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# "Relationships between Caudal Fin Shape and Ecomorphotype in extant Sharks"

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# 2. Abstract

Since sharks inhabit this planet for more than 200 million years, they are of big interest for researchers. The interplay between morphological and behavioural adaptations and the constantly changing environment is an important part in scientific shark studies. A perfectly adapted body plan with sophisticated senses is a reason for their long existence. A very prominent characteristic of sharks is the heterocercal caudal fin shape in which the vertebra extends into the elongated dorsal lobe. The caudal fin, as the main locomotory organ in sharks, can be very diverse in shape and therefore, it is of tremendous importance to understand why different caudal fin shapes occur and how strong the influence of factors such as the environment they live in, is on the morphology of the caudal fin.

In this thesis, the goal is to quantitatively assess the relationships between the caudal fin shape of various extant shark species and their associated ecomorphotypes. Through geometric morphometric analyses it was possible to display connections between the caudal fin shape and the ecomorphotype although different limitations (e.g. ontogeny) occurred due to a small number of individuals. It was possible to show clean separations and clusters between species, which leads to the assumption, that more than one caudal fin design is present in modern sharks. Furthermore, the classification of ecomorphotypes is valid for all extant shark species and ontogenetic changes were not included. Therefore, it is important to take into account that ecomorphotype to a species. Additionally, it is possible, that sexual dimorphism is the reason for some species [e.g. Shortfin mako (*Isurus oxyrinchus*)] to display intraspecific variations in caudal fin shape.

#### 3. Introduction

#### 3.1. General

Modern sharks (Chondrichthyes: Elasmobranchii) are marine predators with a fossil record that extends back at least 200 million years (Maisey 2012). The oldest articulated fossil shark-relative even stretches back to the Devonian about 400 million years ago (Miller et al. 2003; Hara et al. 2018). Since sharks inhabit this planet for such a long time, it is of tremendous interest for researchers how these animals managed to survive and what behavioural and morphological changes they went through to become such successful vertebrates. To date, there are more than 500 species of sharks, divided into nine orders and 34 families that have been described (Weigmann 2016). A perfectly adapted body plan with sophisticated senses is a reason for their long existence (Coates et al. 2018). The main characteristics of Chondrichthyes are a cartilaginous endoskeleton, paired jaws and five to seven gill slits (Compagno et al. 2005; Boisvert et al. 2019).

Since sharks belong to Chondrichthyes, the complete internal skeleton consists of poorly mineralized cartilage. A lot of this cartilage skeleton, such as the jaws, is covered in a layer of mineralized plate-like structures that consist of calcium salts, the so-called tesserae, which are as strong as bones but not as heavy (Dean et al. 2015; Boisvert et al. 2019).

The jaw is not attached to the cranium and the teeth are arranged in multiple rows. Sharks are polyphyodont, which means that they continuously produce, use and lose teeth (Tucker and Fraser 2014; Boisvert et al. 2019; Fraser et al. 2020).

Another evident characteristic of sharks is their skin. Almost the entire body surface is covered in dermal denticles, also known as placoid scales. These scales are similar to their teeth in composition. The main body of a tooth, which is composed of dentine, sits on a flat base and is covered by enameloid. The function of the dermal denticles is predominantly a protection from predators or parasites, a better hydrodynamic efficiency, a placement of sensory organs and, in some cases (*Scyliorhinus canicula*), a feeding function (Southall and Sims 2003; Boisvert et al. 2019).

Besides the protruding appearance of the jaws and teeth, the locomotion in sharks is of major interest. Not only the skin plays an important role but also the morphology of the pectoral fins and especially the caudal fin, as its main locomotory organ (Lauder and Di Santo 2016).

In extant sharks, three different swimming modes (anguilliform, carangiform and thunniform) exist (Maia et al. 2012, Lauder and Di Santo, 2016). Anguilliform sharks are characterized by an "eel-like" swimming behaviour where the entire trunk and caudal fin undulates at high amplitude. Specimens using a carangiform swimming mode show reduced lateral movements, which are mostly conducted by the posterior half of the body. The thunniform swimming mode shows the slightest lateral movements, which are executed by the caudal fin, starting at the caudal peduncle (Maia et al. 2012; Sternes and Shimada 2020). Sternes and Shimada (2020) found out, that the swimming modes show a strong correlation with the body form.

Tomson and Simanek (1977) created a classification of sharks based on different body forms. They divided 56 extant shark species into a total of four different body forms using simple morphometric measurements. This got revisited by Sternes and Shimada (2020) who classified 470 species of extant sharks into two main body forms ("shallow-bodied" and "deep-bodied") using landmark-based geometric morphometric analyses. They postulated that the major variations, and therefore the most important factors to determine the body form are expressed in the precaudal body area and not in the caudal fin. Furthermore, they assume that all sharks possess, except some specializations, one basic caudal fin design.

#### 3.2. Caudal fin

First and foremost, the so-called heterocercal shape of the caudal fin is an outstanding characteristic of sharks and early fishes (Webb and Smith 1980; Thomson 1975). Louis Agassiz (1833) defined the term "heterocercal" as tails that are composed of asymmetrical lobes, where the dorsal lobe, comprising the most posterior or terminal part of the vertebral column, is larger than the ventral lobe (Lauder 2000, Moreira et al. 2018). Although, the shape of a sharks' caudal fin can be distinctly different (Thomson 1976, Thomson and Simanek 1977, Scacco et al.

2010), the general caudal fin skeleton anatomy is uniform. The skeleton consists of epaxial and hypaxial components. The epaxial component comprises basidorsal, interdorsal and



Figure 1. Anatomical illustration of the caudal fin skeleton (taken from Moreira et al. 2018).

supraneural cartilages, while the hypaxial component encompasses haemal spines, basiventral cartilages and, in some case e.g. the tiger shark *Galeocerdo cuvier*, prehypochordal cartilages. The vertebral centra depict the boundary between epaxial and hypaxial components. The basidorsal cartilages are located at the dorsal edge of each vertebral centrum and are connected with interdorsal cartilages, which are located dorsally between the vertebral centra. The connection between basidorsal



and interdorsal cartilages creates а neural arch wherein the caudal nerve proceeds towards the posterior tip of the caudal fin. The supraneural cartilages are situated dorsally along the neural



Figure 2. Illustration of the model created by Alexander (1965).

arch. The hypaxial part contains paired and connected basiventral cartilages, located at the ventral edge of the vertebral centra. The caudal vein and artery are surrounded

