Importance of the keels of boxfishes for passive stability during swimming

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Aquatic habitats are characterised by random disturbances in the flow field; therefore, during locomotion, aquatic animals will be subjected to a large number of external forces that may throw their body out of balance. Aquatic animals can actively correct these destabilising forces with fin or body movements. Furthermore, the general body proportions and/or the presence of specific structures on the body can also passively dampen disturbances. A distinction can be made between bodies that are hydrodynamically stable and hydrodynamically unstable. When a body is inherently stable it will be subject to passive course stabilisation: when it slightly deviates from its aligned position in the flow due to external factors, the body will automatically return to its equilibrium position in the flow, without active intervention. An inherently unstable body, on the other hand, would rotate even further away from its aligned position in the flow should there be no active intervention.

In boxfish, the body is completely covered by a shell of fused hexagonal bony plates, known as the carapace. This rare feature is shared by all members of the Ostraciidae family, even though the body geometry varies greatly between species. Boxfish have accurate control over manoeuvres which is essential for foraging in their spatially complex habitat such as coral reefs. In fish, propulsion is usually driven largely by undulation of the body. Since the rigidity of the carapace disallows bending of the body, boxfish depend solely on their five fins for locomotion; the body is also not streamlined. This situation is very similar to many rigid man-made aquatic vessels in which high movement efficiency is strongly pursued and thus boxfishes morphology has fuelled several studies of bio-inspired design in aquatic engineering sciences.

A general feature of the carapace of boxfish is the presence of longitudinal ridges, the keels. The keels on the carapace were hypothesised to be a critical factor for different hydrodynamic properties, namely, (H1) reduced drag for forwards swimming, (H2) generating stabilising yaw and pitch torques to help boxfish to maintain straight swimming trajectories, and (H3) providing resistance against rolling. Evidence for the drag reduction hypothesis (H1) was already found in other marine vertebrates, such as the leatherback sea turtle (Dermochelys coriacea) in which longitudinal ridges suppress separation of the boundary layer. Whether the keels of boxfish contribute to drag reduction, however, remained untested. The hypothesis that the keels contribute to stabilising rectilinear swimming by generating self-stabilising yaw and pitch torques (H2) was inferred from vortical flows and pressures measured experimentally near the keels of boxfish. However, recent studies demonstrated that the overall torque by the flow past the carapace under yaw and pitch angles of attack is not self-stabilising but rather destabilising. Considering that permanent course stabilisation would make manoeuvring energetically costly and boxfish spent a considerable part of their time manoeuvring, an unstable body may be energetically beneficial. However, whether the keels are involved with either increasing stability or increasing instability remained unstudied. Finally, the hypothesis that keels in Ostraciidae damp roll rotations (H3), corresponds to the function of keels in boats and other engineered aquatic vehicles. In these systems, keels are ubiquitous as a passive stability system to reduce the tendency to roll by increasing the hydrodynamic resistance against roll rotation.

The aim of this study was to gain more insight into the hydrodynamic function of the keels. For five boxfish species with different carapace shapes, we investigated the effect of the keels on: drag coefficients of the carapace (H1), induced moment coefficients of the carapace in a pitch or yaw angle of attack (H2), rotational drag moment coefficients and rotational added mass moment coefficients for imposed roll (H3). To do so, two sets of three-dimensional boxfish surface models were prepared: a first set of control models (obtained by laser scanning museum specimen), and a second set of “modified models” (obtained by digitally reducing the size of the keels from the control models). Hydrodynamic properties were calculated using computational fluid dynamics (CFD).

In the first type of CFD simulations, a steady water flow was simulated over a stationary boxfish carapace model at different angles of attack. The drag force (H1) was determined for the models with their rostro-caudal axis parallel with the incoming water flow. To measure the (de)stabilising pitch and yaw moments in a static setup (H2), boxfish models were placed in a flow at a slight pitch or yaw angle, respectively. This was a representation of the boxfish no longer oriented in line with its direction of motion. In the second type of CFD simulations, the resistance against roll rotation (H3) was determined by calculating the roll moment as a function of time during a short period during which we imposed a roll rotation of constant acceleration on the body of the boxfish in stagnant water. This was a mathematical approach to simulate the effect of an external torque on the fish's body. In natural situations, this could be the result of variable water currents, or of the fish’s fin forces during manoeuvring.

From the CFD output, we could calculate the drag coefficient (H1), the pitch and yaw moment coefficient (H2), and the rotational drag moment coefficient and rotational added mass moment coefficient (H3) for the control model and the modified model with reduced keels. To obtain a better understanding of the measured forces, moments and coefficients related to the presence of keels and the different body shapes, contour plots were created of the pressure experienced by the carapace surface, as well as 3D iso-surfaces of the vorticity.

This study confirmed that the boxfish body is inherently unstable for pitch and yaw rotation, although it seems unlikely that the keels play a prominent role in shaping these characteristics. No relationship could be discovered between the presence of keels and drag reduction or, passive stability, as these parameters were only very weakly affected by the presence of keels and differences being inconsistent. For all five species, the pressure patterns and 3D iso-vorticity surfaces were almost identical in the control models and the modified models. However, all species showed a strong increase in roll resistance by the presence of keels. Especially the damping of roll by drag torques increased considerably, with for some species the rotational drag moment coefficient for roll rotation being doubled, despite the reductions in keel height being relatively small. This demonstrates that the body in possession of keels will be brought out of balance less quickly. This was also reflected in the pressure plot, positive and negative high-pressure areas that counteract the roll rotation were larger in the control model than in the modified model. Our results strongly suggest that a significant part of the body's roll resistance can be attributed to the keels.

It can be stated that the objective of this study, to gain more insight into the function of the keels, was met. Some previous misunderstandings were clarified. The long-standing theory that keels cause drag reduction and enable passive stability for pitch and yaw, was proven incorrect. The roll-resistance-increase-hypothesis for keels in boxfish, which was tested for the first time, proved to be promising and was strongly supported by the obtained results. Further research is needed to capture how exactly this increased roll resistance is of use to the boxfish during certain swimming movements.