Hammer it out: shifts in habitat are associated with changes in fin and body shape in the scalloped hammerhead (*Sphyrna lewini*)

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Major shifts in habitat often occur during life history and can have significant impacts on the morphology and function of an animal; however, little is known about how such ecological changes influence the locomotor system of large aquatic vertebrates. Scalloped hammerheads (*Sphyrna lewini*) are large sharks found in warm temperate and tropical waters. Smaller scalloped hammerheads are generally found in near-shore habitats, but as they grow larger, individuals spend time in deep-water, pelagic habitats. We measured a number of morphological traits of scalloped hammerheads, ranging from 32 to 130 cm, to determine whether there are allometric changes in morphology in association with this shift in habitat. We found that head morphology, caudal fin area and lateral span scaled with negative allometry, whereas the lengths of their pectoral, dorsal and caudal fins, and their pectoral and caudal fin aspect ratios, scaled with positive allometry. Furthermore, the largest shark in our dataset exhibited an optimal body fineness ratio for locomotor efficiency. This suggests that the changes in ecology have profound influences on the functional morphology of scalloped hammerheads. We discuss how these drastic morphological changes relate to potential changes in scalloped hammerhead swimming function and performance.

ADDITIONAL KEYWORDS: ecology – form – function – morphology – shark.

INTRODUCTION

As organisms grow larger in body size, they sometimes experience changes in ecology and their life history (Calder, 1984; Schmidt-Nielsen; 1984; LaBarbera, 1989). Such shifts in habitat can strongly impact animal function (Koehl, 1996; Higham *et al.*, 2021) by imparting new functional demands. This, in turn, can cause changes in morphology in order to execute these functions effectively (Wainwright & Reilly, 1994; Wainwright *et al.*, 2002). For fishes, changes in habitat and diet not only cause changes in body, head and jaw morphology, but also impact growth patterns through ontogeny (Svanbäck & Eklöv, 2002; Ward-Campbell & Beamish, 2005; Fu *et al.*, 2016). Among larger fishes, such as sharks, these types of changes can lead not only to a shift in trophic level from a mesopredator to an apex predator, but also to shifts in marine habitats (Tricas, 1984; Grubbs, 2010; Fu *et al.*, 2016).

Changes in habitat in aquatic organisms are well documented, although most of the focus has been on freshwater fishes. For example, juvenile bluegill sunfish (*Lepomis macrochirus*) are often restricted to highly vegetated littoral habitats, whereas adults tend to be in open water (Mittelbach & Osenberg, 1993). This, in turn, influences both predation and feeding biology. Bluegill sunfish shift to feeding on zooplankton in open water as they increase in size, which has a cascade of changes in selective pressures. In largemouth bass (*Micropterus salmoides*), a closely related species, a change in diet from littoral invertebrates to fish typically occurs during the first year (Olson, 1996). Likewise, marine Eurasian perch (*Perca fluviatilis*), which occupy two different habitats, exhibit differences in head, body and fin shapes, which affect the diets of the two groups (Svanbäck & Eklöv, 2002). Specifically, perch in the littoral habitat have deeper bodies, larger heads and longer fins compared with those in the pelagic habitat. Another classic example is the three-spined stickleback (*Gasterosteus aculeatus*), which exhibit drastic morphological

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changes when shifting habitats, with pelvic spines emerging when they move from a vegetative habitat to an open-water habitat (Sillet & Foster, 2000; Spoljaric & Reimchen, 2011). Nevertheless, given the magnitude of marine habitats, tracking and understanding how changes in ecology and performance are linked is challenging.

Scalloped hammerheads [*Sphyrna lewini* (Griffith & Smith, 1834)] are large apex predators with a worldwide distribution, but they are generally found in warm temperate and tropical seas (Roff *et al.*, 2016; Wells *et al.*, 2018; Ebert *et al.*, 2021). Scalloped hammerheads are seasonally migratory and are often observed in large schools (Klimley *et al.*, 1988; Ebert *et al.*, 2021). Interestingly, smaller scalloped hammerheads [30–90 cm total length (TL)] are generally found in near-shore, shallow-water habitats, whereas larger individuals (> 90 cm TL) are generally found in deep-water, pelagic habitats (Clarke, 1971; Klimley, 1987; Duncan & Hollland, 2006; Hoyos-Padilla *et al.*, 2014; Ebert *et al.*, 2021; Estupiñán-Montaño *et al.*, 2021). Additionally, these different habitats present different prey types, where smaller scalloped hammerheads tend to feed on benthic prey, such as isopods, octopods and scorpion fish, compared with the larger pelagic individuals that consume larger and more evasive prey, such as deep-water squid and pelagic crabs (Gallagher & Klimley, 2018). Furthermore, the ability to forage on deep-water squid requires frequent vertical migrations, which has been well documented in scalloped hammerheads (Klimley, 1993; Bessudo *et al.*, 2012; Ketchum *et al.*, 2014).

Given the shift in both habitat and feeding requirements, changes to the locomotor system are likely to be important. Specifically, the caudal fin is responsible for generating thrust in sharks (Ferry & Lauder, 1996), and it has been proposed that caudal fin shape is crucial for the ability to capture certain types of prey. For example, lamnid sharks (e.g. mako sharks, porbeagle, salmon and white sharks) have a stiff, symmetrical, lunate caudal fin (Thomson & Simanek, 1977; Lingham-Soliar, 2005b), which is thought be essential for catching evasive prey, such as seals, swordfish and tuna (Stillwell & Kohler, 1982; Tricas, 1984; Ebert *et al.*, 2021). In contrast, most sharks have a highly asymmetrical caudal fin, which is likely to be used for swimming slowly and for rapid manoeuvres for prey capture (Thomson & Simanek, 1977; Webb, 1984; Maia *et al.*, 2012).