Figure 3. Illustration of the model created by Grove and Newell (1936).

by haemal arches, which are the result of the joined basiventral cartilages. The haemal spines in the anterior diplospondylic (two or more vertebrae per muscle segment) caudal region are not connected with the haemal arches whereas the haemal spines in the posterior diplospondylic caudal region are attached to the basiventral cartilages. The posterior haemal spines, close to the terminal tip, are reduced and no basiventral cartilage is present (Moreira et al. 2018; Fig. 1). The strong morphological differences between heterocercal and homocercal caudal fins go along with disparities in locomotion behaviour. The classical theory of heterocercy, postulated by Schulze (1894) and Ahlborn (1896), implies that the ventral lobe is led by the dorsal lobe during lateral tail beats, which result in a dorsoventrally asymmetrical locomotion. This causes a lift force on the tail created by a ventral and posterior deflection of the surrounding water. Confirmation of this theory occurred first through models (Grove & Newell 1936; Affleck 1950) and by Alexander (1965) using cropped shark tails (Fig. 2, 3). More topical research (Ferry and Lauder 1996; Lauder 1999) corroborates the classical theory of heterocercal tail function in sharks but contradicts the assumption of pectoral fins engender lift forces during steady horizontal locomotion (Wilga and Lauder 2000; 2001).

Unlike in homocercal fins, where a posteriorly directed jet is produced through a single vortex ring, two jets are created in heterocercal fins. A small dorsal vortex ring with counter-rotating centres, producing the first jet, is surrounded by a bigger vortex ring which produces a second jet as a result of flow generation through the ventral tip. This creates a dorso-ventrally directed jet force that leads to an opposite and antero-dorsally directed reaction force, dorsal to the centre of mass producing a torque around the centre of mass, which gets counteracted by a torque that generates lift forces due to a positive angle of the body to the flow. The pectoral fins are not actively used during steady horizontal locomotion but play a role during initiation and execution of rising and sinking manoeuvres (Lauder 2000; Wilga and Lauder 2002; 2004). Since the caudal fin is known to be the primary locomotive structure (Ferry and Lauder 1996; Wilga and Lauder 2004), it plays an important role for a shark, not only for steady movements or manoeuvring but also for predation, gill ventilation, predation avoidance and reproduction (Webb 1988; Maia et al. 2012; Kim et al. 2013). Due to the high diversity in caudal fin shapes (e.g. four different types of caudal fin shape in the order of lamniforms) and the use of specific habitats, it is possible that the morphology of the caudal fin is related with the lifestyle (Kim et al. 2013).

# 3.3. Ecomorphology

Recognizing and understanding connections between the morphology and ecology of diverse organisms is the primary aim of ecomorphological researches (Norton et al. 1995). Accordingly, ecomorphology is the study of the relationship between the ecological role of an individual and its morphological adaptations (Kriwet 2008). The beginning of ecomorphological research reaches far back in history. It is assumed that probably the first ecomorphological connections between habitat and body form was drawn in the ancient Hindu text "Sushruta-samhita" whereby parts of this text can even be pre-dated to Aristotle (Lindsey 1978; Motta 1995).

A real upsurge in ecomorphological research started in the early 1950's when vertebrate morphology started to become much more diverse. The creation and extension of new fields such as functional morphology and evolutionary morphology aroused attention and interest, not only for morphologists, but also for evolutionary biologists, ecologists or systematists (Bock 1990; Bock 1994; Norton et al. 1995). Techniques, like high-speed and x-ray cinematography and electromyography made it possible to observe movements of structures and muscle activities in animals.

Ecologists also addressed questions concerning e.g. community structures, partitioning of habitats or the concept of the niche during the 1950's and 1960's which led to the minting of the term "Ecomorphology" in an article by Karr and James in 1975, which examined connections between morphological structures and the environment from an ecological point of view (Karr and James 1975; Bock 1994).

#### 3.4. Ecomorphotype

To better understand the connections between morphology and ecology, sharks were divided in so called ecomorphotypes (Compagno 1990). An ecomorphotype describes a specific aggregation of taxa based on similar features such as morphology, behaviour and habitat, while taxa do not necessarily have to be phylogenetically closely related (Compagno 1990). Since Compagno (1990), classification of ecomorphotypes comprises all chondrichthyans described at that time, a new allocation of ecomorphotypes solely for extant sharks, which encompasses ca. 390 shark species divided into 18 ecomorphotypes, has been established by Martin (2003).

In this study, nine different ecomorphotypes are compared (Tab. 1). The Anguillobathic (AB) ecomorphotype is represented by only one living species, the frilled shark (Chlamydoselachus anguineus). The tiger shark (Galeocerdo cuvier) and the great white shark (Carcharodon carcharias) are characteristic examples for the Eurytrophic Littoral (ETL) ecomorphotype. The brownbanded bamboo shark (Chiloscyllium punctatum) represents the Leptobenthic Littoral type (LBL). The Macropelagic (MAP) ecomorphotype comprises the oceanic whitetip (Carcharhinus longimanus) and the common thresher shark (Alopias vulpinus). The smalltooth sand tiger (Odontaspis ferox) represents the Mesobathic (MB) ecomorphotype, the smallspotted catshark (Scyliorhinus canicula) depicts the Mesobenthic Littoral (MBL) ecomorphotype, the blacktip reef shark (Carcharhinus melanopterus), whereas the whitetip reef shark (*Triaenodon obesus*) and sand tiger shark (*Carcharias taurus*) belong to the Mesotrophic Littoral (MTL) ecomorphotype. The shortfin mako (Isurus oxyrinchus) and porbeagle shark (Lamna nasus) represent the Tachypelagic (TP) ecomorphotype. The here included sharpnose sevengill shark (Heptranchias perlo) has not yet been assigned to any ecomorphotype (= undetermined, UN).

