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Learning From the Fins of Ray-Finned Fish for the Propulsors of Unmanned Undersea Vehicles

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Introduction

ilitary and civilian studies have identified that two of the most significant technological obstacles to deploying unmanned undersea vehicles (UUVs) are energy and autonomy (Nicholson & Healey, 2008; Office of the Secretary of Defense, 2009). The energy and the rate it is used (power) limit the duration and distance of operations and bound the type of activity that can occur even for short periods. Autonomy defines the degree to which humans must supervise UUV operations and provides UUVs with the ability to react to external stimuli without human intervention. Among the enabling technologies that are critical for solving the challenges associated with energy and autonomy are more effective propulsors (Office of the Secretary Defense, 2009). Propulsors are required to provide increased maneuverability, stealth, and endurance for the widespread range of missions envisioned for UUVs, from long duration sensing in the open ocean to mine countermeasures in very shallow, high-energy water.

ABSTRACT

Advanced propulsors are required to help unmanned undersea vehicles (UUVs) overcome major challenges associated with energy and autonomy. The fins of rayfinned fish provide an excellent model from which to develop propulsors that can create forces efficiently and drive a wide range of behaviors, from hover to lowspeed maneuvers to high-speed travel. Although much is known about the mechanics of fins, little is known about the fin's sensorimotor systems or how fins are regulated in response to external disturbances. This information is crucial for implementing propulsive and control systems that exploit the same phenomena as the biological fins for efficiency, effectiveness, and autonomous regulation. Experiments were conducted to evaluate the in vivo response of the sunfish and its pectoral fins to vortex perturbations applied directly to the fish and to the fins. The fish and the fins responded actively to perturbations that disturbed the motion of the fish body. Surprisingly, perturbations that deformed the fins extensively did not cause a reaction from either the fins or the body. These results indicate that the response of the pectoral fins to large deformations is not reflexive and that fin motions are regulated when it is necessary to correct for disturbances to the motion of the fish. The results also demonstrate a benefit of compliance in propulsors, in that external perturbations can disturb the fins without having its impact be transferred to the fish body. Keywords: biorobotics, flapping fins, vortex pertubations, sensory-based control

Fish are important biological models from which to learn methods of propulsion that are effective and efficient over a wide range of operating conditions. Bony fish, such as the bluegill sunfish (Lepomis macrochirus) and the swordfish (Xiphias gladius), are able to hover, swim and maneuver at low speeds, manipulate the orientation of their bodies, conduct acrobatics to escape or to attack prey, and, especially for the swordfish, sustain high swimming speeds. These behaviors can be accomplished in smooth water and in high-energy flows and relate directly to the behaviors desired for UUVs. The remarkable swimming

abilities of these fish are due, in large part, to the fish having multiple, highly actuated, flexible fins that are able to create and to modulate large-magnitude forces.

A great deal is known about the mechanisms that contribute to the production of hydrodynamic forces by flapping the fins and the fish body. Forces are created through the dynamic interaction of the fins, the body, and the fluid, which results in energy being added to, or taken from, the fluid. A review of seminal work that explains the way in which marine animals control vorticity is presented in Triantafyllou et al. (2002) and Zhu et al. (2002). Numerical and experimental studies of flexible fins with two-dimensional kinematics (heaving and pitching) include, but are in no way limited to, studies of McHenry (1995), Liu and Bose (1997), Prempraneerach et al. (2003), Triantafyllou et al. (2005), Fish et al. (2006), Lauder et al. (2006), Mittal et al. (2006), Lauder and Madden (2007), and Zhu and Shoele (2008). Recent studies that considered deformable fins with complex kinematics are presented in, for example, Shoele and Zhu (2009), Dong et al. (2010), and Tangorra et al. (2010).

In contrast to our understanding of the mechanics of fins and of hydrodynamic forces, little is known about how fishes sense their interaction with the water and use sensory information to regulate the fins. Knowledge of fin sensorimotor control is critical if engineered systems are to take full advantage of the mechanisms used by fins to create forces efficiently and to react to changes in the environment.