Sharks exhibit a wide range of pectoral fin shapes, and this can probably be attributed to differences in ecology (Maia *et al.*, 2012). However, a recent analysis of a limited number of species suggests this might not be the case, because external morphology was not significantly different among sharks with different ecology (Hoffmann *et al.*, 2020). Despite the lack of difference in external morphology, there were considerable differences based on internal morphology, such as the amount of skeletal support, between benthic and pelagic sharks (Hoffmann *et al.*, 2020). Nevertheless, benthic sharks have shorter and more rounded pectoral fins (Wilga & Lauder, 2000, 2001; Maia *et al.*, 2012), whereas the pectoral fins of truly pelagic sharks are long and narrow, most probably for improved lift-to-drag ratio (Vogel, 1994; Alexander, 2003; Maia *et al.*, 2012). Functionally, pectoral fins are responsible for vertical movements in the water column (Maia *et al.*, 2012). In contrast, benthic sharks routinely use their pectoral fins for station-holding (Wilga & Lauder, 2001). This division highlights the importance of considering pectoral fin morphology and function when considering ecological differences among sharks and other fishes.

Considering the drastic differences in the ecology of shallow- and deep-water habitats, it is likely that different morphological traits of scalloped hammerheads might be favoured in each habitat. Do the pectoral fins of scalloped hammerheads exhibit allometric growth, given the reliance on vertical migrations for foraging in deep-water habitats? Does this also lead to a more symmetrical caudal fin and/or changes to other parts of the body? To answer these questions, we measured 50 museum specimens of *S. lewini* (over a range of body sizes from 32 to 130 cm TL), gathering 13 morphometric linear measurements and five area measurements for each specimen. We followed the methods of Irschick & Hammerschlag (2014) and Higham *et al.* (2018), because these measurements specifically address lengths and areas of the head, pectoral, dorsal and caudal fins, and overall 'girth' of the shark body. From these data, we aimed to address whether there are any morphological differences present in *S. lewini* and discuss the implications of these results in relation to the life history of this shark.

MATERIAL AND METHODS

SAMPLES

We examined specimens of *S. lewini* from the following four institutions: California Academy of Sciences (CAS), San Francisco, CA, USA; Field Museum of Natural History (FMNH), Chicago, IL, USA; Natural History Museum of Los Angeles County (LACM), Los Angeles, CA, USA; and Scripps Institution of Oceanography (SIO), University of California, San Diego, CA, USA. The Supporting Information (Table S1) lists all samples of *S. lewini* examined in this study.

In our study, we used preserved museum specimens, unlike others, who have used live sharks (Irschick & Hammerschlag, 2014; Fu *et al.*, 2016; Irschick *et al.*, 2017). That said, several studies (Reiss & Bonnan, 2010; Anhelt *et al.*, 2020) have examined ontogenetic change using museum specimens. Thus, despite the potential for shrinkage of specimens, we are confident that we captured true changes in form, because all the specimens were measured in the same conditions. Additionally, we acknowledge that scalloped hammerheads are long-lived species, and adults can reach TLs of 400 cm (Ebert *et al.*, 2021). However, given that there are significant logistical challenges in housing and maintaining such large specimens, we are constrained to museum specimens of a maximum TL of 130 cm. Furthermore, scalloped hammerheads are listed as critically endangered by the International Union for Conservation of Nature, and they are highly sensitive to non-lethal sampling (Gallagher *et al.*, 2014); thus, any capture and measurement of larger live individuals might have a negative impact on the population. Lastly, it is known that scalloped hammerheads become highly migratory and are found in offshore habitats at ~100 cm TL (Klimley, 1987; Hoyos-Padilla *et al.*, 2014). Thus, we are confident about the use of museum specimens in our study.

MORPHOLOGICAL MEASUREMENTS

To document morphological differences in *S. lewini*, we followed the approach of Irschick & Hammerschlag (2014) and Irschick *et al.* (2017) and quantified the following morphological measurements (Fig. 1) using a standard metric tape measure (accurate to 1 mm): (1) cephalofoil or head size (EE), the distance between the inner part of the eyes; (2) lateral span (LS), the distance (i.e. around the curved dorsal side of the shark) from the insertion point of the anterior edge of one pectoral fin to the insertion point of the other pectoral fin; (3) frontal span (FS), the distance (i.e. around the curved dorsal side of the shark) from the insertion point of the anterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin; (4) proximal span (PS), the distance spanning (i.e. around the curved dorsal side of the shark) from the insertion point of the posterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin; (5) caudal keel circumference (CKC), the total circumference at the base of the tail as measured at the caudal keel; (6) pectoral fin length (PFL), the linear distance from the insertion of the pectoral fin at the distal edge to the tip of the pectoral fin when fully extended; (7) dorsal fin 1 (DF1), the distance from the anterior insertion point of the dorsal fin to the tip of the dorsal fin; (8) dorsal fin 2 (DF2), the distance from the tip of the dorsal fin to the posterior insertion point of the dorsal fin; (9) dorsal fin 3 (DF3), the distance horizontally across the shark body between the anterior and posterior insertion points of the dorsal fin; (10) caudal fin 1 (CF1), the linear distance from the dorsal insertion of the caudal fin to the dorsal tip of the caudal fin; (11) caudal fin 2 (CF2), the linear distance from the dorsal tip of the caudal fin to the ventral tip of the bottom part of the caudal fin; (12) caudal fin 3 (CF3), the the linear distance from the bottom anterior edge of the caudal fin to the bottom posterior edge of the caudal fin; and (13) precaudal length (PCL), the linear distance from the tip of the snout to the precaudal pit, which is a longitudinal notch on the caudal peduncle directly on the anterior side of the caudal fin.