# 3.5. Goals

The goal of this study is, to quantitatively assess the relationship of the caudal fin shape with the ecomorphotype, because there is a general assumption that variations in caudal fin shape among different ecomorphotypes occur. However, Sternes and Shimada (2020), conversely, assumed that there is only one basic caudal fin design in sharks. Thus, the present study intends to solve this contradiction providing novel information derived from sharks, including prenatal growth stages.

| Anguillobathic        | Chlamydoselachus<br>anguineus |
|-----------------------|-------------------------------|
| Eurytrophic Littoral  | Galeocerdo cuvier             |
|                       | carcharias                    |
| Leptobenthic Littoral | Chiloscyllium punctatum       |
| Macropelagic          | Carcharhinus<br>Iongimanus    |
|                       | Alopias vulpinus              |
| Mesobathic            | Odontaspis ferox              |
| Mesobenthic Littoral  | Scyliorhinus canicula         |
|                       | Carcharhinus<br>melanopterus  |
| Mesotrophic Littoral  | Triaenodon obesus             |
|                       | Carcharias taurus             |
|                       | Isurus oxyrinchus             |
| Tachypelagic          | Lamna nasus                   |
| Undetermined          | Heptranchias perlo            |

Table 1. Ecomorphotypes with corresponding species and fin shapes, based on Martin (2003). Scale bars = 1 cm.

### 4. Material and methods

#### 4.1. Specimens

The specimens used in this study were provided by the Department of Palaeontology at the University of Vienna and the Natural History Museum Vienna. Additionally, pictures, contributed by Prof. Dr. Jürgen Kriwet, were added to this study. In total, 73 individuals where used to establish the caudal fin form, comprising the common thresher shark [Alopias vulpinus (Bonnaterre, 1788)] (n = 4; juveniles = 4), the oceanic whitetip shark [Carcharhinus longimanus (Poey, 1861)] (n = 1; prenatal = 1), the blacktip reef shark [Carcharhinus melanopterus (Quoy and Gaimard, 1824)] (n = 2; juveniles = 2), the sand tiger shark [Carcharias taurus (Rafinesque, 1810)] (n = 1; juveniles = 1), the great white shark [Carcharodon carcharias (Linnaeus, 1758)] (n = 5; embryos = 5), the brownbanded bamboo shark [Chiloscyllium punctatum (Müller and Henle, 1838)] (n = 5; juveniles = 3, adults = 2), the frilled shark [*Chlamydoselachus anguineus* (Garman, 1884)] (n = 8; embryos = 8), the tiger shark [Galeocerdo cuvier (Péron and Lesueur, 1822)] (n = 7; embryos = 7), the sharpnose sevengill shark [Heptranchias perlo (Bonnaterre, 1788)] (n = 5; embryos = 5), the shortfin mako shark [Isurus oxyrinchus (Rafinesque, 1810)] (n = 2; juveniles = 2), the porbeagle shark [Lamna nasus (Bonnaterre, 1788)] (n = 2; juveniles = 2), the smalltooth sand tiger shark [Odontaspis ferox (Risso, 1810)] (n = 1; juveniles = 1), the lesser spotted dogfish [Scyliorhinus canicula (Linnaeus, 1758)] (n = 27; embryos = 7, juveniles = 10, adults = 10) and the whitetip reef shark [Triaenodon obesus (Rüppel, 1837)] (n = 3; embryos = 1, juveniles = 2). Pictures of each specimen were taken with a DSLR (Olympus E 520) in a lateral position with the head displaying the left side. Each photo contains a scale bar for measuring the total length (TL) of each specimen, which is used to determine the age. Species such as the picked dogfish (Squalus acanthias) were excluded from the analyses due to the absence of a subterminal notch and therefore the absence of a comparable homologous point. Staging was not performed due to the small number of individuals. Analysing ontogenetic trajectories was beyond the scope of the thesis.

# 4.2. Geometric morphometrics

Photos of the caudal fin of the examined specimens (see above) were imported into the software program tpsUtil (version 1.78) (Rohlf 2004) to capture landmark coordinates for further analyses. The TPS files were then imported into the program tpsDig2 (version 2.12) (Rohlf 2004) to digitize the coordinates. A total of 32 coordinates where set, 5 landmarks were placed as true and/or fixed landmarks and 27 landmarks were placed as semi-landmarks and combined into four curves to capture the caudal fin shape. All fixed landmarks were placed on homologous points: the first and second fixed landmarks were placed on the upper and lower origin of the caudal fin, the third landmark on the ventral lobe tip, the fourth was placed on the subterminal notch of the upper lobe and the fifth was placed at the tip of the caudal fin, which was determined as an elongation of the vertebra that separates the dorsal and ventral lobes (Figs. 4, 5). Between the first and the fifth fixed landmark, 13 semilandmarks were positioned creating a curve, which emulates the dorsal caudal margin. The second and third fixed landmarks form, together with three semilandmarks, a curve from the lower origin to the ventral tip. The third curve, containing the third and fourth fixed landmarks and eight semi-landmarks, outlines the postventral margins. The fourth curve comprises the fourth and fifth fixed landmarks and three semi-landmarks, which encompass the terminal ventral lobe with the subterminal and terminal margin starting from the subterminal notch to the posterior tip.



Figure 4. Anatomical description of caudal fin structures (taken from Compagno et al. 2005).



Figure 5. Shape of the caudal fin of *Scyliorhinus canicula* showing the location of the fixed landmarks (pink) and semi-landmarks (light blue).

# 4.3. Statistical analyses

First, a Generalized Procrustes Analysis (GPA) was executed to superimpose, rotate and align the shapes. This removes the differences in size, rotation and location (Gower 1975; Rohlf and Slice 1990). All landmarks are evenly distributed along their individual curves, starting and ending with fixed landmarks. The semi-landmarks were allowed to slide between two neighbouring landmarks to minimize the bending energy between the reference- and target point and to optimize the location of the semi-landmarks (Gunz and Mitteroecker 2013). The aligned coordinates were then subjected to a Principle Component Analysis (PCA) to ascertain the variance among all specimens. The mean shape for all specimens was estimated with the *mshape* function to visualize the deviation of all shapes from the mean.

Additionally, the coordinates were subject to an analysis of variance (ANOVA) to identify any differences between shape and ecomorphotype groups. This was assessed with the *procD.Im* function from *geomorph* with 999 iterations, considering the residuals permutations to estimate the significance. A comparison between sexes was performed to detect gender specific shape variations.

All statistical analyses were conducted with the statistical freeware program RStudio (R Core Team 2019) using the R package *geomorph* (Adams et al. 2019). Therefore, a classifier containing all specimens and categories used for this study was compiled in a "comma separated value" (CSV) format.

# 5. Results

# 5.1. Exploratory analysis of the raw data

During comparison of all digitized landmarks, no individual mark appeared to be above the upper quartile (Fig. 6). This shows that no outliers were produced due to an inaccurate digitizing of landmarks or higher disparity from the rest of the group. The maximum deviation from the mean shape (Fig. 7) occurs in *Chiloscyllium punctatum*, which is placed in the upper quartile (Fig. 6). The slightest deviation from the mean is displayed in *Scyliorhinus canicula* (Fig. 6).

