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Ocean Ecology: Understanding and Vision for REsearch

Physiological, Ecological, and Evolutionary Consequences of the Hydrodynamics of Individual Organisms

M. A. R. Koehl

Department of Integrative Biology
University of California at Berkeley
Berkeley, CA 94720-3140

I. INTRODUCTION

A. Scope of Topic

Processes operating at the level of individual organisms can determine the properties of populations, communities, and ecosystems. This "white paper" focuses on how a mechanistic, organismal-level understanding of mass and momentum exchange between marine organisms and the surrounding water can provide predictive insights to studies in ocean ecology. Conversley, the evolution of organsimal-level traits (physiological, morphological, behavioral) cannot be understood without studying the ecological context in which natural selection operates. Therefore, this paper also mentions how information about the physical and biological oceanographic context in which populations live can enhance investigations of the evolution of organismal-level traits affecting hydrodynamic performance.

This paper focuses on small-scale exchange of momentum and mass between individuals and the surrounding water on the spatial scale of microns to meters. Organismal-level aspects of momentum exchange include organisms pushing on the water (e.g. swimming, creation of feeding or respiratory currents) and ambient flow imposing loads on organisms (e.g. deformation, damage, or removal of benthic organisms by waves and currents). Organismal-level aspects of mass exchange include the supply of dissloved materials (e.g. oxygen, nutrients) to the exchange surfaces of individuals; the dispersal, sensing, and tracking of chemical cues; the transport and capture of particluate food for suspension-feeders and deposit feeders; the removal of dissolved and solid wastes of organisms; the transport and mixing of gametes of macrophytes and spawning animals; and the dispersal and settlement of propagules (e.g. larvae, spores, rafters). This topic includes not only the small-scale water flow involved in these aspects of mass and momentum exchange, but also organismal morphology, behavior, physiology, and mechanical properties that affect mass and momentum exchange. Biofluiddynamical subjects that are covered in other white papers are not discussed in detail here, even though they represent important aspects of how water flow affects important ecological and evolutonary processes: flow effects on larval settlement and on soft-substratum benthos should be covered in the Butman and Davis paper, on dispersal of chemical cues should be discussed in the Zimmer-Faust paper, and on transport at scales greater than meters should be addressed in the Malone and Botsford paper.

B. Brief History

The history of organismal-level biomechanics and biofluiddynamics can more accurately be described as the convergence of work by researchers from different fields than as the evolution of a single discipline. Fluid dynamicists (e.g. G. I.

Taylor, J. Lighthill, T. Wu), physicists (e.g. E. M. Purcell), and applied mathematicians (e.g. S. Childress, C. Peskin) have worked on biological flow problems, while bioengineers (e.g. T. McMahon) who usually addressed medical or sports problems have sometimes studied non-human creatures. In the more recent blossoming of the field of biomimetics, engineers designing such man-made things as composite materials, sensors, and robots, have studied basic biological designs for ideas. In biology, the European approach of quantifying organismal form (e.g. D'Arcy Thompson) and locomotion (e.g. J. Gray), and then of applying engineering analyses in studies of functional morphology (e.g. R. M. Alexander, J. D. Currey, W. Nachtigall, C. Pennycuick, T. Weis-Fogh), was popularized during the past two decades among biologists in the USA by books by Wainwright (solid mechanics) and Vogel (fluid dynamics). Simultaneously, some animal and plant physiologists and physiological ecologists interested in respiration, circulation, thermoregulation, and energetics (e.g. K. Schmidt-Nielsen, C. R. Taylor, P. Nobel, W. Porter) have incorporated engineering analyses in their work, as have some neurobiologists interested in locomotory motor control, mechanoreception, or olfaction. Some evolutionary biologists (e.g. K. Leim) and paleontologists (e.g. S. Stanley) have also used biomechanics/biofluiddynamics as a tool in their analyses of the process of adaptation, the sources of evolutionary novelty, and the functions of exctinct organisms. Although many of the studies that have grown out of these various traditions have used marine organisms, their impact on oceanography has been small, probably for two reasons: 1) the species studied (chosen as tractable systems for addressing basic biomechanical, physiological, or evolutionary questions) often were not of oceanographic importance, and 2) the spatial scale of fluid flow analyzed was smaller than that studied by physical oceanographers, and the levels of biolgical organization studied (organismal, organ system, tissue, and celluar) were lower than those important to most biological oceanographers (ecosystem, community, population).