The focus of this paper will be on the pectoral fins of sunfish and, in particular, on how and when sunfish alter the use of the pectoral fins in response to external perturbations. We begin with an overview of pectoral fin swimming in sunfish and briefly present robotic fins that produce and modulate forces like the biological fins. A series of experiments where the biological fin is perturbed during steady swimming is then presented. These experiments address the response of the fins in the context of using the fins to control and stabilize the fish body.

Ray-Finned Fish and Robots Sunfish Swimming

The ability of the sunfish to control the magnitude and direction of its pro-

pulsive forces is due to its ability to modulate the kinematics, coordination, and mechanical properties of its fins and muscular tail (Tangorra et al., 2010, 2011). Hydrodynamic forces are created through an exchange of energy between the propulsive surfaces and the surrounding fluid. As the fish moves through the water, vortices develop along the body and fins, the propulsive structures bend and store energy, and the vortices are shed into the flow along with directed jets (Triantafyllou et al., 2002; Dong et al., 2010). The complex motions that cause this exchange of energy are the result of driven motions of the fin rays and a dynamic interaction of the deformable fin surfaces with the water. The forces created by fins are, therefore, modulated through changes to the kinematics of the fin and active adjustments of fin's mechanical properties (Lauder et al., 2006; Mittal et al., 2006; Akhtar et al., 2007; Tangorra et al., 2010). The changes may be subtle, as in steady swimming where the stiffness of the fin rays is gradually increased with speed, but where the motions of the fins are approximately the same. Or the changes may be obvious, as when the fish interrupts a cyclic swimming pattern and uses a stiff, impulsive fin motion to slow the fish and turn it away from an obstacle (Gottlieb et al., 2010).

Ray-Finned Robotic Systems

Robotic fins (Figure 1) have been developed that produce motions, forces, and flows like the biological fins (Tangorra, Davidson et al., 2007; Phelan, Tangorra et al., 2010; Tangorra, Lauder et al., 2010). These fins were designed originally as physical models with which to conduct experimental studies that would have been difficult to conduct with the living fish

FIGURE 1

Biorobotic models of the sunfish pectoral fin (A) and caudal fin (B). The pectoral fin is instrumented with strain gages along the fin rays and pressure sensors along the body plate in order to model distributed sensing in the sunfish. Modified versions of the robotic pectoral and caudal fins, as well as dorsal and anal fins, are implemented on a fish robot (C). The fish robot can swim freely or be attached to a rigid mast (shown) so that forces can be measured. The grooves in the side of the fish body are used for pressure lines and ports.



(Tangorra, Phelan et al., 2011). The fins are comprised of fin rays, each with multiple actuated degrees of freedom (DOF), within a thin, flexible webbing. The geometries of the fin rays were defined so that the stiffness of the robotic fin was proportional to that of the biological fin across the fin's chord and span. The architecture of the robotic fin provides a great degree of control over the fin's motions and mechanical properties, which enables the magnitude and direction of the force produced by the fin to be easily modulated (Figure 2). Gross changes to the profile of the fin's force can be made by changing the fin's gait

FIGURE 2

Thrust (horizontal) and lift (vertical) forces for pectoral fins executing normal and modified steady swimming gaits. By making relatively small changes to fin stiffness (A) and fin motions (B), the forces can be moved throughout the thrust-lift plane. Normal, full-fin steady swimming for three levels of stiffness (A). The gait was modified slightly by altering the phase angle between fin rays by 30° (B, red) or by using just the upper or lower half of the fin (B, green). The magnitude of the force can also be altered simply by changing the frequency of the fin beat.



pattern, for example, by switching from a steady swimming gait to the pattern used by the fish for a turn maneuver. Smaller changes to the force profile can be made by changing the frequency of the fin beat and/or by changing phase relationships between fin rays (Figure 2A). Considerable changes to the magnitude and direction of the force can also be made by adjusting the mechanical properties of some, or all, of the fin rays. When the mechanical properties of the fin rays are under active control, as in the fish, changes to the force profile can happen very quickly since the driven motions of the fin do not have to be changed.