All Specimens



Figure 6. Overview of all specimens displayed and listed following their Procrustes Distance from the mean shape. The distance to the median (continuous blue line) and the upper quartile (dashed line at the top) condense the total distance from the mean shape. Displayed names are picture names and therefore irrelevant for this figure.



Figure 7. Mean shape of all 5 specimens of *Heptranchias perlo* (left) and one female example specimen of *H. perlo* from the sample pool used in this study (right). Representing the mean for all species. Scale bar = 5 cm.

# 5.2. Shape

The shape of each specimen, using two-dimensional landmark coordinates multiplied by their scale factor, is shown in Figure 8. The coordinate values reach from 9.759 to 1236.704 (Tab. 2).



Figure 8. Plot of each specimen using the landmark coordinates as a reference before aligning them with Generalized Procrustes Analysis.

Table 2. Main values for landmark coordinates displayed in Fig. 4

| Min.  | 1 <sup>st</sup> Qu. | Median  | Mean    | 3 <sup>rd</sup> Qu. | Max.      |  |
|-------|---------------------|---------|---------|---------------------|-----------|--|
| 9.759 | 72.172              | 138.483 | 251.773 | 316.336             | 1.236.704 |  |

# 5.3. Generalized Procrustes Analysis

After the Generalized Procrustes Analysis, all shapes were superimposed, scaled to a unit-centroid size and rotated until the coordinates are aligned as near as possible to the equivalent points (Fig. 9).



Figure 9. Aligned and superimposed coordinates of all specimens after Generalized Procrustes Analysis (GPA). The landmarks of each specimen are displayed in grey and the mean shape is shown with black connected points.

#### 5.4. General shape variations described by principle components

The PCA is used to find specific patterns in a dataset whereby similarities and differences within the dataset can be revealed to explain existing variances. In this study, the first 10 PCs explain more than 99% of the overall variation (Tab. 3). PC1 describes in the positive scores a more rounded terminal upper lobe. The curvature expands downwards to the subterminal notch. The lower lobe has a more triangular shape with a more evenly connected upper and lower postventral margin. The shape in the negative scores is characterized by a more downwardly directed and curved dorsal lobe, which ends in an acute angled posterior tip. The preventral- and lower postventral margin form a hook-shaped anterior ventral lobe that extends to the subterminal notch and ceases in a more angled terminal ventral lobe. A fiercely elongated and thin dorsal lobe is described by PC2 in the positive scores which leads to an extremely sharp angled posterior tip. The preventral and lower postventral margin show a smaller, hook shaped anterior lower lobe. The upper postventral margin is more elongated and the terminal ventral lobe smaller. PC2 describes a more rounded dorsal and terminal lower lobe in the negative scores. The anterior ventral lobe is shorter, the lower postventral margin smaller and the subterminal notch is more distinct (Fig. 10).

|      | Standard  | Proportion of | Cumulative |
|------|-----------|---------------|------------|
|      | deviation | Variance      | Proportion |
| PC1  | 0.1546    | 0.4279        | 0.4279     |
| PC2  | 0.1227    | 0.2695        | 0.6974     |
| PC3  | 0.0917    | 0.1505        | 0.8479     |
| PC4  | 0.06248   | 0.06986       | 0.91777    |
| PC5  | 0.04260   | 0.03247       | 0.95025    |
| PC6  | 0.03123   | 0.01746       | 0.96771    |
| PC7  | 0.02225   | 0.100886      | 0.97657    |
| PC8  | 0.02079   | 0.00774       | 0.98430    |
| PC9  | 0.01702   | 0.00519       | 0.98949    |
| PC10 | 0.01241   | 0.00276       | 0.99225    |

Table 3. Standard deviation, proportion of variance and cumulative proportion explained by the first 10 Principle Components.



Figure 10. Principal Component Analysis (PCA) displaying pre- and postnatal specimens (points) within each genus (convex hulls) and deformation extrema for PC1 and PC2. There is no salience regarding the distribution of pre- and postnatal specimens. Maximum and minimum deformation for all shapes (black) superimposed with the average shape (grey). A = minimum deformation PC1, B = maximum deformation PC1, C = minimum deformation PC2, D = maximum deformation PC2. For PC1 the minimum deformation happens to be in *Carcharodon carcharias* whereas the maximum deformation appears in *Chlamydoselachus anguineus*. *Scyliorhinus canicula* displays the minimum deformation and *Alopias vulpinus* the maximum deformation for PC2.

#### 5.5. Shapes of individuals

The shapes of each species were averaged and superimposed with the mean shape for better comparison (Fig. 11, Tab. 1). *Alopias vulpinus* is characterized by an extremely elongated and downwardly bent dorsal lobe, which ends in an acute posterior tip. The ventral lobe contains a comparably small anterior ventral lobe, which is accompanied by an extended upper postventral margin, ending in the subterminal notch and a small terminal lobe.

The dorsal lobe of the sandtiger shark, *Carcharias taurus* runs horizontally with a slightly downwards bending terminal end. The ventral lobe consists of a smaller, hook-shaped anterior lobe with a short lower postventral margin and a distinct, angular shaped terminal lobe.

The white shark, *Carcharodon carcharias* possesses a very high, round and downwardly directed dorsal lobe. The anterior ventral lobe is hook- shaped with a posteriorly pointing ventral tip. The lower and upper postventral margins are curved, leading to an angular shaped terminal lobe. The upper fin origin is located further anterior than the lower one. The terminal upper lobe is rounded and connects with an angled ventral terminal lobe. A posterior notch is not clearly visible and the preventral margins seems to be evenly connected to the lower and upper posteroventral margins, forming one united anterior ventral lobe form together a circular shaped posterior fin. Due to the absence of a clearly visible posterior notch, the lower and upper postventral margins seem to connect evenly and form a triangular shaped anterior ventral lobe.

An elongated and slightly bent dorsal lobe can be seen in *Galeocerdo cuvier*. The anterior ventral lobe is hook-shaped and the ventral tip points to the posterior end. A prolate upper postventral margin leads to a shallow recessed subterminal notch. A comparable short subterminal margin forms together with an extended terminal margin a wide angled ventral terminal lobe. The dorsal lobe is elongated, slightly bent and horizontally directed. The anterior ventral lobe is comparably small and pointing downwards. A short lower postventral margin connects with an elongated upper postventral margin. The subterminal and terminal margins form an orthogonal and pronounced ventral terminal lobe.