Although oceanographers have long understood the importance of the physics of the ocean to biological processes, they have mainly focused on biological-physical interactons at spatial scales larger than that of individual organisms. In the field of marine ecology (i.e. using marine systems to study basic ecological questions), investigating the role of physical factors in determining population and community structure and organism distribution has gone in and out of vogue and has not focused on mechanisms at the organismal level. However, some notable exceptions in oceanography and marine ecology during the past few decades have included organismal-level biofluiddynamical studies of feeding and recruitment of soft-substraum benthos (discussed in Butman white paper), of food capture by zooplankton (e.g. M. Koehl, R. Strathmann, J. Yen), of nutrient uptake by phytoplankton and bacteria (I need help here with names of some early workers in this area), and of mechanisms of particle aggregation in the water column (I need help here too). Furthermore, quantitative engineering studies of wave- and current-swept organisms (e.g. Koehl, Denny) have revealed mechanisms responsible for differences in the susceptibility of different types of benthos to physical disturbance, while engineering analysis of basic designs of digestive systems (e.g. Penry, Jumars) has provided insights in foraging ecology.

C. Significance of Previous Discoveries and Insights

This smorgasboard of organismal-level biofluiddynamical and biomechanical studies done in a variety of fields has shown that general physical rules apply across taxa and can provide powerful tools for understanding and predicting how organisms interact with their physical environments. Furthermore, since the performance of an organism is the crucial link between its phenotype and its ecological success, organismal-level mechanistic research can be used in concert with other tools to gain insights about issues in ecology (e.g. foraging, competition, disturbance, keystone species, functional groups) and evolution (e.g. adaptation, interpretation of fossils, and origin of novelty), as reviewed in Schoener (1986), May, et al. (1989), and Koehl (1996). Mechanistic analyses of how function depends on biological form have revealed morphological constraints on habitat use, on ecological interactions such as competition or predation, and on reproductive strategies. Quantitative organismal-level studies also enhance theoretical ecology by elucidating factors that can be ignored versus those that must be included in mechanistic ecological models, by testing the assumptions of such models, and by providing realistic values for parameters used in model calculations.

II. STATE OF THE FIELD

A. Accepted Knowledge

Within the field of biomechanics/biofluiddynamics, it is accepted that basic principles of fluid and solid mechanics are very useful in telling us how organisms work. Engineering analyses have revealed the mechanisms by which organisms do physical things such as swim, run, burrow, capture food or molecules, chew, fight, and resist external loads imposed by e.g. predators or ambient water flow. Such quantitative mechanical approaches have also revealed basic rules about how organismal morphology determines performance of these biologically-important functions, and about the physical constraints on organisms of different sizes and body designs.

Although it is accepted that quantitative mechanistic analyses help us sort out how organisms work, not everyone agrees that such information is useful in addressing larger scale evolutionary, ecological, or oceanographic problems. For example, although the paradigm that morphology affects performance, which in turn affects fitness, is the cornerstone of modern "ecomorphology", there is disagreement about whether mechanistic information is necessary for such analyses, which are usually done by statistical correlation. Other areas that are still subject to debate at the interface between biomechanics and evolutionary biology include whether or not quantitative optimality approaches are useful, and whether or not studies of form and function are worth pursuing if not done in a phylogenetic context. Similarly, many ecologists and oceanographers contend that, when studying or modeling processes at the population, community, or ecosystem level, it is sufficient to know THAT organisms do certain things (e.g. eat, migrate, spawn, wash away) at particular rates, but not necessary to know HOW these functions are performed or to know the organismal-level mechanisms determining their rates. Conversely, others argue that a multiplicity of approaches and that information about function across a range of levels of organization enhances our ability to answer questions and make predictions about ecological oceanographic processes.

B. Examples of Exciting Recent Findings and Doors They Open to the Future

There are a number of exciting recent advances in studies of trophic interactions of marine organiams, of life history strategies and dispersal, and of benthic community structure in which mechanstic organismal-level studies are playing an important role.