In addition to linear measurements, we obtained digital images of the head, first dorsal fin, pectoral fin and caudal fin. We used IMAGEJ to calculate the area of the various fins and head (Fig. 1). Subsequently, we calculated the aspect ratio (AR) of each fin, defined as L^2/S, where L and S are the length and area of the fin, respectively.

Furthermore, to investigate body shape diversity attributable to changes in habitat, we measured the fineness ratio (Porter *et al.*, 2009, 2011). The fineness ratio is associated with a minimum drag coefficient and can be defined as L/d, where L is the body length and d the profile height. In this case, we used PCL as L and FS as d. We calculated the fineness ratio of each individual and regressed these values against PCL to tease out any trends through ontogeny.

SCALING AND STATISTICAL ANALYSIS

We determined the scaling relationships using the power-law function $y = mx^b$, where in this case, x = PCL (body length in centimetres), y is the variable of interest, and b is the scaling exponent. All data were $\log_{10}$-transformed before analyses. Linear and area measurements have expected isometric slopes of 1.0 and 2.0, respectively. To compare the scaling exponents with those expected from isometry, the 95% confidence interval of the slope was first calculated. If the expected value fell within the confidence interval, the relationship was considered isometric, but an exponent below or above the expected value was considered negative or positive allometry, respectively. The significance of each regression was assessed using a cut-off of $P < 0.05$.

RESULTS

All morphological variables were significantly correlated with body length. An overwhelming
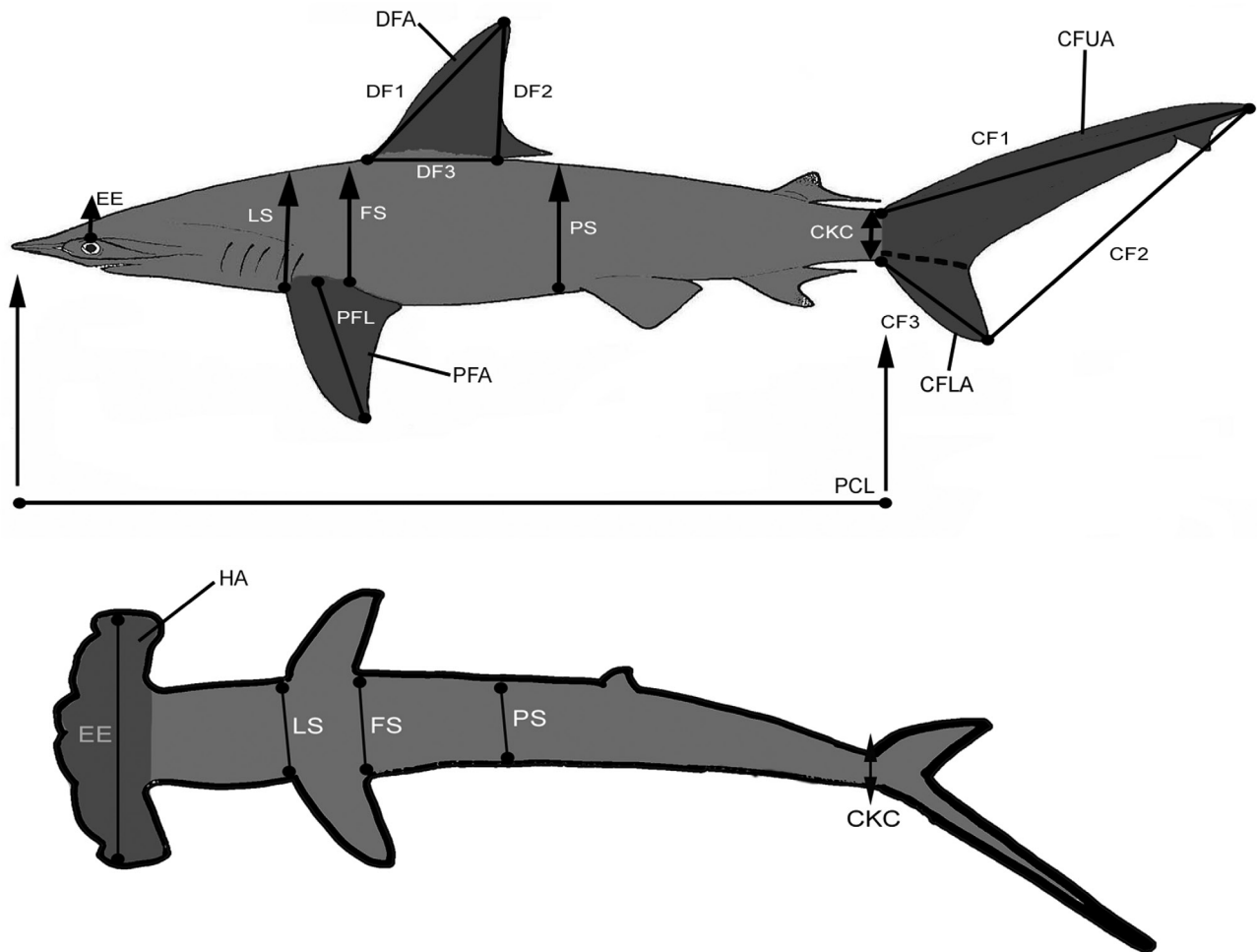
Figure 1. Diagram of scalloped hammerhead with morphological variables measured in this study (for more detailed descriptions of each measurement, see the Material and Methods section). The top image is a lateral view and the bottom image a ventral view. Abbreviations: CFA, caudal fin area; CF1, caudal fin 1, the linear distance from the dorsal insertion of the caudal fin to the dorsal tip of the caudal fin; CF2, caudal fin 2, the linear distance from the dorsal tip of the caudal fin to the ventral tip of the bottom part of the caudal fin; CF3, caudal fin 3, the linear distance from the bottom anterior edge of the caudal fin to the bottom posterior edge of the caudal fin; CKC, caudal keel circumference, total circumference at the base of the tail as measured at the caudal keel; DFA, dorsal fin area; DF1, dorsal fin 1, distance from the anterior insertion point of the dorsal fin to the tip of the dorsal fin; DF2, dorsal fin 2, distance from the tip of the dorsal fin to the posterior insertion point of the dorsal fin; DF3, dorsal fin 3, distance horizontally across the body of the shark between the anterior and posterior insertion points of the dorsal fin; EE, distance between the inner part of the eyes; FS, frontal span, the distance (i.e. around the curved dorsal side of the shark) from the insertion point of the anterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin; LS, lateral span, the distance (i.e. around the curved dorsal side of the shark) from the insertion point of the anterior edge of one pectoral fin to the insertion point of the other pectoral fin; PCL, precaudal length; PFA, pectoral fin area; PFL, pectoral fin length, the linear distance from the insertion of the pectoral fin at the distal edge to the tip of the pectoral fin when fully extended; PS, proximal span, the distance spanning (i.e. around the curved dorsal side of the shark) from the insertion point of the posterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin.