The mako shark, *Isurus oxyrhinchus* possesses a lunate shaped caudal fin. The dorsal lobe is slightly bent and pointing downwards. A proportional large anterior ventral lobe, directed downwards, is connected through a shallow recessed subterminal notch with a small ventral terminal lobe.

The dorsal lobe of the mackerel shark, *Lamna nasus* is slightly bent and oriented downwards. The ventral lobe is, considering it is a heterocercal fin, large, pointing downwards and leads to a distinct ventral terminal lobe with an extended terminal margin.

A slightly bent and downwardly directed dorsal lobe can be found in the small tooth tiger, *Odontaspis ferox*. A small anterior ventral lobe, pointing downwards, leads to a well distinct, angled ventral terminal lobe.

The catshark, *Scyliorhinus canicula* shows a more horizontal oriented dorsal lobe with a rounded terminal part. Due to the absence of a clearly visible posterior notch, the lower and upper postventral margins seem to connect evenly and form a triangular shaped anterior ventral lobe. A clearly distinct, angular-shaped ventral terminal lobe is present.

The dorsal lobe of the caudal fin in the whitetip reef shark, *Triaenodon obesus* is slightly bent and pointing downwards. The anterior ventral lobe is slender and shows a sharp angle at the ventral tip. A posterior notch is clearly discernible. The subterminal margin is comparably long and therefore a distinct ventral terminal lobe is extant.

Members of the requiem shark genus, *Carcharhinus* display a curved dorsal lobe, which becomes rounded down at the end. The anterior ventral lobe is broad with a round ventral tip. A posterior notch is present. A long subterminal margin creates a distinct ventral terminal lobe.



Figure 11. Plot: PCA with convex hulls around each specimen belonging to the same genus: Scyliorhinus , Carcharhinus , Triaenodon , Galeocerdo Chiloscyllium Chlamydose Chus , Carcharodon , Alopias *eptranch* , Odontaspis Carcharias . Fin illustrations: average shape of each genus (coloured) , Lamna , Isurus superimposed with the mean shape (grey). The colours of the averaged shapes correspond to

#### those of the genera used in the plot. 5.6. Shape variations between groups

The Principal Component Analyses for orders, families, genera, ecomorphotypes and sexes are displayed in Figure 12. The main percentage of shape variance described through PCA is 42.6% for PC1 and 27.2% for PC2. PC3 explains 15% and PC4 ca. 7% of the variation (Tab. 3). Orders significantly differ from each other (p = 0.001) and explain 36% of the overall variation (Tab. 4). The shape variation among the orders displays a large overlap between the orders (Fig. 12). Hexanchiformes, represented by *C. anguineus* and *H. perlo*, are described by PC2 exclusively and by PC1 predominantly, with positive scores. The caudal fin of these sharks is characterized by a short anterior ventral and a comparably long, horizontally oriented dorsal lobe. Carcharhiniform sharks predominantly comprise a curved and downwardly directed dorsal lobe and a distinct anterior and terminal ventral lobe. The Lamniformes, including *A. vulpinus*, *L. nasus*, *I. oxyrhinchus*, *C. carcharias*, *C.* 

*taurus* and *O. ferox*, are highly diverse in terms of caudal fin shape and show, primarily, an elongated, curved dorsal lobe, a clearly distinct anterior ventral lobe and a distinct, angular ventral terminal lobe. The only representative of the Orectolobiformes in this study is *C. punctatum* that is characterized as described above (see section 'Shapes of individuals').



Figure 12. Principal Component Analysis (PCA); convex hulls around specimens belonging to the same order and percentage of variance being explained by PC1 and PC2

|            | Df | SS     | MS       | Rsq     | F      | Z      | Pr(>SS) |
|------------|----|--------|----------|---------|--------|--------|---------|
| Log(size)  | 1  | 0.7146 | 0.71459  | 0.17764 | 15.337 | 38.871 | 0.001   |
| Residuals  | 71 | 33.082 | 0.04659  | 0.82236 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Orders     | 3  | 14.471 | 0.48237  | 0.35973 | 12.923 | 53.007 | 0.001   |
| Residuals  | 69 | 25.756 | 0.03733  | 0.64027 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Families   | 7  | 29.807 | 0.42581  | 0.74096 | 26.56  | 74.308 | 0.001   |
| Residuals  | 65 | 10.421 | 0.01603  | 0.25904 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Genera     | 12 | 34.386 | 0.286549 | 0.85479 | 29.432 | 80.269 | 0.001   |
| Residuals  | 60 | 0.5842 | 0.009736 | 0.14521 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Species    | 13 | 34.527 | 0.265594 | 0.8583  | 27.49  | 81.103 | 0.001   |
| Residuals  | 59 | 0.57   | 0.009661 | 0.1417  |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Eco        | 8  | 30.889 | 0.38612  | 0.76786 | 26.462 | 75.566 | 0.001   |
| Residuals  | 64 | 0.9338 | 0.01459  | 0.23214 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Sex        | 2  | 0.2173 | 0.108664 | 0.05402 | 19.988 | 14.796 | 0.064   |
| Residuals  | 70 | 38.054 | 0.054363 | 0.94598 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |
| Orders     | 3  | 14.471 | 0.48237  | 0.35973 | 49.26  | 53.007 | 0.001   |
| Eco        | 6  | 16.885 | 0.28141  | 0.41973 | 29.126 | 64.728 | 0.001   |
| Orders:Eco | 2  | 0.2978 | 0.14890  | 0.07403 | 15.412 | 43.441 | 0.001   |
| Residuals  | 61 | 0.5894 | 0.00966  | 0.14651 |        |        |         |
| Total      | 72 | 40.227 |          |         |        |        |         |

Table 4. Procrustes ANOVA for 73 sharks. Significance is highlighted with bold values.

