Great hammerhead sharks swim on their side to reduce transport costs

Nicholas L. Payne¹,²,*, Gil Iosilevskii³,*, Adam Barnett⁴, Chris Fischer⁵, Rachel T. Graham⁶, Adrian C. Gleiss⁷ & Yuuki Y. Watanabe¹,⁸

Animals exhibit various physiological and behavioural strategies for minimizing travel costs. Fins of aquatic animals play key roles in efficient travel and, for sharks, the functions of dorsal and pectoral fins are considered well divided: the former assists propulsion and generates lateral hydrodynamic forces during turns and the latter generates vertical forces that offset sharks’ negative buoyancy. Here we show that great hammerhead sharks drastically reconfigure the function of these structures, using an exaggerated dorsal fin to generate lift by swimming rolled on their side. Tagged wild sharks spend up to 90% of time swimming at roll angles between 50° and 75°, and hydrodynamic modelling shows that doing so reduces drag—and in turn, the cost of transport—by around 10% compared with traditional upright swimming. Employment of such a strongly selected feature for such a unique purpose raises interesting questions about evolutionary pathways to hydrodynamic adaptations, and our perception of form and function.

¹ National Institute of Polar Research, Tachikawa 190-8518, Japan. ² Department of Life Sciences, University of Roehampton, London SW15 4JD, UK. ³ Faculty of Aerospace Engineering, Technion, Haifa 32000, Israel. ⁴ College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia. ⁵ Ocearch, Park City, Utah 84068, USA. ⁶ MarAlliance, San Pedro, PO Box 283, Belize. ⁷ School of Veterinary and Life Sciences, Centre for Fish and Fisheries Research, Murdoch University, Murdoch, Western Australia 6150, Australia. ⁸ SOKENDAI (The Graduate University for Advanced Studies), Tachikawa 190-8518, Japan. * These authors contributed equally to this work. Correspondence and requests for materials should be addressed to N.P. (email: nick.payne@roehampton.ac.uk).
like other mobile aquatic animals, sharks have evolved a set of morphological traits that facilitate efficient travel in water; a streamlined body shape and assortment of fins are conspicuous examples. Almost all sharks are negatively buoyant, and use their pectoral fins to generate vertical hydrodynamic force that counters gravity. In contrast, the dorsal fin assists in propulsion and turning through the generation of lateral forces. The prevailing view is that the roles of the pectoral and dorsal fins in sharks are clearly divided in this way.

By measuring body posture of great hammerhead sharks *Sphyrna mokarran* swimming in the wild, we show that this species regularly swims rolled on their side. Because this implies a reconfiguration of the function of their fins during locomotion, we conducted a series of modelling experiments to explore the hydrodynamic consequences of this unusual rolled swimming. Our results show that *S. mokarran* generate lift with their dorsal fin by swimming on their side, and that doing so is a more efficient way to travel than is swimming upright. These findings question the paradigm of the division of labour in shark fins, and highlight that efficient travel is a strong selective agent in driving the evolution of animals.

**Results**

**Observations of rolled swimming.** We tagged two wild great hammerhead sharks with accelerometer loggers that allow the estimation of body pitch and roll angles as they swim freely in their environment (see Methods, Supplementary Fig. 1 and Supplementary Notes 1 and 2); one at the Great Barrier Reef, Australia, and another off the Mesoamerican Reef, Belize. Unexpectedly, the shark tagged at the Great Barrier Reef spent ~90% of the 18 h deployment period (which was from early evening till late morning) swimming on its side at absolute roll angles between 50° and 75° (Fig. 1a,b and Supplementary Fig. 2). The shark exhibited this rolling behaviour whether it was ascending, descending or swimming at constant depth, and alternated between rolling to the left and right sides approximately every 5–10 min. An onboard video camera visually confirmed the observations (Supplementary Movie 1). The shark tagged off Belize exhibited a very similar pattern; it was recorded spending approximately every 5–10 min. An onboard video camera visually confirmed the observations (Supplementary Movie 1). The shark tagged off Belize exhibited a very similar pattern; it was recorded spending approximately every 5–10 min.
Energy savings. Energy expenditure per distance swam (commonly termed the ‘cost of transport’, COT) is defined as:

\[
C = \frac{P_0}{v} + \frac{D}{\eta m}
\]  

(5)