General models about the physical mechanisms involved in particle capture and particle deposition on the substratum, as well as quantitative experimental studies of the hydrodynamics of feeding by a variety of suspension-feeding and deposit-feeding organisms (from copepods to corals, from polychaetes to protozoans) are elucidating the effects that water flow, that particle size and shape, and that feeding-appendage morphology, size, stiffness, kinematics, and adhesiveness can have on rates of particle capture. Such information should permit us to understand mechanisms responsible for selective feeding, and thus the physical constraints on foraging strategies of organisms of different designs. It should also enable us to better predict the effects of ambient flow or community compositon on the flux of material between the water column and the benthos, and through important components of planktonic food webs. Such mechanistic information about the design of particle-capturing devices should also enhance studies of the evolution of feeding modes in various lineages of aquatic organisms.

Recent experimental studies measuring effects of steady shear or of small-scale turbulence on feeding rates or behaviors of various planktonic organisms, coupled with general models of how turbulence might affect encounter rates of small organisms, suggest that organismal-level studies of the physical mechanisms by which turbulence affects trophic interactions could be a rich area of future study. There is still much to be learned about how turbulence characteristics of various parts of the ocean translate into the temporal and spatial patterns of local shear encountered by organisms of various sizes, and how that in turn affects swimming mechanics, feeding-current production, and the encounter, capture, and retention of food by organisms of different morphologies and sizes. Such organismal-level mechanistic informaton could greatly enhance our ability to predict the effects of turbulence on food web dynamics, and to better understand the functinal morphology and the distribution in the ocean of organisms using differnt types of feeding techniques.

Mechanistic approaches similar to those used in research on particle feeding are also being used to model the the physical processes involved in particle aggregation, break-up, and sinking in the water column. The development of such predictive theories at a time when it is technically possible (via diving, ROV's, and submersibles) to observe and sample marine snow in the field poses exciting possibilities for making significant progress in understanding the flux of material between the surface waters and the benthos in the ocean.

Recent efforts in modelling and measuring the mechanisms of capture of molecules by marine organisms (e.g. during nutrient uptake, gas exchange, olfaction) is following a similar course to the above-mentioned mechanistic studies of particle capture. We should be able to develop predictive physical rules governing how the morphology and size of organisms or their molecule-capturing structures, the diffuson coefficients of the molecules, and the small-scale water flow relative to the organisms' surfaces affect rates of molecule capture. Such a basic mechanistic theory should help us understand such diverse processes as nutrient uptake by bacteria, food location by deep-sea carrion feeders, mate-finding by zooplankton, gas exchange by corals, or photosynthesis by kelp or phytoplankton. Now is also an exciting time for learning about the hydrodynamics of how dissolved materials are mixed and moved by ambient water flow in the ocean (see white papers by Butman and Davis, and by Zimmer-Faust).

Several lines of ongoing organismal-level research should yield information that can be integrated to produce a better understanding of foraging strategies used by organisms of diverse body designs and sizes in various parts of the ocean. The possibility of coupling insights from studies of the mechanics and energetics of various modes of locomotion and mechanisms of food capture by marine organisms, with principles learned in investigations of the physics of how mechanical and chemical cues in the water are transmitted and used by organisms to locate their prey and avoid their predators, and then meshing those concepts with the general models of mechanisms of digestion (described above) holds great promise for a comprehensive overview of foraging. Such basic mechanistic informaton should also elucidate physical constraints on tropic interactions, and thus may enhance our understanding of marine food webs. Much information that could be incorporated into such a comprehensive framework is already being gathered by researchers studying evolutionary and biomechanical questions. For example, fish are a popular system for the study of evolutonary novelty and the process of adaptation, hence a lot of information is being gathered about how the morphology of fish heads affects the hydrodynamics of food capture and the mechanics of food biting/crushing. Fish are also popular systems for studying the fluid dynamics and energetics of paddling and of undualtory swimming by animals of differnt body shapes and sizes. Similarly, various benthic arthropods are being used as systems to study the mechanics, energetics, and hydrodynamic constraints on underwater and amphibious legged locomotion, while their antennules are being used as systems to study the design of olfactory sensors, their behavior to study strategies for following odor plumes, and their claws to investigate the design of biological crushing and cutting tools as well as the evolutionary "arms race" between predators and prey.

