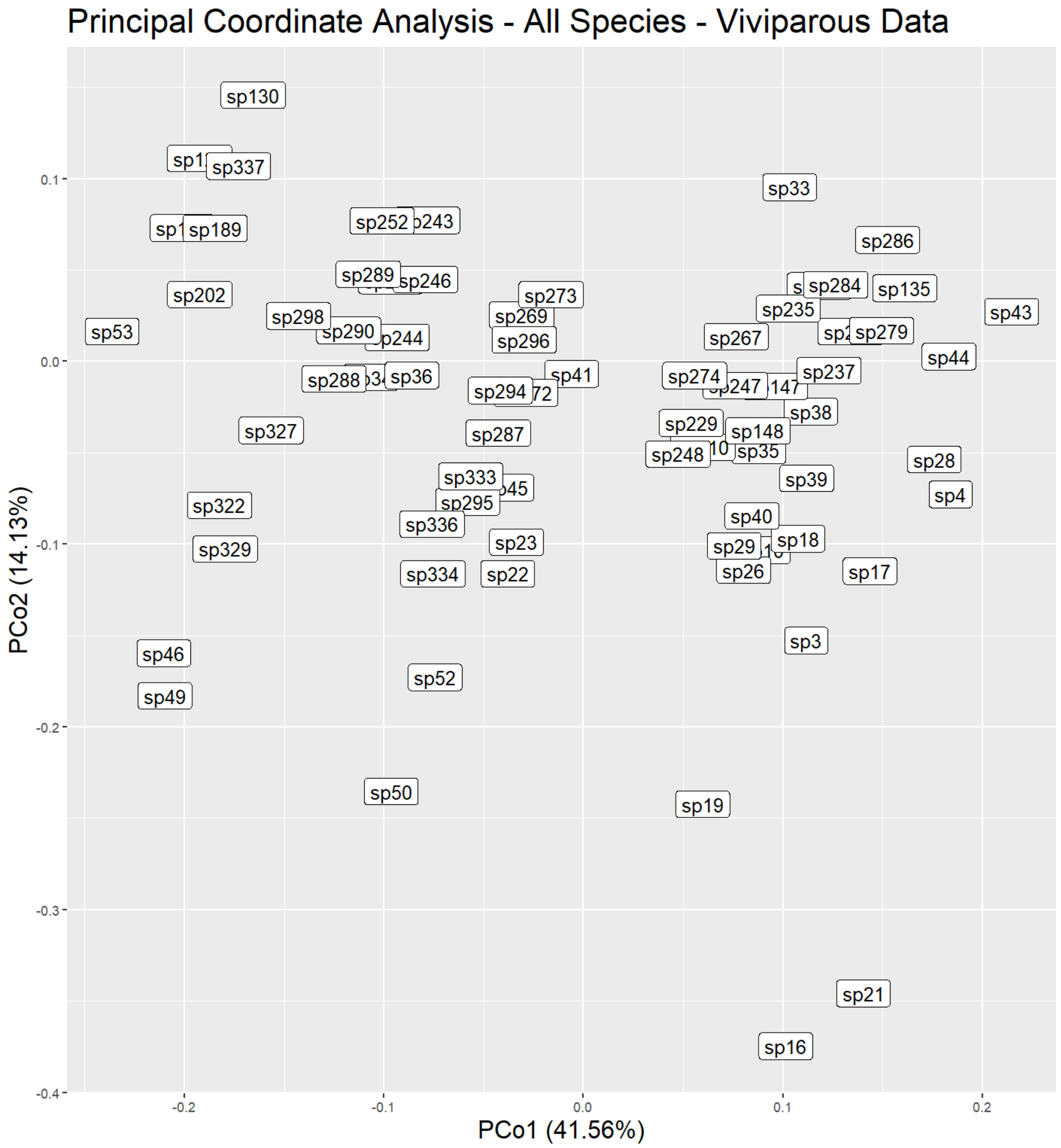

Figure 1A Principal Coordinate Analysis plot of the all-species 'species x trait matrix' with viviparous data substitutions for the five species from the *Bythaelurus* genus without mode of reproduction data. The X-axis and Y-axis represent the two main coordinate axes, and the percentage of variance explained by each axis is in parentheses. A guide for the species labels in this plot is provided in Appendix Table 1A.

