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Life in turbulent waters: unsteady biota–flow interactions across scales

Aquatic organisms generate and are subject to a plethora of physical forces that are ultimately related to the movement of the water body in which they reside. In particular, turbulence exposes organisms to rapidly varying conditions across a wide range of spatial scales, from small-scale (microscopic) changes to meso-scale eddies and circulations found in lakes, oceans, and connecting water bodies such as rivers and estuaries. Turbulence is often characterized by the dissipation rate of turbulent kinetic energy (ε), which varies over about six orders of magnitude in lakes and around nine orders of magnitude in the oceans. The strength of turbulent motions also controls the transfer of key properties within aquatic environments, as well as the flux across the pelagic–benthic and water–air boundaries. Modern laboratory facilities have allowed for turbulent conditions to be carefully controlled, while advances in field instrumentation and processing techniques have improved characterization of turbulence. Combined, these new capabilities have provided novel insights into the connections between physical and biological or geochemical processes.

This special issue of *Limnology and Oceanography* explores how organisms experience and respond to turbulence at different length and time scales, and how the effects on individual behavior influence the ecosystem-scale responses. The contributions in this issue add to the breadth of knowledge in this area. This breadth is also demonstrated in the companion virtual issue online at https://aslopubs.onlinelibrary.wiley.com/doi/toc/10.1002/(ISSN)1939-5590.life-turbulent-waters. The virtual issue, which also includes many papers from *Limnology and Oceanography: Fluids and Environments*, is intended as a living and growing compilation of flow-biota studies that showcases manuscripts from the 1960s to present, with a steady increase in numbers beginning in the early 1990s. We emphasize the advances on flow–biota interactions rather than the large number of seminal papers on physical aspects of turbulence and influence of turbulent flux on water bodies that have also been published in *Limnology and Oceanography*. While the papers in the special issue encompass a wide range of topics, several key themes nonetheless emerge.

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Special Issue: Life in turbulent waters: exploring unsteady biota-flowinteractions across scales. *Edited by: Josef Ackerman, Danielle Wain, RafaelTinoco, Hidekatsu Yamazaki, Mimi Koehl, and Deputy Editors Julia C. Mul-larney, Steeve Comeau, and Elisa Schaum.*

Several of the new contributions focus on the behavioral or ecophysiological responses of mostly marine planktonic organisms to turbulent motions across different spatial scales. There are, however, several contributions that demonstrate that freshwater zooplankton exhibit both similar and contrasting responses compared with marine zooplankton. Du Gurung et al. (2024) examined how the swimming behavior of freshwater *Daphnia magna* responds to multiple stimuli. The *Daphnia* were exposed to changes in hydrodynamic conditions mimicking larger-scale Langmuir circulation cells ($10^{-7} < \varepsilon < 10^{-5}$ $m^2\ s^{-3}$), light exposure, and contact with oil, which hinders swimming ability. Aggregations of *Daphnia* were observed within a "Goldilocks" zone—when flow velocities were faster than still water but slower than typical swimming speeds, which is similar to observations with marine zooplankton. Conversely, Ruszczyk et al. (2024) found that the swimming response of freshwater copepod, *Hesperodiaptomus shoshone*, to turbulence differed from marine copepods. Their laboratory experiment examined the response of *Hesperodiaptomus* to turbulence using a Burgers' vortex apparatus to mimic small-scale dissipative eddies. The results revealed linear swimming trajectories in both male and female copepods at all turbulence levels, which contrasts with the spiral swimming trajectories reported in marine species (*Acartia tonsa*, *Temora longicornis*, and *Calanus finmarchicus*). The authors presented several plausible explanations for the difference in swimming in *Hesperodiaptomus* including the differences in setal arrays, their ecological niches, and the limited mixing in freshwater pond environments.

Other studies focused on an isolated component of turbulence—vorticity. Goulet et al. (2024) examined whether exposure to vorticity would affect the intertwined responses of swimming and feeding behaviors of freshwater *Daphnia magna*. They found that clearance rates of algae increased with small levels of vorticity but declined as vorticity increased. This ramp-like or unimodal feeding response to hydrodynamic forcing has been found in other freshwater and marine organisms. Goulet et al. (2024) determined that the normal hop-sink swimming ability of *Daphnia* was also affected by vorticity, which reduced the number of hops and their ability to orient. The swimming response to vorticity may explain the feeding response in freshwater *Daphnia*, but it contrasts with a lack of response to vorticity in marine copepods (*A. tonsa*), perhaps due to the stronger swimming ability of the latter taxon.