majority of the variables had R^2 values > 0.75 (Table 1). Eye to eye, frontal span, proximal span, caudal keel circumference, dorsal fin 1, dorsal fin 3, caudal fin 1, caudal fin 2 and dorsal fin area all scaled with isometry. Lateral span, caudal fin upper area, caudal fin lower area, caudal fin area, and head area all scaled with negative allometry. Pectoral fin length, dorsal fin 2, caudal fin 3, pectoral fin area, pectoral fin aspect ratio, and caudal fin aspect ratio exhibited positive allometry (Figs 2–4; Table 1). For body fineness ratio,

Table 1. Scaling relationships for the variables examined in this study. NA=Not applicable.

Variable	N	R^2	P-value	Expected slope	Observed slope	SE of slope	Lower confidence interval	Upper confidence interval	Scaling
Eye to eye	49	0.96	< 0.001	1.00	0.929	0.024	0.857	1.001	Isometric
Head area	28	0.93	< 0.001	2.00	1.746	0.09	1.533	1.901	Negative
Lateral span	50	0.81	< 0.001	1.00	0.794	0.059	0.676	0.913	Negative
Frontal span	50	0.79	< 0.001	1.00	0.875	0.068	0.739	1.012	Isometric
Proximal span	50	0.76	< 0.001	1.00	0.874	0.076	0.721	1.026	Isometric
Caudal keel circumference	50	0.92	< 0.001	1.00	0.888	0.039	0.769	1.006	Isometric
Pectoral fin length	50	0.93	< 0.001	1.00	1.172	0.064	1.078	1.267	Positive
Pectoral fin area	28	0.94	< 0.001	2.00	2.171	0.01	1.987	2.355	Positive
Pectoral fin aspect ratio	28	0.24	< 0.01	0	0.328	0.11	0.144	0.488	NA
Dorsal fin 1	48	0.94	< 0.001	1.00	0.968	0.035	0.866	1.070	Isometric
Dorsal fin 2	48	0.90	< 0.001	1.00	1.287	0.058	1.127	1.453	Positive
Dorsal fin 3	50	0.92	< 0.001	1.00	1.015	0.038	0.922	1.108	Isometric
Dorsal fin area	27	0.91	< 0.001	2.00	2.039	0.013	1.769	2.258	Isometric
Dorsal fin aspect ratio	27	0.009	0.645	0	−0.052	0.112	−0.28	0.208	NA
Caudal fin 1	50	0.98	< 0.001	1.00	1.01	0.018	0.946	1.055	Isometric
Caudal fin 2	50	0.96	< 0.001	1.00	1.09	0.033	0.989	1.192	Isometric
Caudal fin 3	50	0.91	< 0.001	1.00	1.203	0.033	1.034	1.373	Positive
Caudal fin upper area	29	0.92	< 0.001	2.00	1.725	0.012	1.549	1.892	Negative
Caudal fin lower area	29	0.86	< 0.001	2.00	1.87	0.015	1.655	2.176	Negative
Caudal fin total area	29	0.91	< 0.001	2.00	1.752	0.019	1.594	1.936	Negative
Caudal fin aspect ratio	29	0.29	< 0.001	0	0.45	0.114	0.200	0.623	NA

values ranged from 1.9 to 4.8. The slope observed was 0.013, with an R^2 value of 0.2 ($P < 0.05$). The largest value of 4.8 belonged to the largest individual in our study. All other individuals ranged from 1.9 to 2.7.