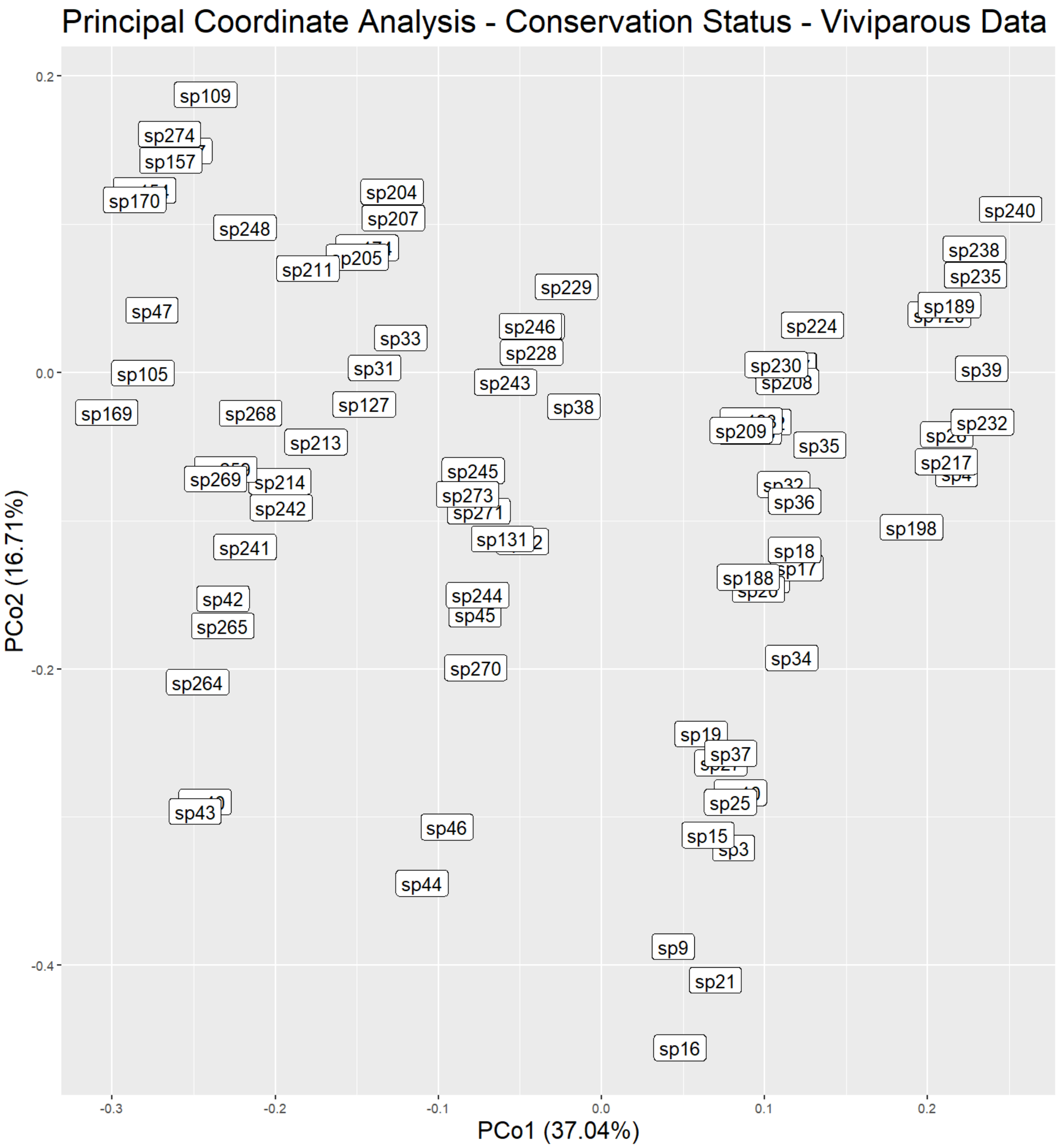

Figure 2A Principal Coordinate Analysis plot of the conservation status ‘species x trait matrix’ with viviparous data substitutions for the five species from the *Bythaelurus* genus without mode of reproduction data. The X-axis and Y-axis represent the two main coordinate axes, and the percentage of variance explained by each axis is in parentheses. A guide for the species labels in this plot is provided in Appendix Table 6A.

Appendix B. Tables

Table 1A List of all oceanic shark species examined in this study (337 total species). The species codes used for all statistical tests in this study are included to the left of the species name.

All Oceanic Shark Species

sp1	*Alopias pelagicus*
sp2	*Alopias superciliosus*
sp3	*Alopias vulpinus*
sp4	*Asymbolus submaculatus*
sp5	*Carcharhinus albimarginatus*
sp6	*Carcharhinus altimus*
sp7	*Carcharhinus falciformis*
sp8	*Carcharhinus galapagensis*
sp9	*Carcharhinus longimanus*
sp10	*Carcharhinus signatus*
sp11	*Carcharodon carcharias*
sp12	*Cetorhinus maximus*
sp13	*Isurus oxyrinchus*
sp14	*Isurus paucus*
sp15	*Lamna ditropis*
sp16	*Lamna nasus*
sp17	*Megachasma pelagios*
sp18	*Mustelus canis*
sp19	*Prionace glauca*
sp20	*Pseudocarcharias kamoharai*
sp21	*Rhincodon typus*
sp22	*Scymnodalatias albicauda*
sp23	*Scymnodalatias oligodon*
sp24	*Sphyrna lewini*
sp25	*Sphyrna mokarran*
sp26	*Sphyrna zygaena*
sp27	*Apristurus brunneus*
sp28	*Asymbolus occiduus*
sp29	*Carcharhinus obscurus*
sp30	*Cephaloscyllium sufflans*
sp31	*Cephaloscyllium umbratile*
sp32	*Galeorhinus galeus*
sp33	*Heterodontus ramalheira*
sp34	*Heteroscymnoides marleyi*
sp35	*Hypogaleus hyugaensis*
sp36	*Mollisquama mississippiensis*
sp37	*Mustelus higmani*
sp38	*Mustelus lenticulatus*
sp114	*Centrophorus harrissoni*
sp115	*Centrophorus isodon*
sp116	*Centrophorus lesliei*
sp117	*Centrophorus longipinnis*
sp118	*Centrophorus moluccensis*
sp119	*Centrophorus seychellorum*
sp120	*Centrophorus squamosus*
sp121	*Centrophorus uyato*
sp122	*Centrophorus westraliensis*
sp123	*Centrophorus zeehaani*
sp124	*Centroscyllium excelsum*
sp125	*Centroscyllium fabricii*
sp126	*Centroscyllium granulatum*
sp127	*Centroscyllium kamoharai*
sp128	*Centroscyllium nigrum*
sp129	*Centroscyllium ornatum*
sp130	*Centroscyllium ritteri*
sp131	*Centroscymnus coelolepis*
sp132	*Centroscymnus owstonii*
sp133	*Centroselachus crepidater*
sp134	*Cephaloscyllium albipinnum*
sp135	*Cephaloscyllium cooki*
sp136	*Cephaloscyllium fasciatum*
sp137	*Cephaloscyllium formosanum*
sp138	*Cephaloscyllium hiscosellum*
sp139	*Cephaloscyllium isabellum*
sp140	*Cephaloscyllium signourum*
sp141	*Cephaloscyllium silasi*
sp142	*Cephaloscyllium speccum*
sp143	*Cephaloscyllium stevensi*
sp144	*Cephaloscyllium variegatum*
sp145	*Cephaloscyllium zebrum*
sp146	*Cephalurus cephalus*
sp147	*Chlamydoselachus africana*
sp148	*Chlamydoselachus anguineus*
sp149	*Cirrhigaleus asper*
sp150	*Cirrhigaleus australis*
sp151	*Cirrhigaleus barbifer*
sp227	*Galeus springeri*
sp228	*Gollum attenuatus*
sp229	*Gollum suluensis*
sp230	*Halaelurus quagga*
sp231	*Hemitriakis abdita*
sp232	*Heptranchias perlo*
sp233	*Hexanchus griseus*
sp234	*Hexanchus nakamurai*
sp235	*Hexanxhus vitulus*
sp236	*Holohalaelurus favus*
sp237	*Holohalaelurus grennian*
sp238	*Holohalaelurus melanostigma*
sp239	*Holohalaelurus punctatus*
sp240	*Holohalaelurus regani*
sp241	*Iago garricki*
sp242	*Iago omanensis*
sp243	*Isistius brasiliensis*
sp244	*Isistius plutodus*
sp245	*Mitsukurina owstoni*
sp246	*Mollisquama parini*
sp247	*Mustelus albipinnis*
sp248	*Odontaspis noronhai*
sp249	*Oxynotus bruniensis*
sp250	*Oxynotus caribbaeus*
sp251	*Oxynotus centrina*
sp252	*Oxynotus japonicus*
sp253	*Oxynotus paradoxus*
sp254	*Parascyllium sparsimaculatum*
sp255	*Parmaturus albimarginatus*
sp256	*Parmaturus albipenis*
sp257	*Parmaturus angelae*
sp258	*Parmaturus bigus*
sp259	*Parmaturus campechiensis*
sp260	*Parmaturus lanatus*
sp261	*Parmaturus macmillani*
sp262	*Parmaturus melanobranchus*
sp263	*Parmaturus pilosus*
sp264	*Parmaturus xaniurus*

