



Ecological fluid mechanics: interaction between living organisms and environments

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Ecology is the study of interconnections among living organisms, including humans, and their physical and chemical environments. Landscapes that host these environments are inclusively named ecosystems where the biological, physical, and chemical components form an interacting network of energy flow and material cycling from inorganic to organic and back to inorganic elements. Ecosystems around the world, whether aquatic or terrestrial, have been adapting to ever-growing pressures from changing climate and human (anthropogenic) activity. Ecological fluid mechanics seeks to understand the vital interconnection between living organisms and the physical/chemical world. As such, it is a truly interdisciplinary branch of environmental fluid mechanics. A scientist or engineer might quantify how fluid flow distributes nutrients and other chemicals affecting the organism's physiology and metabolism.

Ecosystems include the biological interactions of ecological community with its corresponding food web, a process mediated by ecological fluid mechanics. The organism/community interaction and ecological fluid mechanics can determine how ecosystems function. For example, physical and chemical processes control a fundamental property of aquatic ecosystems, namely, the balance of organic material production (autotrophy) and decomposition (heterotrophy). The autotrophy-heterotrophy balance underlies the photosynthesis to respiration ratio, dissolved oxygen balance and overall water quality, and determines whether the aquatic ecosystem will be a potential sink or source for carbon dioxide in the atmosphere.

Ecological fluid mechanics operates over a wide range of spatial and temporal scales within the food web. The spatial scales range from the size of individual microorganisms such as bacteria to that of watersheds. The corresponding temporal scales vary from the time it takes microorganisms to absorb nutrients (μ s) to the time associated with organism growth (years). A conceptual classification of these spatial and temporal scales in a watershed containing a corresponding aquatic network could be compartmentalized into organism, reach, network, and watershed scales (Fig. 1). At the organism scale, thin layers with molecular-diffusion dominant transport mechanism regulate the supply and release of nutrients. The flux of nutrients through these thin layers is controlled by the difference in chemical concentration across them, i.e. from the waterside to the organism side. While

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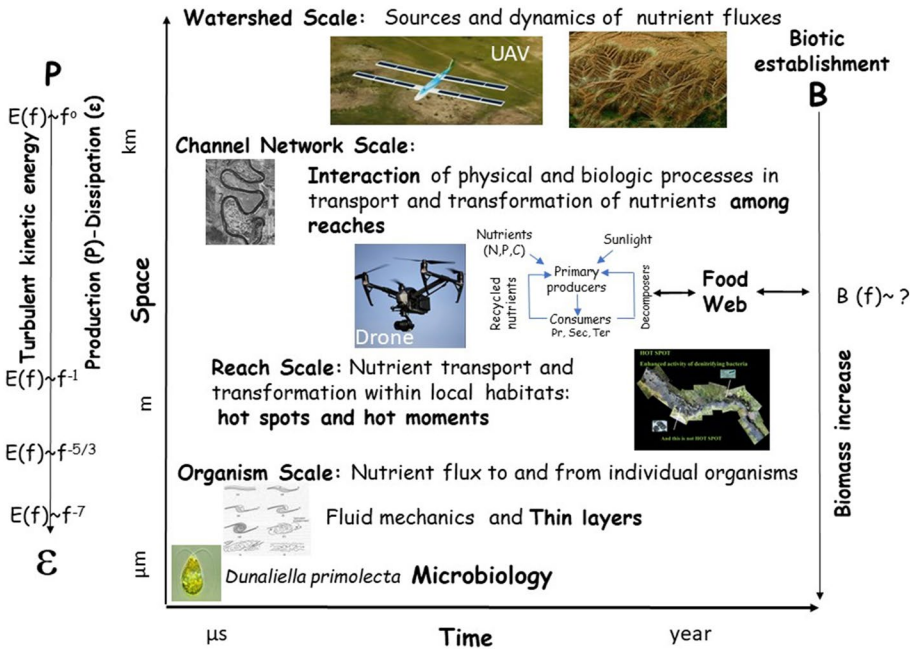


