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Introduction to the Symposium-Unsteady Aquatic Locomotion with Respect to Eco-Design and Mechanics

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SYMPOSIUM

Introduction to the Symposium—Unsteady Aquatic Locomotion with Respect to Eco-Design and Mechanics

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Synopsis The importance of unsteadiness in the aquatic environment has come to the forefront in understanding locomotor mechanics in nature. The impact of unsteadiness, starting with control of posture and trajectories during aquatic locomotion, is ultimately expressed in energy costs, morphology, and fitness. Unsteadiness from both internal and external perturbations for aquatic animals is important at scales ranging from micro to macro to global.

Introduction

Animals must operate in the aquatic environment, which is in a constant state of change and therefore unsteady by nature. Unsteadiness in animals is due to self-induced instabilities and external perturbations, which poses a challenge to functioning in open water (Webb 1997; Weihs 2002). Animals can use self-induced instabilities to accomplish a number of tasks efficiently, including saving energy through intermittent locomotion and diving, capturing prey with high accelerations, escaping from predators using high maneuverability, and avoiding obstacles by turning and breaking (Weihs 1974; Nishimoto and Herrnkind 1978; Williams et al. 1999, 2004; Domenici 2001; Domenici et al. 2004; Maresh et al. 2004). External perturbations are associated with currents, tidal oscillations, wave action, and turbulence (Webb et al. 2010). Turbulence for aquatic animals is important at scales ranging from micro (i.e., plankton) to macro (i.e., effects of waves) to global (i.e., biogenic mixing). To meet the challenges of inherently unsteady movements and unsteady environments, aquatic animals have adapted morphologies and behaviors that not only act to enhance stability, but can also take advantage of the unsteadiness. Organisms have evolved mechanisms that utilize unsteadiness in an adaptive manner, including the capture of vortex energy, using tidal transport, and reducing drag in swarms and schools (Weihs 1973b; Liao et al. 2003a, 2003b; Fish 2010). Furthermore, the unsteady turbulence that animals produce themselves can have ramifications for the mixing of water and for global climatic change (Fig. 1).

Biological and engineering studies of locomotor mechanics and energetics throughout the 20th century primarily explored steady-state conditions for self-correcting and stable organisms and vehicles. These studies were the foundation for many ideas in the understanding of the evolution, behavior, and ecology of swimmers and flyers. While an immense amount of data has been collected on organisms swimming under controlled conditions of still water or steady flows, the late recognition of the ubiquity of unsteadiness in locomotion and behavior means little is known of how organisms deal with these real-world challenges (Webb and Weihs 1994; Webb and Cotel 2010; Webb et al. 2010; Heatwole and Fulton 201~~2~~). 3

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Nature is characterized by unsteadiness. In terms of locomotion, organisms are frequently unstable in posture, exhibit changes in speed and trajectories, are not self-correcting when in motion, and experience conditions greatly exacerbated by environmental turbulence (i.e., changing currents, eddies, and vorticity). All these internal and external contributions

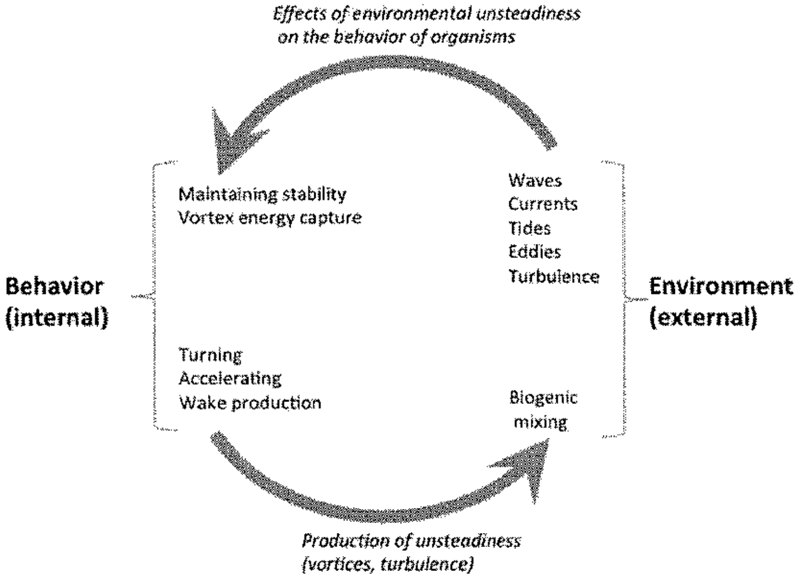

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Fig. 1 Swimming in an unsteady world: the internal perturbations that arise as a result of the organisms' behavior as well as the responses to environmental unsteadiness are listed on the left. Shown on the right is the unsteadiness of the aquatic environment, including the contribution of biological mixing in the ocean.