Appendix Table 1A Continued

sp39	*Mustelus stevensi*
sp40	*Odontaspis ferox*
sp41	*Pristiophorus japonicus*
sp42	*Scyliorhinus cervigoni*
sp43	*Scyliorhinus haeckelii*
sp44	*Scyliorhinus retifer*
sp45	*Scymnodalatias sherwoodi*
sp46	*Squalus acanthias*
sp47	*Squalus albifrons*
sp48	*Squalus crassispinus*
sp49	*Squalus formosus*
sp50	*Squatina albipunctata*
sp51	*Squatina dumeril*
sp52	*Squatina nebulosa*
sp53	*Zameus squamulosus*
sp54	*Aculeola nigra*
sp55	*Apristurus albisoma*
sp56	*Apristurus ampliceps*
sp57	*Apristurus aphyodes*
sp58	*Apristurus australis*
sp59	*Apristurus breviventralis*
sp60	*Apristurus bucephalus*
sp61	*Apristurus canutus*
sp62	*Apristurus exsanguis*
sp63	*Apristurus fedorovi*
sp64	*Apristurus garricki*
sp65	*Apristurus gibbosus*
sp66	*Apristurus herklotsi*
sp67	*Apristurus indicus*
sp68	*Apristurus internatus*
sp69	*Apristurus investigatoris*
sp70	*Apristurus japonicus*
sp71	*Apristurus kampae*
sp72	*Apristurus laurussonii*
sp73	*Apristurus longicephalus*
sp74	*Apristurus macrorhynchus*
sp75	*Apristurus macrostomus*
sp76	*Apristurus manis*
sp77	*Apristurus manocheriani*
sp78	*Apristurus melanoasper*
sp79	*Apristurus microps*
sp80	*Apristurus micropterygeus*
sp81	*Apristurus nakayai*
sp152	*Cirrhoscyllium japonicum*
sp153	*Ctenacis fehlmanni*
sp154	*Dalatias licha*
sp155	*Deania calcea*
sp156	*Deania hystricosa*
sp157	*Deania profundorum*
sp158	*Deania quadrispinosa*
sp159	*Echinorhinus brucus*
sp160	*Echinorhinus cookei*
sp161	*Eridacnis barbouri*
sp162	*Eridacnis radcliffei*
sp163	*Eridacnis sinuans*
sp164	*Etmopterus alphus*
sp165	*Etmopterus benchlyi*
sp166	*Etmopterus bigelowi*
sp167	*Etmopterus brachyurus*
sp168	*Etmopterus brosei*
sp169	*Etmopterus bullisi*
sp170	*Etmopterus burgessi*
sp171	*Etmopterus carteri*
sp172	*Etmopterus caudistigmus*
sp173	*Etmopterus compagnoi*
sp174	*Etmopterus decacuspidatus*
sp175	*Etmopterus dianthus*
sp176	*Etmopterus dislineatus*
sp177	*Etmopterus evansi*
sp178	*Etmopterus fusus*
sp179	*Etmopterus gracilispinis*
sp180	*Etmopterus granulosus*
sp181	*Etmopterus hillianus*
sp182	*Etmopterus joungi*
sp183	*Etmopterus lailae*
sp184	*Etmopterus litvinovi*
sp185	*Etmopterus lucifer*
sp186	*Etmopterus marshae*
sp187	*Etmopterus molleri*
sp188	*Etmopterus parini*
sp189	*Etmopterus perryi*
sp190	*Etmopterus polli*
sp191	*Etmopterus princeps*
sp192	*Etmopterus pseudosqualiolus*
sp193	*Etmopterus pusillus*
sp194	*Etmopterus pycnolepis*
sp265	*Pentanchus profundicolus*
sp266	*Planonasus indicus*
sp267	*Planonasus parini*
sp268	*Pliotrema kajae*
sp269	*Pliotrema warreni*
sp270	*Pristiophorus delicatus*
sp271	*Pristiophorus lanae*
sp272	*Pristiophorus nancyae*
sp273	*Pristiophorus schroederi*
sp274	*Pseudotriakis microdon*
sp275	*Schroederichthys maculatus*
sp276	*Schroederichthys saurisqualus*
sp277	*Schroederichthys tenuis*
sp278	*Scyliorhinus boa*
sp279	*Scyliorhinus cabofriensis*
sp280	*Scyliorhinus capensis*
sp281	*Scyliorhinus comoroensis*
sp282	*Scyliorhinus hachijoensis*
sp283	*Scyliorhinus hesperius*
sp284	*Scyliorhinus meadi*
sp285	*Scyliorhinus torrei*
sp286	*Scyliorhinus ugoi*
sp287	*Scymnodalatias garricki*
sp288	*Scymnodon ichiharai*
sp289	*Scymnodon macracanthus*
sp290	*Scymnodon ringens*
sp291	*Somniosus antarcticus*
sp292	*Somniosus cheni*
sp293	*Somniosus longus*
sp294	*Somniosus microcephalus*
sp295	*Somniosus pacificus*
sp296	*Somniosus rostratus*
sp297	*Squaliolus aliae*
sp298	*Squaliolus laticaudus*
sp299	*Squalus acutipinnis*
sp300	*Squalus albicaudus*
sp301	*Squalus altipinnis*
sp302	*Squalus bahiensis*
sp303	*Squalus bassi*
sp304	*Squalus blainville*
sp305	*Squalus boretzi*
sp306	*Squalus brevirostris*
sp307	*Squalus bucephalus*