The designs of the robotic fins were modified and the fins implemented on a freely swimming biorobotic fish (Figure 1). Modifications included placing actuators within the fish body adjacent to each fin, using a network of microcontrollers to drive fin motions, and minimizing the number of actuated DOF for each fin ray. The motions and orientation of the robotic fish are controlled by adjusting the propulsive forces created by five rayfinned fins. In this first implementation, the forces are modulated by switching between several fin gaits and by making predetermined changes to fin beat frequencies and to the phase relationships between fin rays.

Sensory-Based Control of Fins

What is clearly missing in this robotic system is the ability to automatically modulate the kinematics and mechanical properties of the fins based on sensory information about the fins and their interaction with the water. The motions of the fins are adjusted based on the forces required to control the robot's body, but sensory information is not being used to exploit the phenomena that are critical to the efficient production of force (e.g., vorticity) nor to adjust behaviors in response to changes in the flow (e.g., speed and turbulence). This is due to the fact that very little is known about the sensory-based control of ray-finned fins (Phelan et al., 2010). The fine level of control that the sunfish has over fin motions and mechanical properties suggests strongly that there is closed-loop control of the fins. However, fundamental questions about the existence of sensory systems intrinsic to fins, about the types of stimuli that elicit responses from fins, about information in the flow that is relevant to propulsive forces, and about the behavior of the fins in response to external perturbations have not yet been answered. This knowledge is vital for the development of fin-based propulsors that take advantage of the phenomena used by fish to produce forces efficiently and that

automatically adjust their behavior in response to disturbances and changes in operating requirements.

Experimental Methods and Equipment Experimentation

Experiments were conducted to evaluate the response of the sunfish's pectoral fins to external perturbations applied to the fin and to the fish's body during steady swimming. Perturbations were created using a vortex generator (Figure 3), which produces a vortex ring that moves through the water and imparts a short duration impulse to the fish (Figure 4). The strength of the vortex was sufficient to deform the pectoral fin or to displace the fish laterally by several millimeters. The vortex is not visible, so it does not elicit a visually mediated response from the fish. The vortex does, however, produce a pressure wave that may be sensed by the fish.

Two bluegill sunfish, with body lengths of 160 ± 10 mm and intact pectoral fins, were used for the experiments. For the experimental trials,

FIGURE 3

The vortex ring generator and vortex (left). Blue dye was added to the vortex generator's cavity to make the vortex visible to the naked eye. The vortex generator comprises an orifice plate (1), two cavity plates (2), a latex membrane (3), and a connector plate (4), which enables the air-line to be connected to the vortex generator.



FIGURE 4

Sunfish in flow tank with vortex generator (A). The sunfish kindly positioned itself in the center of the test area and laser sheet (B). The laser sheet is used with PIV to characterize the vortex as it travels toward the fish.



a sunfish was placed in the working area (280 × 280 × 800 mm) of a 600-l flow tank and was allowed to acclimate for 2 h. The flow rate was set to 100 mm s⁻¹, which equates to a steady swimming speed of approximately 0.6 body lengths s^{-1} . At this speed, sunfish generate swimming forces using primarily their pectoral fins. The tail and the caudal, anal, dorsal, and paired pelvic fins are moved very little but are important for stability. The vortex generator was positioned approximately 150 mm above the tank floor and placed either perpendicular to the fish in order to perturb the fish's body or at a 45° angle to the fish in order to perturb the pectoral fin during its outstroke. A horizontal light sheet (Figure 4) used for particle image velocimetry (PIV) was positioned so that it had the same height as the middle of the vortex generator. The fish was directed into the middle of the test area and light sheet by coaxing it with a wooden dowel. Once the fish was positioned properly, the vortex was launched to strike the fish. Vortices impacted the fish (1) on the body near the tip of the left pectoral fin while the fin rested against the body during the pause between fin beats and (2) at the tip of the left pectoral fin as the fin completed its outstroke.

High-speed (500 fps), highdefinition video (1024 × 1024 pixels) was used to capture the motions of the fish and of the fish's fins. Two cameras (Photron 1024 PCI, Photron USA, Inc., San Diego, CA) were synchronized and positioned so that the ventral and posterior views of the fish were captured.