DISCUSSION

Scalloped hammerhead sharks undergo significant morphological changes in shape that are likely to be associated with major shifts in habitat and ecology. Pectoral fin length and area, pectoral fin and caudal fin aspect ratio, dorsal fin height and the length of the caudal fin lower lobe exhibited positive allometry. These changes point towards an increase in swimming efficiency through reductions in drag, which are indicative of sustained swimming activity. These results suggest that the drastic ecological changes that scalloped hammerheads experience are accompanied by changes in functional demand, leading to allometric patterns of growth.

CAUDAL FIN SHAPE IN DIFFERENT HABITATS

The use of the caudal fin for propulsion is widespread throughout the evolution of fishes (Webb, 1982).

Other fishes can also use other fins for propulsion, whereas the caudal fin is exclusively responsible for generating thrust in most sharks (Gray, 1933; Alexander, 1965; Ferry & Lauder, 1996). However, the shape of the caudal fin varies considerably among species (Thomson, 1976; Sternes & Shimada, 2020), and this is most likely to be related to differences in function (Maia *et al.*, 2012). Sharks with more asymmetric caudal fins tend to swim more slowly but exhibit high manoeuvrability (Maia *et al.*, 2012). Sharks with a more symmetrical caudal fin are faster and often perform long-distance migrations (Lingham-Soliar, 2005a, b; Maia *et al.*, 2012). The caudal fin of scalloped hammerheads in our study transitions from a more asymmetric shape in smaller individuals to a more symmetrical shape in larger, more pelagic individuals (Fig. 3; Table 1). This is likely to be directly associated with the changes in ecology, because smaller scalloped hammerheads live in shallow-water habitats, with limited home ranges. As individuals grow larger and near 100 cm TL, they move into the pelagic realm to perform long-distance migrations (Duncan & Hollland, 2006; Hoyos-Padilla *et al.*, 2014; Ebert *et al.*, 2021; Estupiñán-Montaño *et al.*, 2021). For example, one individual scalloped hammerhead (95 cm TL) travelled 3350 km in a
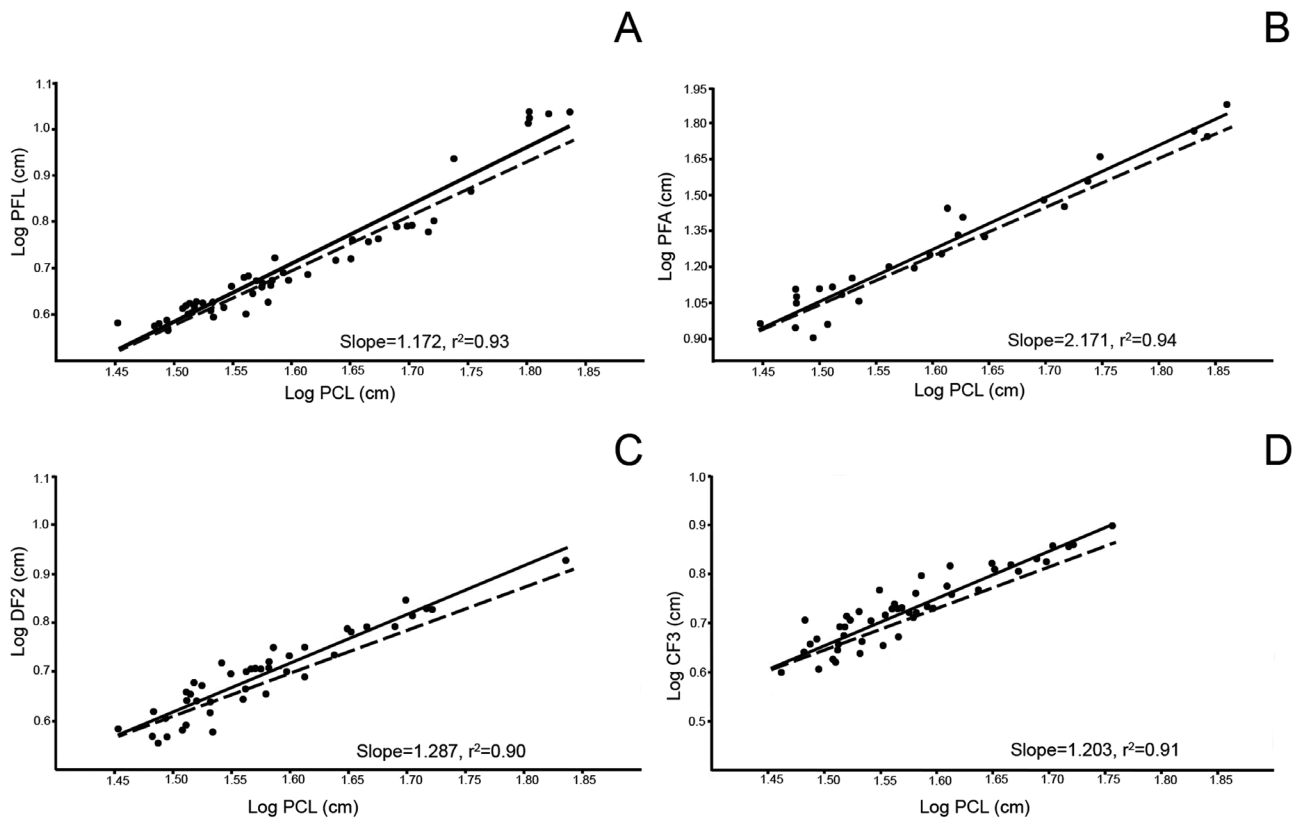
Figure 2. Scaling relationships between $\log_{10}$-transformed values of precaudal length (PCL) and: A, pectoral fin length (PFL); B, pectoral fin area (PFA); C, dorsal fin 2 (DF2, i.e. overall height in length of dorsal fin; and D, caudal fin 3 (CF3, i.e. length of lower lobe). All relationships show positive allometry. Each point on the graphs represents an individual. For how each variable was measured, see Figure 1. The dashed line represents the expected slope under isometry, and the continuous line represents the regression using our data.