Table 1A Continued

sp82	*Apristurus nasutus*	sp195	*Etmopterus robinsi*	sp308	*Squalus chloroculus*
sp83	*Apristurus ovicorrugatus*	sp196	*Etmopterus samadiae*	sp309	*Squalus clarkae*
sp84	*Apristurus parvipinnis*	sp197	*Etmopterus schultzi*	sp310	*Squalus cubensis*
sp85	*Apristurus pinguis*	sp198	*Etmopterus sculptus*	sp311	*Squalus edmundsi*
sp86	*Apristurus platyrhynchus*	sp199	*Etmopterus sentosus*	sp312	*Squalus grahami*
sp87	*Apristurus profundorum*	sp200	*Etmopterus sheikoi*	sp313	*Squalus griffini*
sp88	*Apristurus riveri*	sp201	*Etmopterus spinax*	sp314	*Squalus hawaiiensis*
sp89	*Apristurus saldanha*	sp202	*Etmopterus splendidus*	sp315	*Squalus hemipinnis*
sp90	*Apristurus sibogae*	sp203	*Etmopterus unicolor*	sp316	*Squalus japonicus*
sp91	*Apristurus sinensis*	sp204	*Etmopterus viator*	sp317	*Squalus lalannei*
sp92	*Apristurus spongiceps*	sp205	*Etmopterus villosus*	sp318	*Squalus lobularis*
sp93	*Apristurus stenseni*	sp206	*Etmopterus virens*	sp319	*Squalus longispinis*
sp94	*Apristurus yangi*	sp207	*Euprotomicroides zantedeschia*	sp320	*Squalus megalops*
sp95	*Asymbolus galacticus*	sp208	*Euprotomicrus bispinatus*	sp321	*Squalus melanurus*
sp96	*Asymbolus pallidus*	sp209	*Figaro boardmani*	sp322	*Squalus mitsukurii*
sp97	*Asymbolus parvus*	sp210	*Figaro striatus*	sp323	*Squalus montalbani*
sp98	*Asymbolus rubiginosus*	sp211	*Galeus antillensis*	sp324	*Squalus nasutus*
sp99	*Bythaelurus bachi*	sp212	*Galeus arae*	sp325	*Squalus notocaudatus*
sp100	*Bythaelurus canescens*	sp213	*Galeus atlanticus*	sp326	*Squalus quasimodo*
sp101	*Bythaelurus clevai*	sp214	*Galeus cadenati*	sp327	*Squalus rancureli*
sp102	*Bythaelurus dawsoni*	sp215	*Galeus corriganae*	sp328	*Squalus raoulensis*
sp103	*Bythaelurus giddingsi*	sp216	*Galeus eastmani*	sp329	*Squalus shiraii*
sp104	*Bythaelurus hispidus*	sp217	*Galeus friedrichi*	sp330	*Squatina caillieti*
sp105	*Bythaelurus immaculatus*	sp218	*Galeus gracilis*	sp331	*Squatina formosa*
sp106	*Bythaelurus incanus*	sp219	*Galeus longirostris*	sp332	*Squatina leae*
sp107	*Bythaelurus lutarius*	sp220	*Galeus melastomus*	sp333	*Squatina mapama*
sp108	*Bythaelurus naylori*	sp221	*Galeus murinus*	sp334	*Squatina pseudocellata*
sp109	*Bythaelurus stewarti*	sp222	*Galeus nipponensis*	sp335	*Squatina tergocellata*
sp110	*Bythaelurus tenuicephalus*	sp223	*Galeus piperatus*	sp336	*Squatina varii*
sp111	*Bythaelurus vivaldii*	sp224	*Galeus polli*	sp337	*Trigonognathus kabeyai*
sp112	*Centrophorus atromarginatus*	sp225	*Galeus priapus*		
sp113	*Centrophorus granulosus*	sp226	*Galeus schultzi*		

Table 2A List of all oceanic shallow-water shark species considered in this study (26 total species). Benthopelagic Species are denoted by a ‘*’ symbol. Pelagic species are denoted by a ‘◦’ symbol.

All Oceanic Shallow-Water Shark Species

Alopias pelagicus◦
Alopias superciliosus◦
Alopias vulpinus ◦
Asymbolus submaculatus◦
Carcharhinus albimarginatus *
Carcharhinus altimus *
Carcharhinus falciformis◦
Carcharhinus galapagensis◦
Carcharhinus longimanus◦
Carcharhinus signatus *
Carcharodon carcharias◦
Cetorhinus maximus◦
Isurus oxyrinchus◦
Isurus paucus◦
Lamna ditropis◦
Lamna nasus◦
Megachasma pelagios◦
Mustelus canis◦
Prionace glauca◦
Pseudocarcharias kamoharai◦
Rhincodon typus◦
Scymnodalatias albicauda◦
Scymnodalatias oligodon *
Sphyrna lewini◦
Sphyrna mokarran◦
Sphyrna zygaena◦

Table 3A List of all oceanic wanderer shark species considered in this study (27 total species). Benthic species are denoted by a ‘•’ symbol. Benthopelagic Species are denoted by a ‘*’ symbol. Pelagic species are denoted by a ‘◦’ symbol.

All Oceanic Wanderer Shark Species

Apristurus brunneus •
Asymbolus occiduus ◦
Carcharhinus obscurus◦
Cephaloscyllium sufflans •
Cephaloscyllium umbratile •
Galeorhinus galeus *
Heterodontus ramalheira •
Heteroscymnoides marleyi *
Hypogaleus hyugaensis •
Mollisquama mississippiensis ◦
Mustelus higmani •
Mustelus lenticulatus •
Mustelus stevensi *
Odontaspis ferox *
Pristiophorus japonicus •
Scyliorhinus cervigoni •
Scyliorhinus haeckelii •
Scyliorhinus retifer •
Scymnodalatias sherwoodi *
Squalus acanthias *
Squalus albifrons ◦
Squalus crassispinus ◦
Squalus formosus ◦
Squatina albipunctata *
Squatina dumeril •
Squatina nebulosa •
Zameus squamulosus *

Table 4A List of all oceanic deep-sea shark species considered in this study (284 total species). Benthic species are denoted by a '•' symbol. Benthopelagic Species are denoted by a '*' symbol. Pelagic species are denoted by a '◦' symbol.