# 5.7. Shape variations between families

The families show significant differences (p = 0.001) and explain 74% of the aggregated variation (Tab. 4). It is discernable that Hemiscylliidae, Carcharinidae and Lamnidae are overlapping whereas residual families form separated clusters (Fig. 13). Due to the outstandingly distinct dorsal lobe, described by PC2 in the highest positive scores, the Alopiidae form a clearly separated cluster. A clear separation occurs between Hexanchidae and Chlamydoselachidae, which belong to the Hexanchiformes. Chlamydoselachidae is described by PC1 in the higher positive scores, which depicts a more rounded and circular-shaped terminal fin. Compared to hexanchids, chlamydoselachids show a more triangular-shaped anterior ventral lobe without a clearly visible postventral notch. Scyliorhinids are separated from the remaining carcharhiniform groups. They are described by PC1 only in the positive and by PC2 only in the negative scores and show a rounded terminal fin and a triangular-shaped anterior ventral lobe. Carcharhinids, described solely by PC1 in the negative scores, possess a postventral notch and therefore, show a clearly distinct anterior ventral lobe and a typically heterocercal, longer dorsal lobe. Lamnid

caudal fin shapes occupy a wider area of morphospaces. They are primarily described by PC1 and PC2 in the negative scores and depict a distinct anterior and an angular terminal ventral lobe. Odontaspidids appear to be quite centred in the plot having a postventral notch, which forms a small anterior ventral lobe and a distinct, angular-shaped terminal lobe.



Figure 13. Principal Component Analysis (PCA) with convex hulls around specimens belonging to the same family and percentage of variance being explained by PC1 and PC2.

#### 5.7.1. Shape variations between genera

A stronger separation is detectable on genus level, which provides more detailed information. Genera vary significantly (p = 0.001) and determine 85% of the total variation (Tab. 4). Overlaps only occur between *Chiloscyllium, Carcharodon, Carcharhinus* and *Triaenodon* (Fig. 14). As described above, *Alopias, Chlamydoselachus, Heptranchias* and *Scyliorhinus* form separated clusters. *Lamna* and *Isurus* occupy the central portion of the morphospace and in close distance due to the similar shape. Both show a proportionally large anterior ventral lobe, which leads to a lunate shaped fin. *Galeocerdo* forms a separated cluster and is described by PC1 solely in the negative scores and by PC2 solely in the positive scores. The PC scores mirror the elongated dorsal lobe and a distinct anterior and terminal ventral lobe. The caudal fin of *Carcharias* resembles that of *Heptranchias* in shape and therefore, they are closely located in morphospace occupation. Both possess a

small, acute-angled anterior ventral lobe, a distinct, angular terminal ventral lobe and an elongated dorsal lobe. The only specimen of *Odontaspis* available for this study is occupying the most central position among all specimens in the plot. It has a distinct anterior ventral and an angular terminal ventral lobe. The caudal fin shape of *Carcharodon* is occupying a rather large morphospace area. Overall, the caudal fin displays a hook-shaped, posteriorly oriented anterior ventral lobe and a downwardly oriented dorsal lobe. *Triaenodon* and *Carcharhinus* show an overall similar caudal fin shape. Both show a distinct, thin, hook-shaped anterior ventral lobe and a distinct, angled terminal ventral lobe. The anterior ventral lobe appears to be slenderer in *Triaenodon*.



Figure 14. Principal Component Analysis (PCA) with convex hulls around specimens belonging to the same genus and percentage of variance being explained by PC1 and PC2.

#### 5.7.2. Shape variation between ecomorphotypes

Ecomorphotypes differ significantly from each other (p = 0.001) and feature nearly 77% of the comprehensive variation (Tab. 4). Due to a pairwise comparison of orders with their related ecomorphotypes, it appears that non-significant differences occurred between carcharhiniforms with a "Eurytrophic Littoral" ecomorphotype and hexanchiforms with an "Unknown" ecomorphotype (p = 0.216) and between Carcharhiniforms possessing a "Mesotrophic Littoral" ecomorphotype and lamniforms with an "Eurytrophic Littoral" ecomorphotype and

The analysis reveals an overlap between specimens possessing an ETL, LBL, MTL and MP ecomorphotype. However, the overlap between MP and ETL is caused by the position of *C. longimanus* (Fig. 15). *Alopias vulpinus and C. longimanus* share a MP ecomorphotype but show different fin shapes. The ETL ecomorphotype is represented by prenatal *G. cuvier* and *C. carcharias* and both show, at this ontogenetic stage, a similar fin shape. Both have a clearly distinct, hook-shaped anterior ventral, a distinct, angular terminal ventral and an extended dorsal lobe.

*Chlamydoselachus anguineus* represents the AB ecomorphotype and is characterized by an overall rounded and dorsally elongated fin shape and forms a separated cluster. *Scyliorhinus canicula* is the only representative of the MBL ecomorphotype and shows quite a high distribution in the plot. The younger individuals of *S. canicula* appear to predominately be described by PC2 in the higher negative scores.

The TP ecomorphotype forms a separated cluster as well but edges with the MBL ecomorphotype in one location. The TP ecomorphotype is represented by *I. oxyrhinchus* and *L. nasus* with both having a lunate shaped caudal fin with a distinct terminal ventral lobe.

The MTL ecomorphotype, comprising *C. taurus*, *T. obesus* and *C. melanopterus*, occupy a large morphospace area but share similar shape features such as a small but distinct anterior ventral lobe, a clearly defined, right-angled terminal ventral lobe and a longer dorsal lobe. *Chiloscyllium punctatum*, as representing the LBL ecomorphotype, is partly overlapping with the ETL ecomorphotype but only with the shape of *C. carcharias*. The MB ecomorphotype, depicted by *O. ferox* with one specimen, is located close to the centre of the plot and near to *C. melanopterus*. Currently, there is no ecomorphotype assigned to *H. perlo*, which forms a separated cluster and is primarily described by PC1 in the low negative scores and by PC2 solely in the positive scores.



Figure 15. Principal Component Analysis (PCA) with convex hulls around specimens belonging to the same ecomorphotype and percentage of variance being explained by PC1 and PC2.