\(P_0\) being the standard metabolic rate, \(\eta\) the hydrodynamic propulsion efficiency and \(\eta_m\) the chemomechanical efficiency of the muscles. Given body mass (which we estimated for our Great Barrier Reef shark; see Supplementary Note 4) and temperature (which we measured with our accelerometer loggers), one can estimate the standard metabolic rate\(^{10}\) and, assuming the values for \(\eta, \eta_m\) and \(B/G\) published elsewhere\(^{1,11}\), the COT follows the data shown in Fig. 3b by equations (1)–(3) and (5). An expanded explanation of calculations for drag, metabolic rate and COT is detailed in Supplementary Notes 4 and 5 and Supplementary Figs 8–12. With all the relevant data listed in Supplementary Table 2, the COT estimates are shown in Fig. 3c,d. Again, displaying remarkable congruence with what the sharks actually do in the wild, COT is minimized at the same roll and pitch angles (between 50° and 70°, and 6° and 8°, respectively), and at

Figure 1 | Rolled swimming in great hammerhead sharks *Sphyrna mokarran*. For a to d, roll and pitch angles were measured by an electronic tag attached to a 295 cm shark’s dorsal fin, and monitored as it swam freely at the Great Barrier Reef, northern Australia. (a,c) A typical hour-long time series for that animal. (b,d) Probability distributions of roll and pitch angles based on the last 15 h of the monitoring period for the Great Barrier Reef shark. Images in e,f were taken with a fin-mounted video camera attached to another wild *S. mokarran* (~ 350 cm) as it swam rolled to the left and right (respectively) at South Bimini Island, the Bahamas, at absolute roll angles of ~60° (see Supplementary Movie 2 for examples of this and other wild *S. mokarran* swimming rolled).

Figure 2 | Reconfiguration of lifting surfaces in great hammerhead sharks *S. mokarran*. By swimming rolled, a shark changes the surfaces that generate lift, \(L\), from the pair of pectoral fins at zero roll angle (left) to the combination of the pectoral and dorsal fins at greater roll angles (right). For the great hammerhead, doing so increases the effective span of the lifting surfaces, \(b\). The model to the right is rolled 65°.
the same speeds (between ~0.8 and 1.0 m s⁻¹) exhibited by the wild sharks (Fig. 1 and Supplementary Figs 2 and 3). The gains are significant; ~8% less energy is used to travel a given distance when swimming rolled than when swimming upright (0.8 versus 0.86 mmol ATP per m; Fig. 3c,d).

Discussion

Like many other aquatic animals, great hammerhead sharks have evolved morphological traits that facilitate efficient travel. However, unique among species possessing a dorsal fin, great hammerheads employ a drastic reconfiguration of its traditional role in locomotion. Great hammerheads are also one of the most recently diverged of all shark species (~5 million years ago); therefore, in the context of 450 million years of chondrichthyan evolution, this solution to minimizing travel costs is relatively new. The variable efficiencies of lift generation among other negatively buoyant fish principally arises from the variable pectoral fin morphologies; the blue shark _Prionace glauca_, which has long and narrow pectoral fins, exemplifies selection of this trait. It is therefore curious that the great hammerhead shark has taken such a different route to evolving lifting surfaces.

Hammerheads possess a number of morphological innovations related to their sensory capacity and manoeuvrability: greater lateral flexure of the body and tight turning capacity appear critical to the foraging behaviour of this group that is also related to their unique cranial morphology. These hunting requirements in turn may select for enlargement of the dorsal fin to generate the required lateral forces for performing such manoeuvres.

Our work provides an interesting example of how the evolution of novel morphological characteristics for the purpose of one behaviour can result in a drastic shift in the function of existing morphology. It also further highlights that efficient travel is a strong selective agent in driving the evolution of organisms, in particular those facing substantial costs for movement, such as perpetually active aquatic animals. Understanding how animals reduce the effects of drag on their mobility is an important area of research, not just for zoologists, but also mechanical engineers striving to find biomimetic solutions for man-made designs, and even olympic swimmers trying to break world records (the ‘fish kick’ stroke, where submerged swimmers swim rolled on their side, revolutionized competitive swimming).

With most fully aquatic animals difficult to observe in nature, our work highlights bio-logging technology’s important role in revealing novel hydrodynamic adaptations that change our perception of form and function.