All Oceanic Deep-Sea Shark Species

- *Aculeola nigra* •
- *Apristurus albisoma* •
- *Apristurus ampliceps* •
- *Apristurus aphyodes* ◦
- *Apristurus australis* ◦
- *Apristurus breviventralis* ◦
- *Apristurus bucephalus* •
- *Apristurus canutus* •
- *Apristurus exsanguis* •
- *Apristurus fedorovi* ◦
- *Apristurus garricki* •
- *Apristurus gibbosus* •
- *Apristurus herklotsi* •
- *Apristurus indicus* •
- *Apristurus internatus* ◦
- *Apristurus investigatoris* •
- *Apristurus japonicus* •
- *Apristurus kampae* •
- *Apristurus laurussonii* •
- *Apristurus longicephalus* •
- *Apristurus macrorhynchus* •
- *Apristurus macrostomus* •
- *Apristurus manis* •
- *Apristurus manocheriani* •
- *Apristurus melanoasper* ◦
- *Apristurus microps* •
- *Apristurus micropterygeus* •
- *Apristurus nakayai* ◦
- *Apristurus nasutus* •
- *Apristurus ovicorrugatus* *
- *Apristurus parvipinnis* •
- *Apristurus pinguis*◦
- *Apristurus platyrhynchus* ◦
- *Apristurus profundorum* •
- *Apristurus riveri* •
- *Apristurus saldanha* •
- *Apristurus sibogae* •
- *Apristurus sinensis* •
- *Apristurus spongiceps* •
- *Apristurus stenseni* •
- *Cirrhigaleus asper* •
- *Cirrhigaleus australis* ◦
- *Cirrhigaleus barbifer* •
- *Cirrhoscyllium japonicum* •
- *Ctenacis fehlmanni* •
- *Dalatias licha* •
- *Deania calcea* •
- *Deania hystricosa* •
- *Deania profundorum* •
- *Deania quadrispinosa* •
- *Echinorhinus brucus* •
- *Echinorhinus cookei* *
- *Eridacnis barbouri* •
- *Eridacnis radcliffei* •
- *Eridacnis sinuans* •
- *Etmopterus alphus* ◦
- *Etmopterus benchlyi* ◦
- *Etmopterus bigelowi*◦
- *Etmopterus brachyurus*◦
- *Etmopterus brosei*◦
- *Etmopterus bullisi* ◦
- *Etmopterus burgessi* ◦
- *Etmopterus carteri* ◦
- *Etmopterus caudistigmus* ◦
- *Etmopterus compagnoi* ◦
- *Etmopterus decacuspidatus* ◦
- *Etmopterus dianthus* ◦
- *Etmopterus dislineatus* ◦
- *Etmopterus evansi* ◦
- *Etmopterus fusus* ◦
- *Etmopterus gracilispinis* ◦
- *Etmopterus granulosus* ◦
- *Etmopterus hillianus* ◦
- *Etmopterus joungi* ◦
- *Etmopterus lailae* ◦
- *Etmopterus litvinovi* •
- *Etmopterus lucifer* ◦
- *Etmopterus marshae* ◦
- *Etmopterus molleri* ◦
- *Etmopterus parini* ◦
- *Isistius plutodus* ◦
- *Mitsukurina owstoni* •
- *Mollisquama parini* ◦
- *Mustelus albipinnis* *
- *Odontaspis noronhai* ◦
- *Oxynotus bruniensis* •
- *Oxynotus caribbaeus* •
- *Oxynotus centrina* •
- *Oxynotus japonicus* •
- *Oxynotus paradoxus* •
- *Parascyllium sparsimaculatum* •
- *Parmaturus albimarginatus* •
- *Parmaturus albipenis* •
- *Parmaturus angelae* •
- *Parmaturus bigus* •
- *Parmaturus campechiensis* •
- *Parmaturus lanatus* •
- *Parmaturus macmillani* •
- *Parmaturus melanobranchus* •
- *Parmaturus pilosus* •
- *Parmaturus xaniurus* •
- *Pentanchus profundicolus* •
- *Planonasus indicus* •
- *Planonasus parini* •
- *Pliotrema kajae* •
- *Pliotrema warreni* •
- *Pristiophorus delicatus* ◦
- *Pristiophorus lanae* ◦
- *Pristiophorus nancyae* ◦
- *Pristiophorus schroederi* •
- *Pseudotriakis microdon* •
- *Schroederichthys maculatus* •
- *Schroederichthys saurisqualus* •
- *Schroederichthys tenuis* •
- *Scyliorhinus boa* •
- *Scyliorhinus cabofriensis* ◦
- *Scyliorhinus capensis* •
- *Scyliorhinus comoroensis* •
- *Scyliorhinus hachijoensis* •
- *Scyliorhinus hesperius* •

Table 4A Continued

Apristurus yangi •
Asymbolus galacticus *
Asymbolus pallidus ◦
Asymbolus parvus ◦
Asymbolus rubiginosus ◦
Bythaelurus bachi ◦
Bythaelurus canescens •
Bythaelurus clevai •
Bythaelurus dawsoni •
Bythaelurus giddingsi ◦
Bythaelurus hispidus •
Bythaelurus immaculatus •
Bythaelurus incanus •
Bythaelurus lutarius •
Bythaelurus naylori •
Bythaelurus stewartia •
Bythaelurus tenuicephalus ◦
Bythaelurus vivaldii ◦
Centrophorus atromarginatus •
Centrophorus granulosus •
Centrophorus harrissoni •
Centrophorus isodon •
Centrophorus lesliei •
Centrophorus longipinnis •
Centrophorus moluccensis •
Centrophorus seychellorum •
Centrophorus squamosus •
Centrophorus uyato •
Centrophorus westraliensis •
Centrophorus zeehaani •
Centroscyllium excelsum •
Centroscyllium fabricii •
Centroscyllium granulatum ◦
Centroscyllium kamoharai •
Centroscyllium nigrum *
Centroscyllium ornatum •
Centroscyllium ritteri •
Centroscymnus coelolepis •
Centroscymnus owstonii •
Centroselachus crepidator •
Cephaloscyllium albipinnum ◦
Cephaloscyllium cooki *
Cephaloscyllium fasciatum •
Cephaloscyllium formosanum •
Etmopterus perryi ◦
Etmopterus polli •
Etmopterus princeps •
Etmopterus pseudosqualiolus •
Etmopterus pusillus •
Etmopterus pycnolepis ◦
Etmopterus robinsi •
Etmopterus samadiae ◦
Etmopterus schultzi •
Etmopterus sculptus •
Etmopterus sentosus •
Etmopterus sheikoi ◦
Etmopterus spinax •
Etmopterus splendidus ◦
Etmopterus unicolor •
Etmopterus viator •
Etmopterus villosus •
Etmopterus virens •
Euprotomicroides zantedeschia *
Euprotomicrus bispinatus ◦
Figaro boardmani •
Figaro striatus •
Galeus antillensis •
Galeus arae •
Galeus atlanticus •
Galeus cadenati •
Galeus corriganae •
Galeus eastmani •
Galeus friedrichi •
Galeus gracilis •
Galeus longirostris •
Galeus melastomus •
Galeus murinus •
Galeus nipponensis •
Galeus piperatus •
Galeus polli •
Galeus priapus *
Galeus schultzi •
Galeus springeri ◦
Gollum attenuatus •
Gollum suluensis *
Halaelurus quagga •
Hemitriakis abdita •
Heptranchias perlo •
Scyliorhinus meadi •
Scyliorhinus torrei •
Scyliorhinus ugoi •
Scymnodalatias garricki ◦
Scymnodon ichiharai ◦
Scymnodon macracanthus •
Scymnodon ringens ◦
Somniosus antarcticus *
Somniosus cheni •
Somniosus longus •
Somniosus microcephalus *
Somniosus pacificus *
Somniosus rostratus •
Squaliolus aliae ◦
Squaliolus laticaudus ◦
Squalus acutipinnis •
Squalus albicaudus *
Squalus altipinnis ◦
Squalus bahiensis ◦
Squalus bassi ◦
Squalus blainville •
Squalus boretzi *
Squalus brevirostris •
Squalus bucephalus ◦
Squalus chloroculus •
Squalus clarkae *
Squalus cubensis •
Squalus edmundsi ◦
Squalus grahami ◦
Squalus griffini •
Squalus hawaiiensis *
Squalus hemipinnis *
Squalus japonicus •
Squalus lalannei •
Squalus lobularis *
Squalus longispinis *
Squalus megalops •
Squalus melanurus •
Squalus mitsukurii ◦
Squalus montalbani •
Squalus nasutus ◦
Squalus notocaudatus ◦
Squalus quasimodo ◦
Squalus rancureli •