Table 5. Pairwise comparison of four orders with their associated ecomorphotypes. Pairwise P- values between means are emphasized in blue and Pairwise distances between means are highlighted in orange. P- values higher than 0.05 displayed bold. Carch = Carcharhiniformes; Hex = Hexanchiformes; Lam = Lamniformes; Orec = Orectolobiformes; ETL = Eurytrophic Littoral; MBL = Mesobenthic Littoral; MTL = Mesotrophic Littoral; AB = Anguillobathic; MAP = Macropelagic; TP = Tachypelagic; LBL = Leptobenthic Littoral; UN = Unknown

|           | Carch ETL | Carch MBL | Carch MTL | Hex AB    | Hex UN    | Lam ETL   | Lam MAP   | Lam TP    | Orec LBL |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|----------|
| Carch ETL | 1         | 0.001     | 0.031     | 0.001     | 0.216     | 0.039     | 0.001     | 0.001     | 0.001    |
| Carch MBL | 0.3460067 | 1         | 0.001     | 0.002     | 0.005     | 0.001     | 0.001     | 0.001     | 0.001    |
| Carch MTL | 0.2217350 | 0.2879632 | 1         | 0.001     | 0.045     | 0.306     | 0.001     | 0.028     | 0.004    |
| Hex AB    | 0.3845295 | 0.2353095 | 0.4152878 | 1         | 0.023     | 0.001     | 0.001     | 0.001     | 0.001    |
| Hex UN    | 0.1687910 | 0.2335264 | 0.2435237 | 0.2410450 | 1         | 0.010     | 0.033     | 0.005     | 0.001    |
| Lam ETL   | 0.2336552 | 0.3631587 | 0.1613992 | 0.4729886 | 0.2906489 | 1         | 0.001     | 0.001     | 0.006    |
| Lam MAP   | 0.3035122 | 0.4520532 | 0.4644641 | 0.3374639 | 0.2698519 | 0.4591639 | 1         | 0.001     | 0.001    |
| Lam TP    | 0.3982055 | 0.3534505 | 0.2873379 | 0.3795871 | 0.3370053 | 0.3526846 | 0.4978353 | 1         | 0.001    |
| Orec LBL  | 0.3082377 | 0.4309124 | 0.3163112 | 0.5384203 | 0.3505183 | 0.2965270 | 0.5420483 | 0.5204336 | 1        |

#### 5.7.3. Shape variation between sexes

There is no discernible difference in caudal fin morphology between sexes and both, females and males are almost entirely identical (Fig. 16). The result, received from the Analysis of Variance (ANOVA), also depicts no significant difference between the sexes (p = 0.064) (Tab. 4). There is no salience regarding the distribution of pre- and postnatal specimens at the margins.



Figure 16. Principal Component Analysis (PCA) with convex hulls around specimens belonging to the same sex and percentage of variance being explained by PC1 and PC2.

#### 6. Discussion

The correlation between body form, locomotion and ecological niche in vertebrates has been discussed continuously up to now (e.g., Lindsey 1978; Webb 1984; 1988; Thomson and Simanek 1997; Langerhans and Reznick 2010; Sternes and Shimada 2020). It is evident that the caudal fin is an important structure in locomotion and thus in behaviour. To be able to draw connections between the shape of the caudal fin and the ecomorphotype, it is necessary to reconsider the classification of ecomorphotypes. In this study, nine of eighteen ecomorphotypes, defined by Martin (2003), were used to find relationships. These ecomorphotypes are based on a classification proposed by Compagno (1990) for cartilaginous fishes in general but was optimized solely for extant sharks.

#### 6.1. Shape of species

The grouping of species clearly depicts that almost every species forms its own cluster. Exceptions are *C. carcharias*, *I. oxyrinchus* and *C. melanopterus*. This indicates the occurrence of multiple caudal fin designs in sharks and therefore contradicts the study of Sternes and Shimada (2020) who postulated the presence of only one caudal fin design in the body plan of sharks. It can be assumed that *C. melanopterus* shows a strong variation because the specimens are preserved in alcohol which caused a strong deformation (Fruciano et al. 2020). It is more likely that *C. melanopterus* has a similar caudal fin shape as has *O. ferox*. Adding more specimens of *C. melanopterus* could provide clearer results in terms of shape variation. *Isurus oxyrinchus* is represented with two specimens, which show intraspecific differences in caudal fin shape. Variation due to deformation is plausible but it can be assumed that differences in caudal fin shape could also be related to sexual dimorphism, although, no significant difference between sexes, comparing all species, was detected here. It therefore would be interesting to compare a larger sample of *Isurus oxyrinchus* to identify possible sexual dimorphisms.

Considering *S. canicula*, it is visible that they are arranged in a defined cluster. Specimens appearing further away from the centre of the cluster (Fig. 14), reaching the higher negative PC2 values, are embryos, which display a higher variation in caudal fin shape compared to adults.

### 6.2. Ontogeny and ecomorphotypes

Ontogenetic changes in feeding patterns are well established for the white shark, *C. carcharias* (Klimley 1985; McCosker 1985; Estrada et al. 2006). As a juvenile, the white shark is piscivorous but a dietary shift from primarily fish to marine mammals occurs during ontogeny (Klimley 1985; McCosker 1985). Not only teeth are changing but also the caudal fin shape shows distinct ontogenetic variations. Especially during the embryonic stage, the caudal fin changes extremely from a very heterocercal fin shape at early stages, to an almost complete lunate-shaped caudal fin at birth (Tomita et al. 2018). After birth, juveniles already show a tendency to form a lunate shaped caudal fin but still possess a clearly discernable heterocercal fin. This can be related to a change in feeding strategies (Tricas and McCosker 1984). In my study, only embryos of *C. carcharias* were used, which differ a lot in caudal fin morphology. This would explain the wide distribution of *C. carcharias* in the scatterplot.

The classification of ecomorphotypes is valid for all species and ontogenetic changes in morphology, habitat or diet, however, were not taken into consideration. As a juvenile, *C. carcharias* stays close to the coast and prefers shallow and warmer waters throughout the whole day whereas adults dive deeper and remain at colder waters during the day and sojourn close to the shore during night. Adults also feature a higher activity in terms of greater distance movements (Hoyos-Padilla et al. 2016). Therefore, I suggest to not assigning a species to a specific ecomorphotype but to differentiate between ontogenetic stages within the corresponding species if they show variations in habitat use or prey preferences while growing up. In this case, I would reassign juvenile great white sharks to the MTL ecomorphotype rather than an ETL ecomorphotype.

Further ontogenetic examinations were limited due to the small number of individuals.

#### 6.3. Same ecomorphotype but different shape

It is obvious that species still share the same ecomorphotype even if the shape of the caudal fin differs extremely (e.g. *A. vulpinus* and *C. longimanus*). This can be explained with the fact that both share the same type of habitat. Both species are pelagic, slow swimming species with the ability of rapid burst manoeuvres (Martin 2003; Madigan et al. 2015). It is possible that differences in caudal fin shape occur because of different hunting strategies. *Alopias vulpinus* is assumed to stun its prey through a swipe with its dorsal lobe of the caudal fin and primarily hunts small schooling fishes (Aalbers et al. 2010), whereas *C. longimanus* is a generalist and feeds on teleosts and cephalopods as well as rays, sea turtles, crustaceans, marine mammals and even garbage (Compagno et al. 2005; Bonfil et al. 2008). *Alopias vulpinus* has a very extreme and unique caudal fin shape due to its fiercely elongated dorsal lobe but another reason for the large distance in morphospace between *A. vulpinus* and *C. longimanus* could be that, in this study, only a single specimen of *C. longimanus* was compared to *A. vulpinus* and that the specimen is conserved in alcohol, which could have led to a deformation (Fruciano et al. 2020).