Exciting advances are being made in the study of reproduction and dispersal of marine organisms. Evidence is accumulating about the importance of larval/propagule dispersal and recruitment to the composition of marine communities and the genetic structure of populations in the ocean (see white papers by Botsford & Malone, and by Jackson & Palumbi). At the same time, organismal-level studies of effects of benthic boundary layer flow on larval settlement are revealing the mechanisms responsible for where larvae end up on the substratum (see Butman & Davis white paper). Similarly, new information is being gathered about the effects of organismal-level factors (e.g. the morphology and spawning behavior of benthic animals, the structure of the aggregations they form, and the topography of their immediate neighorhood) on small-scale flow, and hence on gamete mixing and dilution, fertilization success during spawning, and the initial stages of larval transport. Biomechanical studies are revealing the importance of the physical characteristics (e.g. viscosity, bouyancy) of spawned material to fertilization success, and are showing how local shear can either enhance or hinder the joining of egg and sperm. Furthermore, studies are beginning of the physical mechanisms by which motile animals use mechancal and chemical cues in the water to locate mates. Such studies could help lead to a general overview of the spatial and temporal scales over which different sorts of cues (e.g. visual, mechanical, chemical) can be used by organisms of various sizes in different flow habitats in the ocean. (Such a general, mechanistic view of how the ocean environment affects how organisms sense each other would not only help us understand mating strategies, but also other ecologically-important encounters between organisms, such as predator-prey and competitive interactions.)

Both modeling and empirical research on hydrodynamic forces on benthic organisms are becoming more sophisticated and comprehensive, and also are being increasingly well-integrated with ecological studies in rocky shore and coral reef habitats. Our understanding of how the size and shape of an organism can affect the magnitude of the hydrodynamic forces it experiences in different types of ambinet flow regimes is now being extended by recent investigations of: 1) the mechanisms by which an individual's deformability can affect the flow and force it encounters, and 2) the consequences neighboring organisms on hydrodynamic forces experienced. The molecular mechanisms responsible for the mechanical properties of the adhesive structures (e.g. byssal threads, glue) of some sessile organisms are being worked out. Recent studies are also quantifying how the probability of damage or dislodgement of a benthic organism depends on the spatial and temporal distributon of hydrodynamic forces encountered in its habitat. The biophysics of microclimate and of heat and water exchange when in air is being included in mechanistic analyses of intertidal organisms. Integrating this information about organismal design and physical habitat should lead to predictive theories about the susceptibilty of different types of organisms to various regimes of physial disturbance, and hence can contribute to our understanding of mechanisms affecting community structure. Furthermore, patterns are starting to be recognized in life history strategies that correlate with contrasting types of mechaincal designs in physically-stressful habitats. In addition, physical limitations on the foraging patterns of motile organisms in wave- and current-swept habitats is being investigated and related to comunity structure. Wave- and current-swept organisms are also being used in studies of the evolution of mechanical safety factors and of morphological plasticity.

Evidence is accumulating that the impact of a particular species on community structure and ecosystem dynamics depends on the ecological context (e.g. physical conditions, time since disturbance, ecosystem productivity). "Keystone species", now defined as those species whose impact on a commnity or ecosystem is disproportionately large relative to their abundance or biomass, may not be dominant controlling agents in all parts of their range or at all times in the succession of a community. By weaving together an organismal-level understanding of how habitat affects the performance of a sometimes-keystone species, with ecological patterns of the contexts in which it does play an significant role, we may reveal the mechanisms responsible for the context-dependency of their importance. "Functional groups" are suites of species that play equivalent roles in an ecosystem. Understanding the mechanisms responsible for functional equivalency at the organismal level may help us identify the circumstances under which one species can play the same ecological role as another.

C. Current Foci and Rationale for Them

Current foci within the field of organismal biomechanics include both more sophisticated and integrative approaches to studying mechanism, and more effort to interface with evoltuionary biolgists and ecologists. The importance of non-steady-state fluid dynamics in locomotion through fluids (e.g. swimming, flying, running on the substatum) and in mechanical loads imposed on organisms by ambient flow is now recognized and is an active area of inquiry. Investigations of the fluid dynamics at intermediate Reynolds numbers are now beginning to be explored, since so many organisms function in this poorly-understood range at some time during their ontogeny. The role of elastic energy storage in animal movement is currently receivng a lot of attention because it is providing critical information about both the mechanisms and the metabolic costs of various modes of locomotion. There has also been increasing interest in developing integrative approaches to studying animal locomotion, coupling neural control, muscle properties, tissue mechanics, and fluid dynamics in analyzing the limits to performance. Recent technological advances (e.g. "optical tweezers", nanofabrication, confocal microscopes) have permitted biomechanical experiments to be done at the level of embryos, cells, and molecules. Biomimetics (mentioned above) is also a growing area of study. Another recent focus among some biomechanicians has been the incorporation of new phylogenetic and statistical techniques to try to identify morphologcial adaptations, and to sort out features of organisms that are due to their phylogenetic history. There is also now more interest in trying to quantify the physical environments (e.g. fluid-dynamic conditons) under which organisms operate in nature, and to relate mechanical performance to the fitness of organisms in the field.