Table 4A Continued

Cephaloscyllium hiscosellum ◦
Cephaloscyllium isabellum •
Cephaloscyllium signourum *
Cephaloscyllium silasi •
Cephaloscyllium speccum *
Cephaloscyllium stevensi ◦
Cephaloscyllium variegatum ◦
Cephaloscyllium zebrum ◦
Cephalurus cephalus •
Chlamydoselachus africana *
Chlamydoselachus anguineus •
Hexanchus griseus •
Hexanchus nakamurai •
Hexanchus vitulus •
Holohalaelurus favus ◦
Holohalaelurus grennian ◦
Holohalaelurus melanostigma •
Holohalaelurus punctatus •
Holohalaelurus regani •
Iago garricki •
Iago omanensis •
Isistius brasiliensis ◦
Squalus raoulensis ◦
Squalus shiraii ◦
Squatina caillieti •
Squatina formosa •
Squatina leae •
Squatina mapama •
Squatina pseudocellata *
Squatina tergocellata •
Squatina varii •
Trigonognathus kabeyai •

Table 5A List of oceanic species with unknown mode of reproduction (55 total species). The five species for which mode of reproduction could not be inferred are denoted by a '*' symbol.

Species with Unknown Reproductive Data

Apristurus albisoma
Apristurus ampliceps
Apristurus australis
Apristurus bucephalus
Apristurus indicus
Apristurus investigatoris
Apristurus manocheriani
Apristurus micropterygeus
Apristurus ovicorrugatus
Asymbolus occiduus
Bythaelurus giddingsi *
Bythaelurus immaculatus *
Bythaelurus incanus *
Bythaelurus tenuicephalus *
Bythaelurus vivaldii *
Centrophorus seychellorum
Centrophorus zeehaani
Etmopterus brosei
Etmopterus pycnolepis
Galeus corriganae
Galeus friedrichi
Galeus gracilis
Galeus longirostris
Galeus priapus
Galeus schultzi
Gollum suluensis
Hemitriakis abdita
Isistius plutodus
Mitsukurina owstoni
Mollisquama mississippiensis
Mollisquama parini
Odontaspis noronhai
Oxynotus caribbaeus
Parascyllium sparsimaculatum
Parmaturus albimarginatus
Parmaturus albipenis
Parmaturus bigus
Parmaturus campechiensis
Parmaturus lanatus
Parmaturus melanobranchus
Pentanchus profundicolus
Planonasus parini
Pristiophorus lanae
Pristiophorus schroederi
Scyliorhinus hesperius
Scyliorhinus torrei
Somniosus antarcticus
Squalus grahami
Squalus lalannei
Squalus longispinis
Squalus shiraii
Squatina caillieti
Squatina leae
Squatina mapama
Squatina pseudocellata

Table 6A List of oceanic shark species with available conservation status data (274 total species). Non-threatened species have a Least Concern and Near Threatened status given by the IUCN Red List. Threatened species have a Vulnerable, Endangered, or Critically Endangered status given by the IUCN Red List and are denoted by a ‘*’ symbol. The species codes used for all statistical tests in this study are included to the left of the species name.

Oceanic Shark Species with Conservation Status Trait Data

sp1	*Alopias pelagicus* *
sp2	*Alopias superciliosus* *
sp3	*Alopias vulpinus* *
sp4	*Asymbolus submaculatus*
sp5	*Carcharhinus albimarginatus* *
sp6	*Carcharhinus altimus*
sp7	*Carcharhinus falciformis* *
sp8	*Carcharhinus galapagensis*
sp9	*Carcharhinus longimanus* *
sp10	*Carcharhinus signatus* *
sp11	*Carcharodon carcharias* *
sp12	*Cetorhinus maximus* *
sp13	*Isurus oxyrinchus* *
sp14	*Isurus paucus* *
sp15	*Lamna ditropis*
sp16	*Lamna nasus* *
sp17	*Megachasma pelagios*
sp18	*Mustelus canis*
sp19	*Prionace glauca*
sp20	*Pseudocarcharias kamoharai*
sp21	*Rhincodon typus* *
sp22	*Scymnodalatias oligodon*
sp23	*Sphyrna lewini* *
sp24	*Sphyrna mokarran* *
sp25	*Sphyrna zygaena* *
sp26	*Asymbolus occiduus*
sp27	*Carcharhinus obscurus* *
sp28	*Cephaloscyllium sufflans*
sp29	*Cephaloscyllium umbratile*
sp30	*Galeorhinus galeus* *
sp31	*Heteroscymnoides marleyi*
sp32	*Hypogaleus hyugaensis*
sp33	*Mollisquama mississippiensis*
sp34	*Mustelus higmani* *
sp35	*Mustelus lenticulatus*
sp36	*Mustelus stevensi*
sp37	*Odontaspis ferox* *
sp38	*Pristiophorus japonicus*
sp93	*Centrophorus atromarginatus* *
sp94	*Centrophorus granulosus* *
sp95	*Centrophorus harrissoni* *
sp96	*Centrophorus isodon* *
sp97	*Centrophorus lesliei* *
sp98	*Centrophorus longipinnis* *
sp99	*Centrophorus moluccensis* *
sp100	*Centrophorus seychellorum*
sp101	*Centrophorus squamosus* *
sp102	*Centrophorus uyato* *
sp103	*Centroscyllium excelsum*
sp104	*Centroscyllium fabricii*
sp105	*Centroscyllium granulatum* *
sp106	*Centroscyllium kamoharai*
sp107	*Centroscyllium nigrum*
sp108	*Centroscyllium ornatum*
sp109	*Centroscyllium ritteri*
sp110	*Centroscymnus coelolepis*
sp111	*Centroscymnus owstonii* *
sp112	*Centroselachus crepidater*
sp113	*Cephaloscyllium albipinnum* *
sp114	*Cephaloscyllium fasciatum* *
sp115	*Cephaloscyllium formosanum*
sp116	*Cephaloscyllium hiscosellum*
sp117	*Cephaloscyllium isabellum*
sp118	*Cephaloscyllium silasi* *
sp119	*Cephaloscyllium stevensi*
sp120	*Cephaloscyllium variegatum*
sp121	*Cephalurus cephalus*
sp122	*Chlamydoselachus africana*
sp123	*Chlamydoselachus anguineus*
sp124	*Cirrhigaleus barbifer*
sp125	*Cirrhoscyllium japonicum*
sp126	*Ctenacis fehlmanni*
sp127	*Dalatias licha* *
sp128	*Deania calcea*
sp129	*Deania profundorum*
sp130	*Deania quadrispinosa* *
sp185	*Galeus murinus*
sp186	*Galeus nipponensis*
sp187	*Galeus piperatus*
sp188	*Galeus polli* *
sp189	*Galeus priapus*
sp190	*Galeus schultzi*
sp191	*Galeus springeri*
sp192	*Gollum attenuatus*
sp193	*Gollum suluensis*
sp194	*Heptranchias perlo*
sp195	*Hexanchus griseus*
sp196	*Hexanchus nakamurai*
sp197	*Hexanxhus vitulus*
sp198	*Holohalaelurus favus* *
sp199	*Holohalaelurus melanostigma*
sp200	*Holohalaelurus punctatus* *
sp201	*Holohalaelurus regani*
sp202	*Iago garricki*
sp203	*Iago omanensis*
sp204	*Isistius brasiliensis*
sp205	*Isistius plutodus*
sp206	*Mitsukurina owstoni*
sp207	*Mollisquama parini*
sp208	*Mustelus albipinnis*
sp209	*Odontaspis noronhai*
sp210	*Oxynotus bruniensis*
sp211	*Oxynotus caribbaeus*
sp212	*Oxynotus centrina* *
sp213	*Oxynotus japonicus* *
sp214	*Oxynotus paradoxus* *
sp215	*Parmaturus albimarginatus*
sp216	*Parmaturus albipenis*
sp217	*Parmaturus angelae* *
sp218	*Parmaturus campechiensis*
sp219	*Parmaturus lanatus*
sp220	*Parmaturus melanobranchus*
sp221	*Parmaturus pilosus*
sp222	*Parmaturus xaniurus*