Analysis

The linear and rotational velocities of the vortices were analyzed using DaVis (LaVision GmbH, Göttingen, Germany).

The motions of the fish and of the fins were analyzed for two fin beats before and two beats after the impact of the vortex. The coordinates of eight points along the fish body and pectoral were digitized using Matlab (The Mathworks Inc., Natick, MA) and tracked through time. Deformations and curvatures were calculated for the pectoral fin during the impact of the vortex ring. Three points along the fin were selected to characterize the shape of the fin and to define the radius of curvature.

Design of the Vortex Ring Generator

Vortex rings are commonly generated using a piston that moves within a cylindrical cavity and pushes a volume of fluid (the slug) out of the cavity and past an orifice with sharp edges. The movement of the piston causes the boundary layer that develops in the cavity to separate at the orifice's edge and to roll up into a vortex ring that has a toroidal shape. The speed of the piston, the diameter of the orifice pate, and the ratio of cavity length to cavity diameter influence the formation of the vortex and the speed at which the vortex travels. Excellent discussions of vortex generation are presented in Gharib et al. (1998), Allen and Auvity (2002), Shusser et al. (2002), and Mohseni (2006).

The vortex generator that was developed for our experiments is similar to a piston based vortex generator, but the design was modified so that it would be more appropriate for the testing of swimming fish. Two requirements that influenced the design were (1) the vortex generator had to be silent, so that the fish did not hear a mechanism and anticipate the arrival of the vortex, and (2) the system had to be small, so that it could be placed at the side of the flow tank without interfering with the swimming fish. The vortex generator consists of two acrylic plates $(45 \times 55 \times 12 \text{ mm})$ in which a cylindrical cavity is cut (Figure 3). The plates are covered by a 0.3-mm thick aluminum plate with either a 4.0- or 7.5-mm diameter orifice. A latex membrane is sandwiched between the cavity plates and another acrylic plate in which a cylindrical well is cut. This plate is connected via a 6-mm diameter air line (Polyurethane Tubing, NewWay Air Bearings, Aston, PA) to a 60-ml syringe (Becton Dickinson and Company, Franklin Lakes, NJ). A fast push on the syringe plunger causes the latex membrane to expand into the cavity and to exhaust the fluid and create the vortex. The effective length of the cavity can be increased by drawing the syringe plunger back. This draws the latex membrane back into the cylindrical well. Dye was introduced into the chamber via a 1.6-mm diameter hole drilled into the acrylic plate, radial to the cavity. A steel tube was inserted into the hole, and was connected via medical tubing (Scientific Commodities, Inc., Lake Havasu City, AZ) to a syringe filled with food-grade dye. The vortex generator was mounted to an aluminum arm (80/20 Inc., Columbia City, IN) so that it could be positioned within the flow tank.

The force, impulse, and linear velocity of 12 vortices were characterized to better understand the properties of the vortex and how best to actuate the plunger. The force generated by the impact of the vortex was measured (Figure 5b) by shooting the vortex against a plate that was connected to a 2.5 g force transducer (LSB200, JR S-Beam Load Cell, Irvine, CA). The plate was located 100 mm from the orifice of the vortex generator. The vortex was imaged using the high-speed camera as it travelled within the 2-mm thick light sheet. Mean values for vortices created using a 5-mm diameter cavity were: 13 mN force (0.6 mN SE), 0.13 mNs impulse (0.002 mNs SE), and 0.99 m/s velocity (0.01 m/s SE). A 13-mm diameter cavity produced a more powerful but slower vortex: 67 mN force (2.3 mN SE), 1.0 mNs impulse (0.02 mNs SE), and 0.85 m/s velocity (0.01 m/s SE). These values compare well with estimates we have made for the peak force and impulse created by a sunfish pectoral fins. At a swimming speed of 0.5 body length per second, average fin forces are less than approximately 10 mN and the impulse over the fin beat is less than 2.5 mNs.

FIGURE 5

Evaluation of vortex ring's velocity using PIV (A). Force from vortex ring during impact with rigid plate attached to force transducer (B).