Current foci in oceanography and marine ecology that interface with organsmal-level mechanistic research are discussed above in the section on "examples of exciting recent findings and doors they open to the future".

III.EXISTING INFRASTRUCTURE

A. Strengths and Weaknesses of the Technology

There are many technological advances that are enhancing research about organismal-level hydrodynamics and mechanical function. The development of ever more powerful computers and advances in computational fluid dynamics and finite element modeling now permit analysis of flow and mechanical performance of more complex, biologically-relevant models of e.g. organisms, appendages. Fumes and wave tanks have been developed that can mimic biologically-relevant scales of water flow for controlled experiments in the lab. Laser-doppler anemometers, laser-induced flourescence probes, and video particle-tracking velocimetry permit detailed quantificaton of small-scale flow in the lab. Clever optical techniques coupled with high-speed cinematography and video permit the behavior, kinematics, and water flow of small planktonic organisms in aquaria to be visualized in the lab. Field-portable acoustic-doppler and electromagnetic flowmeters with computer data-acquisition systems permit flow to be measured in nature on appropriately small spatial and temporal scales for organismal-level studies. Similarly, field-deployable video systems make it possible to record animal behavior and kinematics as well as tracers of water flow under natural conditions, even in challenging habitats such as wave-swept shores and the deep sea. Videos can now be made in the field at sufficiently high magnification to permit in situ recording of the behavior of planktonic organisms. Field telemetry systems permit tracking and some physiological monitoring of large animals such as seals and tuna.

There are also a number of areas in which technological improvements would be very helpful. For example, high-speed video is necessary for kinematic analysis (e.g. of locomotion, feeding) of most organisms; although there are field portable high-speed video systems that have been developed for studying explosives, similar systems for use underwater would be invaluable for quantifying kinematics in the field under natural conditions. Furthermore, standard user-friendly commercial software is not available yet for motion analysis of organisms in fluids; investigators must write their own or modify systems designed for analyzing human atheletes. Similarly, small field-hardy, waterproof force transducers and displacement transducers are not available off the shelf. Systems that can generate quantifiable realistic temporal and spatial patterns of shear in the lab need to be developed to replace the Cuette cells currently being used in studies of effects of shear on organism function. Methods to tag and follow small individual animals in the water column would be helpful. In addition to new tools, such as the examples just listed, we also need better communication between the diverse scientists gathering data with the technology that already exists. For example, biomechanicians are doing precise quantitative studies in the lab to sort out mechanism, but they don't have information on the physical conditons in field under which the animals or plants have to operate. Similarly, wonderful videos have been made from ROV's and submersibles that could have yeilded invaluable biomechanical information if only they had had a size scale.