Table 6A Continued

sp39	*Scyliorhinus retifer*
sp40	*Squalus acanthias* *
sp41	*Squalus albifrons*
sp42	*Squalus crassispinus*
sp43	*Squalus formosus* *
sp44	*Squatina albipunctata* *
sp45	*Squatina dumeril*
sp46	*Squatina nebulosa* *
sp47	*Zameus squamulosus*
sp48	*Aculeola nigra*
sp49	*Apristurus albisoma*
sp50	*Apristurus ampliceps*
sp51	*Apristurus aphyodes*
sp52	*Apristurus australis*
sp53	*Apristurus breviventralis*
sp54	*Apristurus canutus*
sp55	*Apristurus exsanguis*
sp56	*Apristurus fedorovi*
sp57	*Apristurus garricki*
sp58	*Apristurus gibbosus*
sp59	*Apristurus herklotsi*
sp60	*Apristurus indicus*
sp61	*Apristurus internatus*
sp62	*Apristurus investigatoris*
sp63	*Apristurus japonicus*
sp64	*Apristurus laurussonii*
sp65	*Apristurus longicephalus*
sp66	*Apristurus macrorhynchus*
sp67	*Apristurus macrostomus*
sp68	*Apristurus manis*
sp69	*Apristurus melanoasper*
sp70	*Apristurus microps*
sp71	*Apristurus micropterygeus*
sp72	*Apristurus nakayai*
sp73	*Apristurus nasutus*
sp74	*Apristurus parvipinnis*
sp75	*Apristurus pinguis*
sp76	*Apristurus platyrhynchus*
sp77	*Apristurus profundorum*
sp78	*Apristurus riveri*
sp79	*Apristurus saldanha*
sp80	*Apristurus sibogae*
sp81	*Apristurus stenseni*
sp131	*Echinorhinus brucus* *
sp132	*Eridacnis barbouri*
sp133	*Eridacnis radcliffei*
sp134	*Eridacnis sinuans*
sp135	*Etmopterus alphus*
sp136	*Etmopterus benchlyi*
sp137	*Etmopterus bigelowi*
sp138	*Etmopterus brosei*
sp139	*Etmopterus bullisi*
sp140	*Etmopterus burgessi*
sp141	*Etmopterus carteri*
sp142	*Etmopterus caudistigmus*
sp143	*Etmopterus compagnoi*
sp144	*Etmopterus decacuspidatus*
sp145	*Etmopterus dianthus*
sp146	*Etmopterus dislineatus*
sp147	*Etmopterus evansi*
sp148	*Etmopterus fusus*
sp149	*Etmopterus gracilispinis*
sp150	*Etmopterus granulosus*
sp151	*Etmopterus hillianus*
sp152	*Etmopterus joungi*
sp153	*Etmopterus litvinovi*
sp154	*Etmopterus lucifer*
sp155	*Etmopterus marshae*
sp156	*Etmopterus parini*
sp157	*Etmopterus perryi*
sp158	*Etmopterus polli*
sp159	*Etmopterus princeps*
sp160	*Etmopterus pseudosqualiolus*
sp161	*Etmopterus pusillus*
sp162	*Etmopterus pycnolepis*
sp163	*Etmopterus robinsi*
sp164	*Etmopterus samadiae*
sp165	*Etmopterus schultzi*
sp166	*Etmopterus sculptus*
sp167	*Etmopterus sentosus*
sp168	*Etmopterus sheikoi*
sp169	*Etmopterus spinax* *
sp170	*Etmopterus splendidus*
sp171	*Etmopterus viator*
sp172	*Etmopterus villosus*
sp173	*Etmopterus virens*
sp223	*Pentanchus profundicolus*
sp224	*Planonasus parini*
sp225	*Pliotrema warreni*
sp226	*Pristiophorus delicatus*
sp227	*Pristiophorus lanae*
sp228	*Pristiophorus nancyae*
sp229	*Pristiophorus schroederi*
sp230	*Pseudotriakis microdon*
sp231	*Schroederichthys maculatus*
sp232	*Schroederichthys saurisqualus* *
sp233	*Schroederichthys tenuis*
sp234	*Scyliorhinus boa*
sp235	*Scyliorhinus cabofriensis*
sp236	*Scyliorhinus capensis*
sp237	*Scyliorhinus hesperius*
sp238	*Scyliorhinus meadi*
sp239	*Scyliorhinus torrei*
sp240	*Scyliorhinus ugoi*
sp241	*Scymnodon ichiharai* *
sp242	*Scymnodon ringens* *
sp243	*Somniosus antarcticus*
sp244	*Somniosus microcephalus* *
sp245	*Somniosus pacificus*
sp246	*Somniosus rostratus*
sp247	*Squaliolus aliae*
sp248	*Squaliolus laticaudus*
sp249	*Squalus acutipinnis*
sp250	*Squalus bassi*
sp251	*Squalus boretzi*
sp252	*Squalus brevirostris* *
sp253	*Squalus chloroculus* *
sp254	*Squalus clarkae*
sp255	*Squalus cubensis*
sp256	*Squalus edmundsi*
sp257	*Squalus grahami*
sp258	*Squalus griffini*
sp259	*Squalus hawaiiensis*
sp260	*Squalus hemipinnis* *
sp261	*Squalus japonicus* *
sp262	*Squalus lalannei*
sp263	*Squalus megalops*
sp264	*Squalus mitsukurii* *
sp265	*Squalus montalbani* *