Response to Vortex Perturbations

Perturbation experiments that involved hitting the swimming fish with a vortex ring showed that the fish did not alter the pectoral fin beat during the time course of a single fin stroke but did change the amplitude and timing of the pectoral fin beats subsequent to a vortex impact that perturbed the fish's position.

Response to Vortex Perturbations Applied to the Body

Vortex perturbations that impacted the side of the fish displaced the fish

FIGURE 6

laterally by several millimeters (Figure 6), which is significant relative to the thickness of the fish's body (maximum of approximately 25 mm). The lateral displacement occurred whether the fish had been drifting toward or away from the vortex generator prior to the disturbance and was not accompanied by any obvious change to the roll or yaw of the fish. An active response of the fish to the vortex perturbation was evident in the fishes' motion after a short delay. The soonest the active response occurred was 0.05 s, while the longest delay before a response was evident was 0.20 s. In the majority of trials, the fishes actively

Distance from orifice plate of the left pectoral fin (purple), the right pectoral fin (blue), and the fish at a point between the pelvic fins (green). The distance between the fish and the orifice plate is amplified relative to the fins and is measured at the scale on the right. In this trial, the fish was moving towards the vortex generator and was hit by the vortex at about t = 1.49 (red). The active response of the fish occurred by t = 1.50 (gray). (Color versions of figures available online at: http://www.ingentaconnect.com/content/mtsj/2011/00000045/00000004.)



moved away from the vortex generator after being hit by the vortex (Figure 7). The movement was not particularly quick, but was always faster than the fish's lateral velocity before the perturbation had occurred. In some cases (e.g., Figure 6), the fish actively moved toward the vortex generator after being pushed away from the vortex generator by the impulse. This occurred only when the fish had been drifting towards the vortex generator before the perturbation. In some trials, the fish was startled by the vortex and swam out of the test area. The startled motions were not analyzed quantitatively.

The motions of the pectoral fins during the fin beat subsequent to the perturbation were significantly different from the motions of the pectoral fins prior to the perturbation. However, the pectoral fins did not seem to react quickly to the stimulus. In fact, the initial movement of the fish's body in response to the vortex generally occurred between pectoral fin beats, while the pectoral fins were against the fish body (Figures 6 and 7). Thus, the active motion of the fish was initiated by other fins, which reacted within as little as 0.05 s. Active movement of the pectoral fins did not usually resume until 0.10-0.20 s after the vortex. The frequency of the pectoral fin beats did not change consistently after the perturbation. In three of the eight trials, the frequency of the pectoral fin beat increased from, on average, 1.37 Hz (SD = 0.15) to 1.83 Hz (SD = 0.28). In the other five trials, the frequency of the fin beat decreased from, on average, 1.69 Hz (SD = 0.26) to 1.34 Hz (SD = 0.21). The amplitude of the pectoral fin motions also changed. This altered the force balance between the two pectoral fins and contributed to the movement of the fish body. In the beat after the vortex stimulus, the amplitude of the right pectoral fin (opposite the side of the impact) was consistently smaller than before the vortex. Its motion decreased in all eight trials, on average by 18.9% (SD = 10.9%). The amplitude of the left pectoral fin also changed, but the changes were less consistent. In four trials, the amplitude decreased by, on average, 37.4% (SD = 22.8), while in the other four trials, the amplitude increased by, on average, 8.9% (SD 7.0%). By the second fin beat after the perturbation, the mo-

FIGURE 7

Distance from orifice plate of the left pectoral fin (purple), the right pectoral fin (blue), and the fish at a point between the pelvic fins (green). The distance between the fish and the orifice plate is amplified relative to the fins and is measured at the scale on the right. In this trial, the fish was moving away from the vortex generator and was hit by the vortex at about t = 1.25 (red). The active response of the fish occurred by t = 1.35 (gray). The fish continued to move away from the vortex generator until approximate t = 1.8 s.



tions of the left and right pectoral fins were much more similar to the motions before the fin beat, and were similar to each other.