B. Strengths and Weaknesses of the Intellectual Background

The existing intellectual infrastructure for work in oceanographic organismal-level biofluiddynamics is strong, but perhaps too dispersed. Biological oceanographers already understand the importance of physical factors to ecological processes, and a few are now also coming to see the importance of biological-physical interactions at smaller scales as well. Although physical oceanogrpahers generally study water flow at spatial scales that are too large to be relevant for organismal-level function, engineers do work at the appropriate scales and have developed an intellectual framework and technical expertise that can be applied to marine organisms. Nonetheless, with the exception of researchers studying benthic boundary layers, most oceanogrpahers have not been measuring physical parameters in the field on spatial and temporal scales that are useful to investigators modeling organismal-level functions or trying to design realistic lab experiments. Similarly, although biomechanicians and bioengineers have learned a great deal about the basic mechanics of locomotion and about the structural design of organisms, they have focused most of their efforts on terrestrial vertebrates. Furthermore, the majority of biomechanicians and biofllliddynamicists do not study organisms in nature. While the recent trend among ecologists is to focus on rigorous statistical design of field experiments, technical constraints make these approaches difficult to translate to oceanographic studies in the water column, and to time-consuming equipment-intensive biomechanical field studies. Similarly, the current fad among organismal biologists is to generate phylogenies (the trendiest ones being molecular) and to use statistical approaches to map organismal form and function onto those phyolgenies, while in contrast most oceanographers appear to work in a phylogenetic vacuum. Thus, the intellectual infrastructure necessary for organismal-level mechanistic analyses of marine organisms is active and strong, but it is scattered between departments of oceanography, engineering, mathematics, and biology. Furthermore, the recent trend at universities of separating biologists into cell & molecular departments on the one hand and ecology & evolution departments on the other hand, has left organismal biologists dangling uncomfortably in between. With effort to communicate about the important questions and approaches in each of these disparate disciplines, those studying organismal-level biofluiddynamics can bridge the gaps between these diverse fields, but it is still difficult to envision where to train students who wish to work in this area.

IV. EXCITING FUTURE OPPORTUNITIES AND CHALLENGES

A. How They Would Advance the Field of Biofluiddynamics/Biomechanics

The potential for advances in specific areas of mechanistic organismal research have already been discussed above in section II, C. More generally, if the challenge of marrying such approaches with oceanographic questions can be met, this collaboration could lead to exciting future opportunities in both fields. There are a number of examples of ways that mechanistic organismal research would benefit from better ties with oceanography. The generality of biomechanical principles can be better tested if a wider range of organisms is studied. The biological relevance of features being analyzed can only be determined if the physical environment , life history, and ecological interactions of the organisms are also known. Similarly, studies of the evolution of organsimal-level traits (physiological, morphological, behavioral) of marine creatures will be greatly improved by complementary oceanographic information about the ecological context in which natural selection operates.

B. How They Would Advance Our Understanding of Oceanography, Ecology, and Evolution in General

Section II,B above discusses the potential for advances in specific areas of oceanography that would be possible if organismal-level mechanistic studies were coupled with oceanographic investigations. Furthermore, since the performance of an organism is the crucial link between its phenotype and its ecological success, insights about organismal-level mechanism can be used in concert with other tools to gain insights about basic ecological issues (such as foraging, competition, disturbance, keystone species, and functional groups) and about basic evolutionary issues (such as the process of adaptation, the relationship of morphology to fittness, and the evolutionary origin of novelty). The biggest challenge to these advances is the communications gap between the oceanographers, organismal biologists, ecologists, evolutionary biologists, mathematicians, and engineers whose expertise must be successfully meshed (see section III, B above).

V. SUMMARY

A mechanistic, organismal-level understanding of mass and momentum exchange between marine organisms and the surrounding water can provide predictive insights to studies in ocean ecology. Furthermore, information about the physical and biological oceanographic context in which populations live can enhance investigations of the evolution of organismal-level traits affecting hydrodynamic performance. Organismal-level aspects of momentum exchange include swimming, and creation of feeding or respiratory currents, as well as deformation, damage, or removal of benthic organisms by waves and currents. Organismal-level aspects of mass exchange include the supply of dissloved materials (e.g. oxygen, nutrients) to the exchange surfaces of individuals; the dispersal, sensing, and tracking of chemical cues; the transport and capture of particluate food for suspension-feeders and deposit feeders; the removal of dissolved and solid wastes of organisms; the transport and mixing of gametes of macrophytes and spawning animals; and the dispersal and settlement of propagules (e.g. larvae, spores, rafters). This topic includes not only the small-scale (microns to meters) water flow involved in these aspects of mass and momentum exchange, but also organismal morphology, behavior, physiology, and mechanical properties that affect mass and momentum exchange. Mechanstic organismal-level studies are playing an important role in a number of exciting recent advances that can open doors to future resarch on trophic interactions of marine organiams, on life history strategies and dispersal, and on benthic community structure The biggest challenge to these advances is the communications gap between the oceanographers, organismal biologists, ecologists, evolutionary biologists, mathematicians, and engineers whose expertise must be successfully meshed. If this collaboration is to succeed, not only must we learn the tools of eachother's trades, but we must also come to understand and respect what he important questions and issues are in eachother's fields.

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webmaster@joss.ucar.edu
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