The aforementioned studies demonstrate the advantages of using laboratory studies to reveal relationships between hydrodynamics and organism behavior and ecophysiology, which are difficult to measure in nature. These studies, however, also demonstrate the need to examine these relationships using a diversity of taxa reflective of nature, rather than relying on a limited number of model systems. Moreover, these studies also raise many questions regarding the cascading influences of such behaviors and ecophysiology both within and across trophic levels. We note that one critical factor discussed in several papers within the Special Issue is the importance of ensuring that laboratory experiments are ecologically relevant and that the experiments provide an accurate representation of the spatial and temporal fluctuations of the flow, shear, and vorticity in mimicking such fluctuations encountered by the studied organisms in the field. Indeed, this concern also raises questions regarding the selection of the appropriate descriptor for turbulent conditions, as presented by Franks and Inman (2024). They argue that the dissipation rate of turbulent kinetic energy (ε) does not capture information on the instantaneous spatial structure of turbulent shear at the scale of individual plankton. They suggest the use of a statistical approach using the probability distributions of the microscale motions as a potential way forward in the future.

Another key theme in both the virtual and special issue can broadly be described as the control exerted by large-scale turbulent features on the spatial and temporal distribution of (1) matter relevant for the survival and ecophysiological processes of organisms, and (2) of the organisms themselves. Sato et al. (2024) used a field and modeling study to unravel relationships between coastline type, hydrodynamic regime, and dispersal patterns of larval anemonefishes. Their analysis provided the surprising result that semi-enclosed bays exhibited lower local retention and self-recruitment than open-coast locations. Closer examination revealed that local topographic features drove cross-shore flows and controlled dispersal patterns rather than coastline shape. A multitude of different traits (from dispersal to metabolic traits) are indirectly affected by turbulent dynamics. In an Amazon freshwater stream system, Machado-Silva et al. (2024) explored the effect of hydrodynamic regime on dark carbon fixation in freshwater, an understudied process. Rates of dark carbon fixation were found to be of similar magnitude to heterotrophic production in water and litter, but lower than in sediments. Rates were also greater in lotic relative to lentic systems and although turbulence was not measured, the results highlight the need for further investigation of this process in freshwater systems. Turbulence also affects the flux of matter between water column and benthic habitats. In their review article, however, Porter and Cornwell (2024) caution that use of mesocosm experiments may lead to incorrect conclusions if benthic and water column processes are decoupled. The authors indicate that significant insight can be obtained when realistic regimes for both water column and bottom turbulence are simulated.

A topic featured in the virtual issue (although not represented in the special issue) is how biota that create surfaces (e.g., macroalgae, aquatic vegetation, corals, bivalves, complex benthic or fouling communities) can themselves generate or enhance small-scale turbulence. These organisms, known as ecosystem engineers, change the hydrodynamic environment and can then feedback or engineer the larger ecosystem response, for example, through enhanced nutrient delivery or reducing damaging physical forces. Other related studies included only in the virtual issue explore how freshwater and marine organisms (e.g., planktonic prey of benthic animals, gametes during spawning, propagules and larvae) and materials (e.g., nutrients, oxygen, wastes) travel between the water column and the benthos through the turbulent benthic boundary layer. The virtual issue also contains studies of mechanisms used by microscopic organisms to navigate in turbulent ambient water flow, as well as research on how turbulent ocean waves can dislodge or prune benthic organisms and alter community structure.

Virtual issues are intended to be living and growing issues that provide a useful entry point for, and rich variety of, papers on a particular topic. With this special issue and its accompanying virtual issue, we hope that we have created a living and growing resource for aquatic scientists who study the effects of turbulence on individuals and groups of organisms (including influences on the interactions among species), and the generation of turbulence by the organisms themselves. Thus, we encourage authors to let us know if they think their past or current submissions align with a particular theme, so they can be added to the issue when published, in addition to featuring in the regular published issue.

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