to a seemingly chaotic status are now being recognized as reflecting fundamental questions such as trades-off between stability and maneuverability, especially in fitness-critical situations (i.e., predator–prey interactions), and the expenditure of energy and resources for growth and reproduction that consequently impact the evolution of organisms and the habitats they occupy. Furthermore, an understanding of unsteadiness in the aquatic environment is particularly important compared with terrestrial and aerial locomotion. Aquatic animals do not experience the large differences in density between the organism and the medium that poses primary challenges for terrestrial animals (Daniel and Webb 1987) and that also exacerbates instability in pelagic organisms. The research on aquatic animals has demonstrated the impacts of unsteadiness across taxa over a range of sizes of organisms, and at scales from individual organisms to ecosystems.

At the same time that interest in the biological ramifications of unsteadiness have been recognized, engineers have been concerned with creating autonomous vehicles that can operate in equally turbulent settings for which organisms have evolved novel solutions. In the past 20 years, the rapid growth of interest in unsteadiness in locomotion has been fueled by collaboration between biologists and engineers and the use of new methodologies, notably in computational fluid mechanics, and bio-robotics (Borazjani and Sotiropoulos 2008; Moored et al. 2011; Lauder et al. 2012; Wen and Lauder 2013). The development of Digital Particle Image Velocimetry, a fundamental methodology that allows quantification of flow, has provided new impetus for investigating the behavior of animals in unsteady flow both in the laboratory (Drucker and Lauder 2002) and in the field (Katija et al. 2011; Katija 2012). New scientific advances often occur through overlaps in different fields of study that provide insight for novel solutions to scientific problems and permit paradigm shifts to open new emerging fields.

Mechanics of unsteady swimming

Most previous work on swimming animals has dealt with the ideal situation of organisms swimming either in a flow tunnel with a controlled, laminar flow, or swimming in laboratory tanks filled with still water. While reductionist, these situations may be relevant for the case of organisms migrating at a steady speed, although even in these cases organisms are bound to find perturbations of flow as a result of currents, eddies, and the presence of other organisms. Arguably, however, in most cases marine organisms have to deal with unsteadiness in the system, either because of their own changes in speed and direction, or because of external perturbations. Despite these sources of unsteadiness, organisms need to retain control of their posture and their swimming trajectories in order to accomplish daily tasks such as finding food, escaping from predators, and dealing with tides and currents. Furthermore, scaling, both from the perspective of the properties of the flow (Webb et al. 2010) and the biomechanics of the organisms, is a fundamental issue in unsteady swimming. Due to the differences in size between predators and prey, the scaling of unsteady performance in swimming is a determinant of the outcome of predator–prey interactions for many aquatic species (Domenici 2001; Robinson et al. 2013).

Many different mechanisms are available for addressing problems of postural control by aquatic taxa, but little is known of the dynamics of stability control and maneuverability during aquatic locomotion (Webb 1989, 1997, 2006; Webb et al. 1996; Fish 2002; Fish and Nicastro 2003; Fish et al. 2003; Domenici et al. 2004; Maresh et al. 2004). Yet, the turbulent wakes shed by propulsive movements and the body dominate loss of mechanical energy during locomotion (Weihs 1972; Daniel 1984), and mechanisms that reduce this loss of energy should be expected. Examples explored to date include interactions among multiple propulsors and various parts of the body (Drucker and Lauder 2001, 2002; Catton et al. 2007, 2011; Bartol et al. 2002), body shape (Bartol et al. 2003, 2005), and intermittent swimming behavior (Weihs 1973a, 1974, 1977; Williams et al. 2000). The scale of turbulence shed as eddies by propulsors also provides opportunities for this energy to be captured by conspecifics or similar-sized species, for example in schooling (Weihs 1973b). Surprisingly, organisms have been found to be sources for turbulent mixing at ecosystem scales as well. Indeed, turbulence associated with animals' propulsive systems has ramifications for the mixing of water in the ocean (Huntley and Zhou 2004; Dewar et al. 2006; Katija and Dabiri 2009; Dabiri 2010; Katija 2012), thereby influencing oceanic nutrient recycling and heat transfer related to climatology (Dewar 2009).