Response to Vortex Perturbations Applied to the Fin

The pectoral fins were deformed significantly when struck by the vortex during the fin beat (Figures 8 and 9). The vortex made contact with the left pectoral fin near the end of the fin's outstroke. The vortex bent the tips of the fin rays and progressively bent larger portions of the fin as the vortex travelled towards the fish body. The fin seemed to bend and fold as if it were made from thin paper and exhibited deformations from the tip to the base. The maximum measured curvature of the fin (along fin ray 6) increased from 0.054 mm⁻¹ near the tip and 0.024 mm⁻¹ near the base during unperturbed swimming to 0.113 mm⁻¹ near the tip and 0.029 mm⁻¹ near the base when in contact with the vortex. The vortex remained in contact with the fin while it travelled towards the fish body. This resulted in the pectoral fin being pushed back to the body faster than during an unperturbed instroke. Times ranged from one third to one half of the duration of a normal instroke and were dependent on many

FIGURE 8

Pectoral fin perturbed by vortex during swimming. The mean fin ray curvature after impact was 14.4 mm⁻¹ (0.05 mm SE). Reflective particles are used so that the fluid movement is visible.



FIGURE 9

Ventral view of the fish as the left pectoral fin is hit by a vortex (no dye). The left pectoral fin is hit by the vortex (1). The fin is deformed (2, 3, and 4) and is pushed to the body by the vortex. (5 and 6) The right pectoral fin continues to beat normally. The body is not deflected by the vortex.



variables, including the speed of the vortex, how well contact was made with the fin, and the time of impact within the fin beat.

Despite the severity with which the vortex changed the shape and trajectory of the perturbed fin, the fish did not appear to react to the perturbation or to change its behavior subsequent to the perturbation. During the perturbation, the observed motions of the unperturbed fin and of the fish body were not visibly different from motions prior to the perturbation. Subsequent to the perturbation, the perturbed fin remained against the fish body until the unperturbed fin completed its instroke. Both fins then resumed what appeared to be a normal fin beat. Small differences in the pectoral fin beat and the use of other fins likely occurred to accommodate for differences in propulsive forces produced during the perturbation, but these changes were not visible. Nor were there changes in the motion of the fish body, which was not observed to move laterally or to rotate in yaw.

Discussion

The objective of the experiments was to determine how sunfish respond

to perturbations applied to the body and fins during steady swimming. These experiments provided a contextual understanding of sensory based modulation of pectoral fin function. The experiments produced a mix of expected and surprising results.

As expected, the fishes did alter the amplitude and timing of the pectoral fin beats subsequent to a perturbation that disturbed the lateral position of the fish body. However, the pectoral fins did not respond quickly to the disturbance, but remained against the fish body for durations that were only slightly different from the pauses between fin beats prior to the disturbance. Active movement of the fish's body after the disturbance occurred with a latency of as little as 0.05 s, which is similar to the 0.08 s latency measured by Webb (2004) in response to roll disturbances. The movement of the fish body is believed to have been caused by fins other than the pectoral fins, since the pectoral fins remained against the body for 0.10-0.20 s after the perturbation. When the pectoral fins were moved, the amplitudes of the fins seemed to have been adjusted to help equilibrate the movement of the fish. By the second fin beat after the disturbance, the motions of the

two pectoral fins were synchronized and had amplitudes similar to those before the disturbance.

The delay in the response of the pectoral fins to the vortex and lateral disturbance is different from the response of the fins during experiments where an obstacle was placed in front of the swimming fish (Gottlieb et al., 2010). In those experiments, sunfish altered the motions of the left and right pectoral fins during the outstroke of a steady swimming beat. The changes were not subtle, and the fish did not seem to wait for the next cycle as in the present studies. The pectoral fin on the side of the obstacle stiffened and the fin rays were moved through trajectories that were very different from steady swimming. The fin on the side opposite to the obstacle nearly stopped and served to stabilize the motion of the fish. The difference in the pectoral fins' response to the obstacle and to the vortex and lateral displacement may be related to the fish's perception of the stimuli. The obstacle may have been more threatening than the vortex, which the fish may have interpreted as a common fluidic event. The fish therefore disrupted the steady swimming gait in order to produce large lateral forces that turned the fish away from an unknown obstacle that may have posed a threat. In contrast, the disturbance in motions caused by a fluidic stimulus could be accommodated simply by adjusting motions of the fins within their normal gaits. This would allow the central pattern generator that drives the motions of pectoral fins (Westneat et al., 2004) to continue to produce similar output characteristic rather than having to switch between gaits.