Fig. 1 Space and time scales of ecological fluid mechanics. Organism scale, reach scale, network scale, and watershed scales are compartmentalized habitat sheds. Drone technologies with particle image velocimetry and spectral cameras have been increasingly used to quantify fluid flow, biomass, and physical variabilities over the reach scale. Solar-powered unmanned aerial vehicles (UAV) with Lidar and spectral cameras can be implemented to quantify the terrain and its characteristics, spatial variability of biomass, and physical environments at a watershed scale

the moving fluid generally imposes the waterside concentration, metabolism controls the concentration on the organism side. A combination of physical and chemical conditions at the reach scale can create heterogeneity of amplified physiological and metabolic conditions known as hot spots and hot moments in space and hot moments in time. The occurrence and nature of hot spots and hot moments pose a critical question to be addressed in environmental fluid mechanics. At the network scale, reach scale heterogeneities are connected by various pathways, similar to the organism food web, which can connect, create, or even destroy existing hot spots and hot moments. A particular network of physical and biological processes that amplifies hot spots and hot moments can determine the ecosystem’s functionality. At the watershed scale, which is physically determined by the landscape and convergence of water flows, various climatic and land-use patterns establish the ecosystem network and associated organism habitats.

So how are scales so dissimilar as those of watershed and individual organism get connected? The hierarchy of temporal and spatial fluid mechanics scales in a turbulent flow is effectively visualized by the turbulent kinetic energy spectrum (Fig. 1). Typically, most of the energy production in a turbulent flow is generated by eddies with time scales on the order of minutes and dissipated at a time scale on the order of a second or less. Turbulent energy is systematically transferred from production scales to dissipation scales. The rate of turbulent energy dissipation (ϵ) is a fluid flow property that, through the energy cascade, connects large-scale fluid motion with the much smaller scale physiological

and metabolic responses of microorganisms. Large-scale eddies can transport planktonic organisms through a variety of available nutrients, and therefore provide the conditions needed for biomass increase in the moving fluid. At microscopic scales, the energy dissipation rate with its corresponding velocity gradient effectively controls the thickness of thin layers surrounding aquatic organisms and the associated flux of chemicals to and from these organisms.

Interactions between living organisms and their surrounding environments are necessarily conducted under conditions that enable their physiological and metabolic functioning. What follows is an example of environmental fluid mechanics where filaments of periphyton (substrate attached algae) altered the velocity field and corresponding shear stress in the water adjacent to the filaments, accentuating their nutrient uptake. Under field and laboratory conditions, we studied the biomass heterogeneity and uptake of nutrients by *Cladophora glomerata*, a commonly observed filamentous alga in streams and rivers (Fig. 2a). Commonly, *Cladophora* is a green alga growing as algal mats, often dominating primary production in flowing water. The attached algal mats, sometimes attaining lengths of 5–10 m, potentially control biogeochemical nutrient and carbon cycling. Furthermore, *Cladophora* mats provide refuge for microorganisms, sheltering them from predators and excessive water currents. Bacteria and diatoms such as *Epithemia turgida* colonize *Cladophora* filaments in this way, changing the filaments' color from yellow to rusty red in September. Velocity measurements conducted by acoustic-Doppler velocimetry (ADV) and particle image velocimetry (PIV) in the field revealed turbulent flows in the water above *Cladophora* mats and slow-moving laminar flows inside the mats. One of our objectives was to investigate the uptake of nutrients by *Cladophora* filaments in the mat and how that uptake is connected to the associated water flow fields.

Under laboratory conditions, a water flow containing *Cladophora* filaments was set up and flow velocities measured by digital holography. From these data, velocity gradients were estimated in the proximity of the filaments and the laminar flow skin friction drag coefficient was calculated by $C_D = \frac{8 \tau_s}{\rho U^2} = \frac{8 \mu \left(\frac{du}{dy} \right)_{y=0}}{\rho U^2}$ where C_D is the skin friction drag coefficient, ρ is the water density, U is the discharge velocity, τ_s is the shear stress at the surface of the filament, μ is the dynamic viscosity, u is the local velocity along the filament, and y