Methods

Accelerometer and video data collected from wild sharks. For accelerometer deployments, both sharks were captured by fishing and were fitted with tri-axial accelerometer loggers attached to the dorsal fin using established methods. The 295 cm (total length) female shark captured at the Great Barrier Reef was fitted with a Little Leonardo video camera and PD3GT logger (maximum dimensions 150 × 70 × 30 mm, 260 g in air) that recorded acceleration at 16 Hz and both swim speed, depth and temperature at 1 Hz, and it detached from the shark ~18 h after tagging. Only the last 15 h were used for analysis. The 273 cm male shark captured at the Mesoamerican Barrier Reef near Lighthouse Reef Atoll, Belize was fitted with a ‘daily-diary’ (ref. 17; maximum dimensions 130 × 50 × 35 mm, 260 g in air; Supplementary Fig. 1), which recorded tri-axial acceleration, depth and temperature at 8 Hz. The package detached from the shark 66 h following tagging.

Figure 3 | Hydrodynamics of rolled swimming in great hammerhead sharks _S. mokarran_. (a) Contours of constant lift _C_L_ and (b) drag coefficients _C_D_ for a range of pitch and roll angles, measured through wind tunnel experiments with a physical _S. mokarran_ model. (c) Contours of constant _COT_ for a 2.95 m shark for a range of roll angle and either pitch angles or (d) swimming speeds. _COT_ was estimated from wind tunnel data summarized in _b_, and by assuming values for standard metabolic rate and both chemomechanical and propulsive efficiencies (see Supplementary Notes 4). In _a_, the difference between adjacent contours is 0.2, and in _b–d_, the difference is 0.02.
Both packages were recovered using very high frequency (VHF) telemetry. Analysis and results are detailed in Supplementary Notes 1 and 2 and Supplementary Figs 2 and 3. For the three female sharks (~250, 300 and 350 cm total length) fitted with video cameras in the Bahamas (throughout January to February 2016 at South Bimini Island), each shark was approached underwater by a SCUBA diver, and a miniaturized (71 × 71 × 39 mm, 152 g in air) video camera (GoPro Hero4) was attached to the anterior edge of the dorsal fin with a double-armed clamp as the shark swam by. Video cameras automatically detached from the sharks after 3 h and the footage was examined for evidence of rolled swimming. Examples of rolled swimming in these sharks are shown in Supplementary Movie 2.

**Wind tunnel experiments.** A fifth-scale model of the shark was printed in Full-Cure720. The general drawing can be found in Supplementary Figs 5 and 6; printer-ready files are available on request. The model had replaceable fins, head and neck. All fins had NACA0015 profile. On the basis of the hypothesis that the caudal, anal and second dorsal fins are used mainly for propulsion and not for the generation of lift, the results presented herein have been measured without them. The experiments were repeated with anal and second dorsal fins attached, and the results remained qualitatively the same (Supplementary Fig. 11). The total length of the model was 640 mm, and the part of the model that went into the tunnel was 431 mm long, ending at the caudal end of the anal and second dorsal fins. Its maximal cross-section area (that was used to obtain the drag and lift coefficients) was 3,870 mm².

The experiments were conducted at the subsonic wind tunnel of the Faculty of Aerospace Engineering, Technion. The wind tunnel is of the open type, with a 1 × 1 m square test section, 3 m long. The tunnel is capable of working at 90 m s⁻¹. All experiments were conducted at 50 m s⁻¹. At this speed, the turbulence intensity is estimated at 0.2%. The Reynolds number based on the total length of the model shark (640 mm) was approximately two million. It matches the Reynolds number of a 3 m shark swimming at 0.7 m s⁻¹ in 20°C water.

The forces were measured using a six-component string balance and acquired at 5 kHz. The data were low-pass-filtered at 4 Hz, and block-averaged with 500 samples per block. The lift and side force measured during the experiment were of the order of 1 kg; the drag was of the order of 100 g. Measurement accuracy is estimated at 1 g.

**Data Availability.** The data that support the findings of this study are available from the corresponding author upon request.

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**Author contributions**

N.L.P. and Y.Y.W. conceived the study, and N.L.P. and G.I. wrote the initial draft of the manuscript, to which all authors contributed. N.L.P., Y.Y.W., A.B., K.F., R.T.G. and A.C.G. collected the field data, and G.I. conducted the wind tunnel experiments and analysis.

**Additional information**

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