In terms of organismic evolution, ecology, and behavior, however, turbulence largely in the form of waves and eddies in the environment external to organisms has energies and momentum that can be very large compared with other sources of unsteadiness. The distribution and behavior of plankton, and the settlement of larvae, are influenced by turbulence on a scale larger than the organism (Denny and Shibata 1989; Saiz and Alcaraz 1992; Koehl et al. 2007, 2013). The surge of waves affects the diversity and orientation of marine organisms due to biomechanical and energetic constraints (Nishimoto and Herrnkind 1978; Shanks and Graham 1987; Wyneken et al. 1990; Lohmann and Lohmann 1992; Fulton and Bellwood 2004, 2005; Heatwole and Fulton 2013) and by increasing the availability and diversity of food (Ferreira et al. 2001). Not surprisingly, eddies can negatively affect stability during locomotion (Tritico and Cotel 2010) and turbulence in flow can increase the cost of swimming and reduce swimming performance (Enders et al. 2003; Lupandin 2005). In fish, the increased cost of locomotion can be influenced by individual differences in the ability to adjust their fin beats to the flow environment (Roche et al. 2014). Similarly, organisms tend to choose locations with low intensities of turbulence (Pavlov et al. 2000; Standen et al. 2004; Cotel et al. 2006). Reef fishes subjected to exposed and highly turbulent environments tend to be larger and faster and have higher density (Depczynski and Bellwood 2005). Furthermore, larger waves have been associated with increased mortality (Bodkin et al. 1987). Yet at the same time, aquatic animals can exploit appropriately-sized eddies and wave action, thereby reducing the energic cost of swimming and holding station (Bose and Lien 1990; Liao et al. 2003a, 2003b; Liao 2004, 2008; Przybilla et al. 2010; Taguchi and Liao 2011; Akanyeti and Liao 2013), enhance jumping performance (Sturart 1962), and sense their environment (Dehnhardt et al. 1998, 2001; Schulte-Pelkum et al. 2007; Catton et al. 2011).

Integrating ideas

Research on disturbance in the natural environment and the unsteady behaviors of swimmers is becoming more important, and hence expected to be a major topic in future research both in the laboratory and in the field because of the impact of unsteadiness on the evolution, the energetics of locomotion, and ecology. Understanding the relationship between morphology, behavior, and mechanics of unsteady motions, both intrinsic to organisms as well as arising from the external environment, requires a synthesis from the fields of hydrodynamics, mathematics, engineering, biomechanics, organismal biology, ecology, evolutionary biology, and climatatology, and such synthesis is a goal of the symposium. These interactions will be fundamental to address future challenges such as the study of how organisms can perform intrinsically unsteady maneuvers like turning and accelerating (e.g., fast starts, avoidance of obstacles) in turbulent conditions that mimic those occurring in the field.

The development of highly mobile and stable autonomous underwater vehicles that can deal with perturbations in open water has been a concern for engineers who are attempting to build the next generation of biomimetic robotic vehicles (Moored et al. 2011; Fish et al. 2012). Therefore, a discussion of animals' systems is important to highlight mechanisms (ranging from self-correcting to powered) for control during swimming, and that can be applied to engineered marine systems (Webb 1997; Webb and Cotel 2011; Fish and Lauder 2013). The incorporation of novel structures and mechanisms from animals into the design and function of machines has the goal of improving performance over the current state-of-the-art (Vogel 1998; Fish and Lauder 2006; Allen 2010; Goel et al. 2014).

This symposium emphasizes the union of biological and engineering approaches to answer questions regarding the design of relevant hydrodynamic structures and behavioral mechanisms. This symposium is intended to bring together physiologists, morphologists, engineers, and mathematicians with an interest in unsteady locomotion and serve as a vehicle for fostering collaborations. In addition, bringing together this diverse array of investigators capitalizes on the approach of using animals as biological inspirations for the development of new technologies. This approach seeks common solutions from biology and engineering for increased efficiency and specialization in the marine environment. Analysis of locomotor specializations in animals holds for engineers the possibility that animals can be used as solutions to problems of design for the transfer of technology, whereas biologists can utilize engineering techniques to elucidate the principle factors affecting animals' systems. The union between biologists and engineers in recent years has created a paradigm shift through the biomimetic approach in developing new products and novel solutions to engineering problems. This symposium will help to uncover the principles of form and function, so as to deal with unsteady movement. There is a possibility that the knowledge presented in this symposium can be applied to the design of watercraft. Demonstration of significant practical applications on the association of natural morphologies and performance is likely to attract considerable interest from engineers.

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