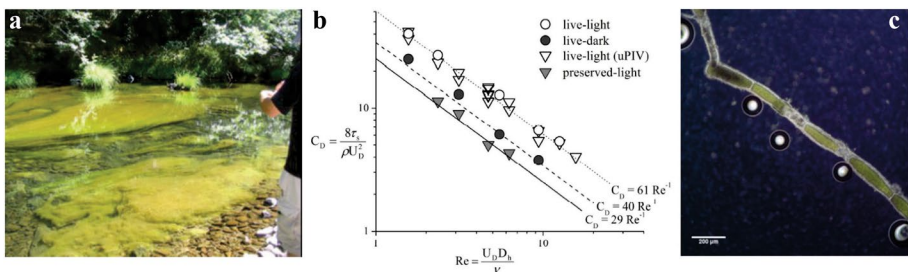


Fig. 2 a A mat of *Cladophora glomerata* in the Eel River (Angelo Range Research Reserve, CA), b Laboratory experimental results under light and dark conditions demonstrating the relationship between the skin friction drag coefficient, C_D , and the Reynolds number, Re . Live-light and Live-dark are live filaments exposed to light and dark conditions, respectively. Preserved-light filaments are dead filaments (soaked in 70% ethanol for 16 h, rinsed, then stored at 4 °C) exposed to light. c Microscopic image of micro-bubbles attached to the surface of a *Cladophora* filament after 3 h light exposure in a solution of growth media and 1 μm seed particles. In collaboration with National Center for Earth-surface Dynamics, Mary Power, and Amy T. Hansen

is the vertical upward distance perpendicular to the surface of the filament. For the associated flow, the power-law relationship $C_D = \frac{A}{R_e}$, A is the constant and R_e is the Reynolds number, depicted by the well-known Moody diagram, was used. In laminar flow, the variable A should be constant and independent of surface roughness. Our laboratory measurements revealed a 1.5 times larger skin friction drag coefficient and shear stress for photosynthesizing filaments (live-light) than for identical non-photosynthesizing (live-dark) filaments (Fig. 2b). Under the light, the filaments produced oxygen microbubbles (Fig. 2c). One possible explanation of the difference in skin friction drag coefficients for photosynthesizing and non-photosynthesizing filaments is the effect of microbubbles attached to the surface of photosynthesizing filaments, elevating the surface roughness and associated drag. Simple laminar flow theory underestimated skin friction drag and nutrient uptake ($J \sim R_e \sqrt{C_D}$) due to photosynthesizing filaments having a skin friction drag 1.5 times greater than theory predicts. The nutrient uptake by the non-photosynthesizing filaments was approximately 50% below that predicted by laminar flow theory. Algal mats of *Cladophora* are made up of thousands of individual filaments and thus act as “multipliers” since the total surface area of filaments can be orders of magnitude larger than what we see in a stream (Fig. 2a). Since the total nutrient uptake (J_T) is proportional to the entire surface area (A_s) of filaments, $J_T \sim J \cdot A_s$, the underestimated nutrient flux can be significant.

Ecological fluid mechanics issues are often investigated at organism scale under controlled laboratory and predominantly steady-state conditions. However, organisms can experience a variety of states that vary in space and time during their active or passive transport through their aquatic habitats. Exploring ecological fluid mechanics at reach, network, and watershed scales has been a particular challenge to the research community. While a “universal” scaling of turbulent kinetic energy has been explored in the field of fluid mechanics, the scaling relationships of organism growth kinetics across the spatial and temporal scales of large ecosystems are poorly understood. The advent of new field measurement technologies, including miniature Lidar, PIV, and spectral imagery by drones and other UAVs promises to better reveal the spatial and temporal heterogeneities of hot spots, hot moments, biomass, and preferential flow and habitat pathways across landscapes. Furthermore, adapting ecological research to a moving reference frame, one that follows an organism in space and time, may well prove advantageous since these organisms experience a variety of physical and chemical conditions through preferential flow paths that likely optimize their growth kinetics. The “*Cladophora*” lesson suggests that simple and widely accepted theory can prove inadequate in capturing the true physiological functioning of living organisms. The altered relationship of C_D versus Re in a laminar flow containing *Cladophora* as described above can be called a biologically-mediated Moody diagram. Scientists and engineers often devote significant effort to employing new ways to measure and characterize ecological environments. Less attention is paid to the understanding of these environments which enable the physiological and metabolic functioning of their resident organisms. In all, *ecological fluid mechanics concerns the interaction of living organisms and the environmental motions in which they reside* and it continues to be a very challenging branch of environmental fluid mechanics.