10.5-month period (Hoyos-Padilla *et al.*, 2014). Thus, a more symmetrical caudal fin with a high aspect ratio would greatly improve the cost of transport for such distances.

PECTORAL FIN SHAPE IN DIFFERENT HABITATS

The aspect ratio of the pectoral fin in scalloped hammerheads increases with body size (Fig. 4; Table 1). For benthic sharks, the pectoral fins do not generate lift but are crucial in vertical movements in the water column and, most probably, manoeuvrability (Wilga & Lauder, 2000, 2001). In contrast, it has been suggested that the higher aspect ratio pectoral fins in pelagic sharks generate lift (Lingham-Soliar, 2005a). However, quantitative data supporting this are lacking. Nevertheless, in general, high aspect ratio fins can achieve greater lift and therefore lower the cost of transport (Vogel, 1994; Alexander, 2003; Biewener & Patek, 2018), which is likely to be necessary for long-distance migrations.

The pectoral fins of scalloped hammerheads appear to follow a similar pattern of benthic and pelagic fishes (Wainwright *et al.*, 2002; Fish & Lauder, 2017). Smaller scalloped hammerheads live a more benthic lifestyle, which corresponds to low aspect ratio pectoral fins, whereas middle-sized and larger scalloped hammerheads are more pelagic and exhibit high aspect ratio pectoral fins. The low aspect ratio pectoral fins probably aid in turning to capture benthic prey, whereas the high aspect ratio pectoral fins provide more lift for the pelagic habitat and long-distance migrations of adults (Fontanella *et al.*, 2013; Martinez *et al.*, 2016). Furthermore, in the pelagic habitat, scalloped hammerheads perform vertical migrations to feed on deep-water prey (Klimley, 1993; Jorgensen *et al.*, 2009; Bessudo *et al.*, 2012; Ketchum *et al.*, 2014). Given that pectoral fins are crucial in vertical movements (Maia *et al.*, 2012), the high aspect ratio pectoral fins of adult scalloped hammerheads are important for lowering the cost of transport.
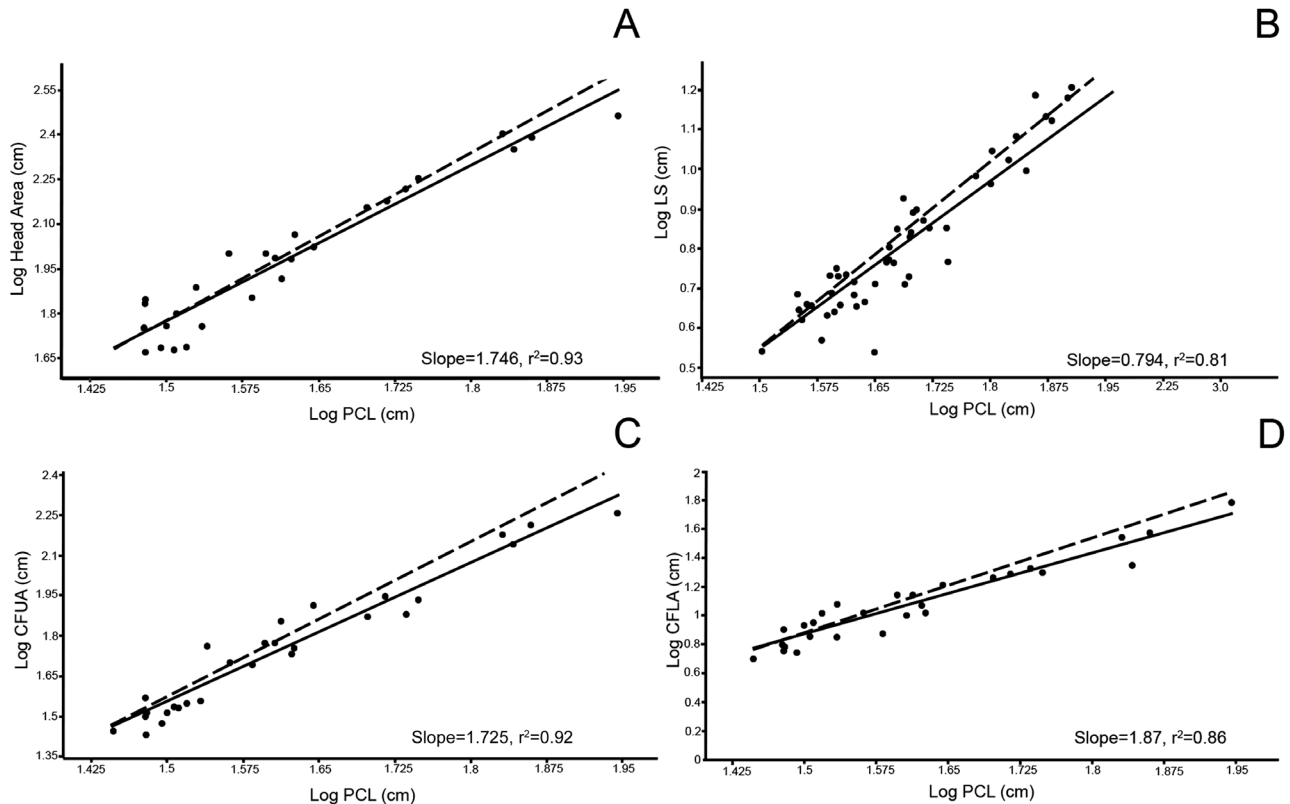
Figure 3. Scaling relationships between $\log_{10}$-transformed values of precaudal length (PCL) and: A, head area; B, lateral span (LS); C, caudal fin upper area (CFUA); and D, caudal fin lower area (CFLA). All relationships show negative allometry. Each point on the graphs represents an individual. For how each variable was measured, see Figure 1. The dashed line represents the expected slope under isometry, and the continuous line represents the regression using our data.