#### 6.4. Ecomorphotype vs. Orders

The pairwise comparison of orders with the associated ecomorphotypes, reveals significant differences among almost every group. Only two comparisons do not

differ significantly. On the one side, it is the relationship between lamniforms with an eurytrophic littoral and carcharhiniforms with a mesotrophic littoral ecomorphotype (p = 0.306) and on the other side it is the relationship between carcharhiniforms with an eurytrophic littoral and hexanchiforms with an unknown ecomorphotype (p = 0.216). The lamniforms with an ETL ecomorphotype are represented by *C. carcharias* and carcharhiniforms with an MTL ecomorphotype consist of *C. melanopterus* and *T. obesus*. The average caudal fin shape of *Carcharodon*, *Carcharhinus* and *Triaenodon* resemble each other with a comparatively low pairwise distance value but possess a different ecomorphotype.

#### 6.5. Unknown ecomorphotype

Comparing *H. perlo*, which represents the hexanchiforms with an unknown ecomorphotype, with *G. cuvier*, the only species in this study within the carcharhiniforms displaying an ETL ecomorphotype, it can be ascertained that there is no significant difference between their caudal fin shapes. Although these species occupy different habitats, similarities in hunting strategies can be recognized. As juveniles, both species mainly hunt for small teleosts whereas the size and diversity of prey increase with age and body size (Lowe et al. 1996; Braccini 2008). A reason for similarities in hunting strategies could be, that it is easier to catch smaller and slower swimming prey while being smaller (younger). This would also explain their similar caudal fin shapes since both species hunt for comparable prey as juveniles. Considering the resemblance of caudal fin shape as well as preferred prey, it can be assumed that both species share a similar ecomorphotype, at least when young. For this study, only embryos of both species were available and therefore, further studies including additional specimens of different ontogenetic stages are necessary to confirm this hypothesis.

#### 6.6. Differences between sexes

There is no significant difference between shape and sexes among all specimens. The sex explains only 5% of the overall variation in caudal fin shape.

# 7. Conclusion

The caudal fin shape of sharks is very diverse, depending on the habitat they live in and their strategy of hunting. The clustering and separation of different species in the plot is an indication for the presence of multiple caudal fin shapes and contradicts the assumption of one caudal fin design in sharks. Special adaptations for an optimal foraging are necessary for a perfect incorporation in a specific environment. The allocation of shark species, in particular ecomorphotypes can be difficult and inaccurate because some species show differences in morphology and behaviour Therefore, ecomorphotypes seemingly throughout their ontogeny. change throughout their ontogeny and need to be taken into account when assigning a specific type to a species by indicating to which ontogenetic stage it refers. Until now, ecomorphotypes are valid for a specific species but ontogenetic changes within that species were not taken into account. Hence, it is important to include ontogenetic changes and consider assigning more than one ecomorphotype to a species in future studies. Furthermore, it can be assumed, that intraspecific variations can be related to sexual dimorphism in some species (e.g. *I. oxyrinchus*). A larger sample of *I. oxyrinchus* is necessary to identify possible sexual dimorphism. Nevertheless, a connection between caudal fin shape and ecomorphotype is clearly present but needs to be further investigated and specified. Therefore, the inclusion of more specimens from different taxa and from different ontogenetic stages is required to better understand the relationships between ecomorphotype and morphological features such as caudal fin or body shape, among others.

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#### 9. Zusammenfassung

Haie leben schon seit mehr als 200 Millionen Jahren auf diesem Planeten und mussten sich im Laufe der Zeit immer wieder an die Änderungen ihrer Umgebung anpassen. Um zu verstehen, wie solch faszinierende Wesen es geschafft haben bis heute an der Spitze ihrer Nahrungskette zu bleiben, sind sie für Forscher von großem Interesse. Das Zusammenhang zwischen Anpassungen, seien sie morphologisch oder verhaltensbezogen, und der sich ständig ändernden Umgebung ist ein wichtiger Bestandteil wissenschaftlicher Hai-Studien. Ein Grund für ihre lange Existenz ist ein perfekt angepasster Körperplan mit hoch entwickelten Sinnen. Ein sehr markantes Merkmal von Haien ist die heterozerkale Schwanzflossenform, bei der sich die Wirbelsäule in den verlängerten dorsalen Lobus erstreckt. Um die effizienteste Fortbewegung in ihrem Habitat zu erreichen, benutzen Haie ihre Schwanzflosse als Hauptantriebsquelle. Diese kann sehr unterschiedlich geformt sein und daher ist es von enormer Bedeutung zu verstehen, warum unterschiedliche Formen der Schwanzflosse auftreten und wie stark der Einfluss von Faktoren, wie der Umgebung, auf die Morphologie der Schwanzflosse ist.

Ziel dieser Arbeit ist es, die Beziehungen zwischen der Schwanzflossenform verschiedener rezenter Haiarten und den damit verbundenen Ökomorphotypen quantitative zu bewerten. Durch geometric morphometrics Analysen war es möglich, Verbindungen zwischen der Schwanzflossenform und dem Ökomorphotypen aufzuzeigen, obwohl aufgrund einer geringen Anzahl von Individuen unterschiedliche Einschränkungen (z.B. Ontogenese) auftraten. Es konnten klare Trennungen und Clusterbildungen der einzelnen Arten aufgezeigt warden, was zu der Annahme führt, dass mehr als ein Schwanflossendesign bei rezenten Haien vorhanden ist. Darüber hinaus ist die Einteilung von Ökomorphotypen für die gesamte Art gültig wobei ontogenetische Veränderungen dabei nicht miteinbezogen werde. Daher ist es wichtig zu berücksichtigen, dass sich Ökomorphotypen scheinbar während der gesamten Ontogenese ändern, wenn ein bestimmter Ökomorphotyp einer Art zugewiesen wird. Zusätzlich kann vermutet werden, dass intraspezifische Variationen der Schwanzflossenform bei einigen Arten [z.B. der kurzflossen Mako (*Isurus Oxyrinchus*)] durch sexuellen Dimorphismus ausgelöst werden.