Table 6A Continued

sp82	*Apristurus yangi*
sp83	*Asymbolus galacticus*
sp84	*Asymbolus pallidus*
sp85	*Asymbolus parvus*
sp86	*Asymbolus rubiginosus*
sp87	*Bythaelurus canescens* *
sp88	*Bythaelurus dawsoni*
sp89	*Bythaelurus giddingsi*
sp90	*Bythaelurus hispidus*
sp91	*Bythaelurus immaculatus*
sp92	*Bythaelurus tenuicephalus*
sp174	*Euprotomicroides zantedeschia*
sp175	*Euprotomicrus bispinatus*
sp176	*Figaro boardmani*
sp177	*Galeus antillensis*
sp178	*Galeus area*
sp179	*Galeus atlanticus*
sp180	*Galeus cadenati*
sp181	*Galeus corriganae*
sp182	*Galeus eastmani*
sp183	*Galeus longirostris*
sp184	*Galeus melastomus*
sp266	*Squalus nasutus*
sp267	*Squalus notocaudatus*
sp268	*Squalus rancureli*
sp269	*Squalus raoulensis*
sp270	*Squatina formosa* *
sp271	*Squatina pseudocellata*
sp272	*Squatina tergocellata*
sp273	*Squatina varii*
sp274	*Trigonognathus kabeyai*

Table 7A List of all oceanic shark species with a lunate caudal fin shape (7 species). All species in this table are epipelagic (shallow-water-pelagic).

Oceanic Shark Species with a Lunate Caudal Fin
Carcharodon carcharias
Cetorhinus maximus
Isurus oxyrinchus
Isurus paucus
Lamna ditropis
Lamna nasus
Rhincodon typus

Table 8A List of all mesothermic oceanic shark species (6 species). All species in this table are epipelagic (shallow-water-pelagic).

Mesothermic Oceanic Shark Species
Alopias vulpinus
Carcharodon carcharias
Isurus oxyrinchus
Isurus paucus
Lamna ditropis
Lamna nasus

Table 9A List of all oceanic shark species with one dorsal fin (6 species). All species in this table reside in the deep sea.

Oceanic Shark Species with One Dorsal Fin
Chalmydoselachus africana
Chalmydoselachus anguineus
Heptranchias perlo
Hexanchus griseus
Hexanchus nakamurai
Hexanchus vitulus

Table 10A List of all oceanic shark species with dorsal spines (121 species). Wanderer species are denoted by a ‘*’ symbol. All other species are deep sea. Species in bold italics only have one dorsal spine. All other species have two dorsal spines.

Oceanic Shark Species with Dorsal Spines

Aculeola nigra
Centrophorus atromarginatus
Centrophorus granulosus
Centrophorus harrissoni
Centrophorus isodon
Centrophorus lesliei
Centrophorus longipinnis
Centrophorus moluccensis
Centrophorus seychellorum
Centrophorus squamosus
Centrophorus uyato
Centrophorus westraliensis
Centrophorus zeehaani
Centroscyllium excelsum
Centroscyllium fabricii
Centroscyllium granulatum
Centroscyllium kamoharai
Centroscyllium nigrum
Centroscyllium ornatum
Centroscyllium ritteri
Centroscymnus coelolepis
Centroscymnus owstonii
Centroselachus crepidater
Cirrhigaleus asper
Cirrhigaleus australis
Cirrhigaleus barbifer
Deania calcea
Deania hystricosa
Deania profundorum
Deania quadrispinosa
Etmopterus alphus
Etmopterus benchlyi
Etmopterus bigelowi
Etmopterus brachyurus
Etmopterus brosei
Etmopterus bullisi
Etmopterus burgessi
Etmopterus carteri
Etmopterus caudistigmus
Etmopterus compagnoi
Etmopterus decacuspidatus
Etmopterus dianthus
Etmopterus dislineatus
Etmopterus evansi
Etmopterus fusus
Etmopterus gracilispinis
Etmopterus granulosus
Etmopterus hillianus
Etmopterus joungi
Etmopterus lailae
Etmopterus litvinovi
Etmopterus lucifer
Etmopterus marshae
Etmopterus molleri
Etmopterus parini
Etmopterus perryi
Etmopterus polli
Etmopterus princeps
Etmopterus pseudosqualiolus
Etmopterus pusillus
Etmopterus pycnolepis
Etmopterus robinsi
Etmopterus samadiae
Etmopterus schultzi
Etmopterus sculptus
Etmopterus sentosus
Etmopterus sheikoi
Etmopterus spinax
Etmopterus splendidus
Etmopterus unicolor
Etmopterus viator
Etmopterus villosus
Etmopterus virens
Heterodontus ramalheira *
Oxynotus bruniensis
Oxynotus caribbaeus
Oxynotus centrina
Oxynotus japonicus
Oxynotus paradoxus
Scymnodon ichiharai
Scymnodon macracanthus
Scymnodon ringens
Squaliolus aliae
Squaliolus laticaudus
Squalus acanthias *
Squalus acutipinnis
Squalus albicaudus
Squalus albifrons *
Squalus altipinnis
Squalus bahiensis
Squalus bassi
Squalus blainville
Squalus boretzi
Squalus brevirostris
Squalus bucephalus
Squalus chloroculus
Squalus clarkae
Squalus crassispinus *
Squalus cubensis
Squalus edmundsi
Squalus formosus *
Squalus grahami
Squalus griffini
Squalus hawaiiensis
Squalus hemipinnis
Squalus japonicus
Squalus lalannei
Squalus lobularis
Squalus longispinis
Squalus megalops
Squalus melanurus
Squalus mitsukurii
Squalus montalbani
Squalus nasutus
Squalus notocaudatus
Squalus quasimodo
Squalus rancureli
Squalus raoulensis
Squalus shiraii
Trigonognathus kabeyai
Zameus squamulosus *

Table 11A List of all oceanic shark species with six or more gill slit pairs (8 species). All species in this table reside in the deep sea.

Oceanic Shark Species with 6+ Gill Slit Pairs	
Chlamydoselachus africana	*Hexanchus nakamurai*
Chlamydoselachus anguineus	*Hexanchus vitulus*
Heptranchias perlo	*Pliotrema kajae*
Hexanchus griseus	*Pliotrema warreni*