DORSAL FIN SHAPE IN DIFFERENT HABITATS

The dorsal fin height of scalloped hammerheads scales with positive allometry (Fig. 2; Table 1). This is highly intriguing, because hammerheads generally possess very tall dorsal fins relative to other sharks (Ebert *et al.*, 2021). Depending on the location along the body axis, the dorsal fin of sharks aids in either stability or thrust production (Lingham-Soliar, 2005c; Maia & Wilga, 2013, 2016). Scalloped hammerheads possess more anteriorly located dorsal fins, which therefore aid in stability. However, scalloped hammerheads are known to perform a peculiar swimming behaviour by swimming on a rolled angle of 90°, otherwise known as side swimming (Royer *et al.*, 2020). Hydrodynamic models on similarly shaped great hammerheads [*Sphyrna mokarran* (Rüppell, 1837)], which also swim on their side at times, indicate that this swimming behaviour might reduce drag or, more importantly, the cost of transport compared with normal, upright swimming (Payne *et al.*, 2016). The large dorsal fin of the hammerhead is hypothesized to generate thrust during rolled swimming. Therefore, the additional

thrust from the dorsal fin reduces the cost of transport from the posterior portion of the body (Payne *et al.*, 2016). Interestingly, all the scalloped hammerheads that swam on their side ranged from subadult to adult (Royer *et al.*, 2020). This suggests that the positive allometry of the dorsal fin facilitates this swimming behaviour in larger individuals. Thus, the larger dorsal fin might benefit larger pelagic scalloped hammerheads when they perform long-distance migrations (Duncan & Hollland, 2006; Hoyos-Padilla *et al.*, 2014; Ebert *et al.*, 2021; Estupiñán-Montaño *et al.*, 2021).

HEAD AND BODY SHAPE IN DIFFERENT HABITATS

The primary function of the hammerhead cephalofoil remains unclear. Previous hypotheses suggested that the cephalofoil increases sensory capabilities, prey capture performance, manoeuvrability and lift (Thomson & Simanek, 1977; Strong *et al.*, 1990; Nakaya, 1995; Kajiura *et al.*, 2003; Mara *et al.*, 2015; Gaylord *et al.*, 2020). However, a recent study indicated that the cephalofoil increases manoeuvrability, but
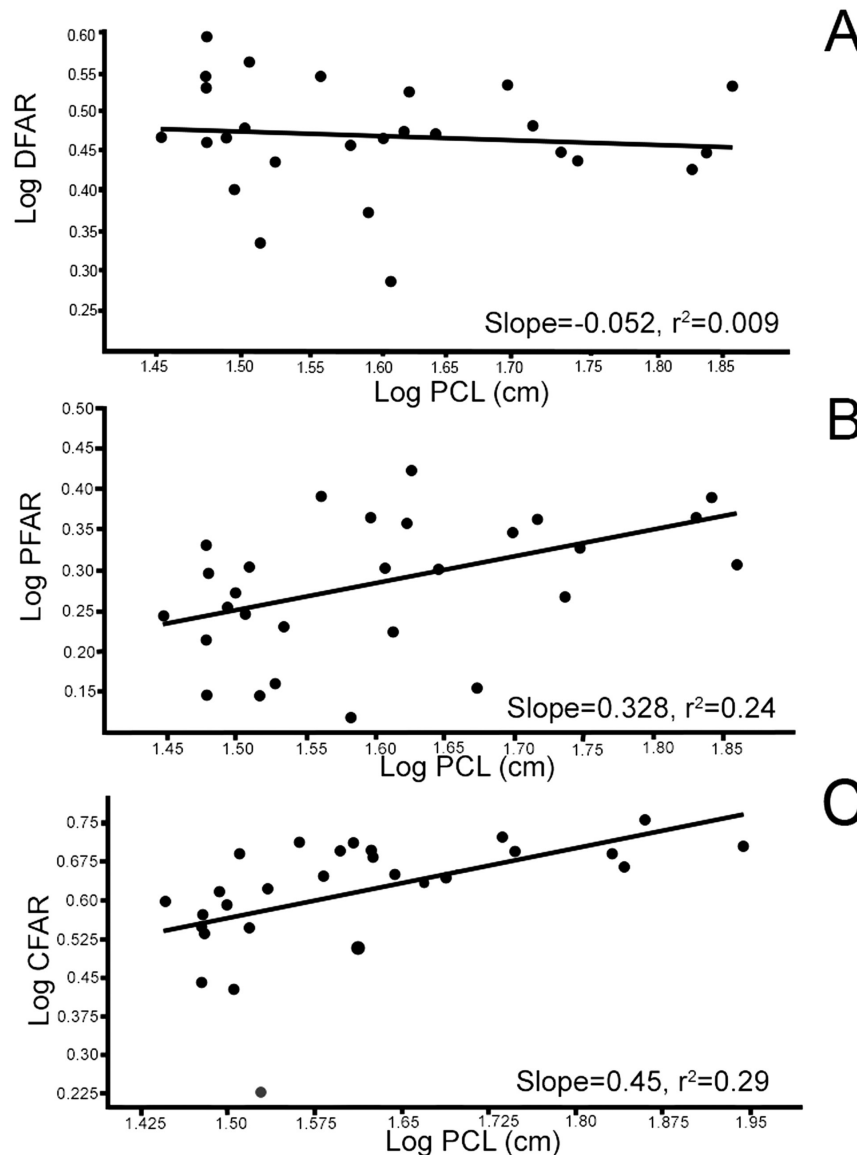
Figure 4. Scaling relationships between log$_{10}$-transformed values of precaudal length (PCL) and: A, dorsal fin aspect ratio (DFAR); B, pectoral fin aspect ratio (PFAR); and C, caudal fin aspect ratio (CFAR). Both PFAR and CFAR were positively related to body size, whereas DFAR was negatively associated with body size. Each point on the graphs represents an individual. The continuous line represents the regression using our data.