Most surprising was the lack of reaction to the vortex when the vortex deformed the pectoral fin at the end

of the fin's outstroke and throughout the instroke. Nerves and free nerve endings exist throughout the fin rays and the fin webbing (experimental findings, M. Hale, University of Chicago), and so it was expected that at least one of the phenomena that the vortex created-pressure, impact, bending-would have elicited a sensory mediated response. The vortex was in contact with the fin for over 100 ms, and so the duration of the stimulus was certainly sufficient for a sensory-mediated response to occur. It was also surprising that neither the motions of the body, nor subsequent beats of the pectoral fins, were clearly different from those before the vortex perturbation. It is highly likely that the left pectoral fin, while being deformed, produced forces that were different from normal. During a normal steady swimming gait, each pectoral fin will produce lateral forces that are similar in magnitude to thrust and lift. Since the fins typically beat synchronously, the lateral forces from the left and right fins balance and cancel. This would not have been the case when the left pectoral fin was deformed, and the unbalanced forces should have accelerated the fish body laterally and/or in roll and yaw. The lack of obvious lateral motion and adjustment to the pectoral fin beat may be due simply to the fish being insensitive to lateral forces. To move the fish laterally, forces must accelerate the mass of the fish and also overcome drag forces and the load from the mass of water against which the side of the fish pushes. Thus, the loss of lateral force during a single fin beat can be easily tolerated because it is difficult for the fish to move sideways. So although studies of biorobotic models of the pectoral fins have shown that the fin's kinematics and mechanical properties must be controlled very carefully to produce forces like the fish (Tangorra et al., 2007, 2010), the mechanics of the fish body do not necessarily require the careful control of forces at all times in all directions.

Conclusions

Perturbation experiments which involved hitting the swimming sunfish with a vortex ring showed that the fish did not alter the pectoral fin beat during the time course of a single fin stroke but did change the amplitude and timing of its motions in beats subsequent to an impact that disturbed the fish's position. Vortices that struck the pectoral fin during the fin's outstroke deformed the fin extensively, but the perturbations did not cause the stroke of the unaffected pectoral fin to change, nor did the perturbation cause changes in the motions of the fish body or in the subsequent strokes of either pectoral fin.

These outcomes suggest that the kinematics of the pectoral fins is modulated by sensory information only when a perturbation results in a disturbance to the fish body, which is the system that the fins are working to control. The pectoral fins did not react quickly when the vortex displaced the fish's body but modulated their motions to help stabilize the displaced fish after other fins had already been engaged. The pectoral fins also did not react reflexively to vortex perturbations that deformed the fins' webbing and fin rays. The fin did not appear to move away from the vortex or to resist the deformation by stiffening. The compliant fin allowed itself to bend and perhaps to shed the load from the vortex, and then altered its motions during the course of the subsequent fin beat.

The results illustrate a benefit of compliant mechanisms within a highly

controllable system. The fins of rayfinned fish have the ability to control forces precisely by altering the kinematics and mechanical properties of individual fin rays. Small changes in either the trajectories or stiffness of fin rays can significantly alter the force that is transferred to the fish (Tangorra et al., 2010). However, it is not always necessary to regulate the fins precisely. By maintaining its flexibility and allowing itself to be deformed, the fin was able to be hit by the vortex-which had sufficient forces to displace the fish-without transferring the full impact of the perturbation to the fish body. Therefore, the fin's passive mechanics made it unnecessary for the fins to be modulated in order to restore the fish to equilibrium. However, when the fish does want to move the quickly-as in a maneuver away from the obstacle-the pectoral fin can be stiffened, the gait changed, and large lateral forces from the fin can be transferred to the fish body.

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