not lift, when comparing the hammerhead cephalofoil with non-hammerhead sharks (Gaylord *et al.*, 2020). This enhanced manoeuvrability would also aid in prey capture performance (Gaylord *et al.*, 2020). Previous studies (Kajiura, 2001; Cavalcanti, 2004) and our study (Fig. 3; Table 1) indicate that the scalloped hammerhead undergoes a change in head shape as individuals grow larger. Specifically, the head area is negatively allometric (Fig. 3; Table 1), and the head itself becomes compressed on the anterior–posterior axis and expands laterally (Cavalcanti, 2004). If the cephalofoil already increases manoeuvrability,

does the change in head shape alter its overall performance? Given that scalloped hammerheads shift their diets from slower benthic prey to quicker pelagic prey (Gallagher & Klimley, 2018; Estupiñán-Montaño *et al.*, 2021), it is possible that this change in head shape might increase manoeuvrability to aid in the capture of more evasive prey. Alternatively, changes in head shape might be attributable to sexual maturity, which is a pattern observed in bonnethead sharks (Kajiura *et al.*, 2005). Future studies should investigate sexual dimorphism in scalloped hammerheads.

The scalloped hammerhead undergoes changes in its body shape with increase in body size. Specifically, the lateral span is negatively allometric (Fig 3; Table 1). The posterior portions of the body (i.e. frontal and proximal spans) remain isometric (Fig. 3; Table 1). Previous work found that large scalloped hammerheads had much narrower trunks compared with the anterior body region (Hoffmann *et al.*, 2017). Combined, these indicate that scalloped hammerheads are becoming more streamlined as a result of shifts in functional demands. For any swimming animal, a streamlined body will reduce drag, which will, in turn, lower the cost of transport (Vogel, 1994; Alexander, 2003; Biewener & Patek, 2018). This is especially important for animals that perform long-distance migrations, including scalloped hammerheads (Hoyos-Padilla *et al.*, 2014).

The optimal fineness ratio to minimize drag is 4.5 (Von Mises, 1945; Schlichting, 1979). Previous studies have investigated how this varies among species of both fishes and whales (Ahlborn *et al.*, 2009; Porter *et al.*, 2009, 2011; Walker *et al.*, 2013). Our values ranged from 1.9 to 4.8, with the largest scalloped hammerhead exhibiting a value of 4.8. Although there was considerable variation in fineness ratio among smaller individuals, it is striking that the highest value was observed in the largest individual and is very close to the optimum of 4.5. This suggests that, at a certain length, the scalloped hammerhead might achieve the optimal fineness ratio to minimize drag for long-distance migrations. Additional data might reveal whether this pattern is consistent among larger scalloped hammerheads.

FUTURE DIRECTIONS

Future studies should quantify the hydrodynamic changes associated with changes in fin and body shape through ontogeny (Long *et al.*, 2010). This will identify the functional consequences of ecomorphological changes that are evident in scalloped hammerheads. Also, more direct measurements of swimming, both in nurseries and in the open ocean, are needed. What speeds do they adopt? How often are manoeuvres executed? What are the costs of transport? Additionally, future studies can potentially investigate the full ontogenetic change in scalloped hammerheads. Furthermore, investigations of possible sexual dimorphism would be useful to make comparisons with patterns seen in other hammerheads (Kajiura *et al.*, 2005).

ACKNOWLEDGEMENTS

DATA AVAILABILITY

The dataset collected during the present study is available in the Supporting Information.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. List of all specimens examined in this study.