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Inside JEB

BIOPHYSICS, BIOENERGETICS AND MECHANISTIC APPROACHES TO ECOLOGY

Biophysics – the study of how the structure of individual plants and animals contributes to their function – has rarely been considered on the ecological scale. However, Mark Denny from Stanford University, USA, has a broader vision. Because the mechanisms that underpin individual performance also play a part in ecological processes, Denny proposes that, 'It's time we move beyond biophysics as an explanation for how an individual organism behaves and start applying the same mechanistic approach to how individuals interact with each other and their environment, to explore the connection between biophysics and ecology'. Guided by this inspiration, Denny has gathered together a collection of reviews and original research addressing the mechanisms that underpin ecological structure and function with the intention of bridging the current knowledge gap between biophysics, biomechanics, physiology and ecology.

Dividing the collection along three themes, Denny initially considers the biological and physical mechanisms that underpin ecology before considering the emergence of large-scale patterns in response to individual small-scale interactions in ecosystems. Finally, he turns to the impact of turbulence on various scales in the ocean and the ecological impact on a wide range of biological processes.

FROM MOLECULES TO ECOSYSTEMS: LINKING PHYSIOLOGY TO ECOLOGY

The collection begins at the molecular level with Herbert Waite and Christopher Broomell's review of the structures and mechanical properties of various biomaterials, with a focus on the byssal threads that anchor mussels to rocks (p. 873). Explaining that mussels – the dominant competitors for space on many rocky shores – depend on the structural integrity of these byssal threads for survival, Waite and Broomell outline the methods used to assess the threads' structural integrity at different length scales under various physiological conditions. They point out that in addition to considering the physical environment, seawater chemistry also significantly impacts the quality and mechanical properties of the byssal thread with implications for the survival of mussel populations.

Continuing the theme of ecomechanics on the molecular scale, Andrew Whitehead, from Louisiana State University, USA, takes a genomics approach to understand the molecular processes that underlie environmental acclimation and adaptation (p. 884). Discussing the analytic techniques routinely applied in comparative genomics, Whitehead describes several ecophysiological case studies on organisms – ranging from comparative studies of bees and wasps to understand the evolution of social behaviour, to studies of killifish addressing acclimation and adaptation to salinity and pollutants.

Changing scale to consider physical interactions within ecosystems, Stacey Combes (p. 903) discusses her work on the mechanisms of predator–prey interactions and Emmanuel de Langre (p. 914) reports on his studies of flow-induced vibrations in plants. With a well-established background in the classical biomechanics of animal flight, Combes and her colleagues have adopted ecological and biomechanical approaches to analyse factors affecting the behaviour of predatory dragonflies pursuing fruit flies in a natural flight arena (p. 903). Describing how prey density influences the dragonflies' success, Combes also discovered that targeted fruit flies rarely take direct evasive action, succumbing to their doom. However, by analysing the fruit flies' trajectories, she discovered that the insects take erratic flight paths to evade their predators.

Considering the influence of wind on plant structures, de Langre draws insight from mechanical engineering theory derived for the nuclear power industry. In a nuclear reactor, vibrations are generated in the tightly packed tubes of the heat exchanger, where heat is transferred from the nuclear core by coolant that flows inside the tubes to heat water outside the tubes to generate steam and drive electricity generation. De Langre shows that these flow-induced vibrations are analogous to the way that tree canopies move in the wind (p. 914). Successfully applying the mechanical engineering theory to plants, de Langre also points out the theory's shortcomings, as it does not take into account growth, adaptation, or the differences between natural and 'engineering' selection. He says, 'A good understanding of these similarities and differences is needed to work efficiently in the application of a mechanistic approach to ecology'.

The collection then moves from the realm of empirical measurement and physical theory to that of theoretical models. Denny notes, 'Ecology is extraordinarily complex. To make sense of this complexity, we need theories that can tell us how to synthesise the details, how to build up from individual interactions to understand how an ecosystem works'. With this in mind, he commissioned three articles (Nisbet et al. 2012, *J. Exp. Biol.* **215**, 892-902; Denny and Dowd 2012, *J. Exp. Biol.* **215**, 934-947; and Basket 2012, *J. Exp. Biol.* **215**, 948-961) discussing the use of theoretical constructs that allow ecologists to make ecological predictions based on physiological and biophysical factors.

Describing dynamic energy budget (DEB) theory, Roger Nisbet explains that the approach uses concepts such as somatic maintenance and energy conductance to calculate an individual's performance (p. 892). Pointing out that this intensely theoretical approach results in abstract combinations of real-life variables that are difficult to disentangle, he also explains that integrating traditional bioenergetic variables, such as metabolic rate, into DEB models had been problematic. However, Nisbet has successfully developed equations, which relate abstract DEB state variables to measurable physiological parameters, to build DEB models of the Pacific bluefin tuna and Pacific salmon that accurately predict both species' life histories.

In Denny's own contribution to this collection of articles, he describes a mathematical simulation – developed in collaboration with Wes Dowd – of how thermal tolerance evolves in limpets (p. 934). Based on an understanding of the thermal physics of intertidal organisms and a statistical description of their physical environment, Denny and Dowd found that rare, random thermal events lead to the evolution of a surprisingly high safety margin in these animals, 5 to 7°C above the maximum body temperature they are likely to encounter in an average year. Pointing out that most limpets are unlikely to experience such high temperatures in their lifetimes, Denny and Dowd suspect that the limpets' generous thermal tolerance is maintained by the rare extreme events that wipe out the least tolerant individuals, shifting the gene pool towards greater temperature tolerance.

Applying knowledge of physical parameters to models of population dynamics, Marissa Baskett has also taken a theoretical approach to model population changes from ecological and evolutionary perspectives, incorporating the effect of environmental factors such as temperature (p. 948). Despite the lack of realism, which limits the predictive power of simple models, she points out that such models can be very useful for determining which factors are more likely to have major ecological impact, allowing the identification of strategies that will best protect the ability of populations and communities to respond to environmental change.

Concluding the section relating physiology to ecology, Michael Kearney, from The University of Melbourne, Australia, and colleagues Alison Matzelle and Brian Helmuth, from the University of South Carolina, USA, warn that the quality of predictions emerging from theoretical models are dependent on the resolution of the input data (p. 922). Describing how mechanistic niche modelling links organismal characteristics to their environment to make ecological predictions, Kearney explains how the frequency with which such physiological inputs are measured can dramatically affect the results that these models yield. Outlining a DEB case study where predictions were made about the fecundity and size of *Sceloporus undulatus* lizards based on climate niche models in which the environmental data were collected at different frequencies, Kearney and his colleagues say, 'Fundamentally different results can accrue given the temporal resolution of input data used, and this is especially important for organisms with limited behavioural thermoregulatory ability (such as sessile or semi-sessile organisms) or organisms living in low-quality habitats'.

MECHANICS AND THE EMERGENCE OF PATTERN

Biology is full of examples of interactions between individuals that result in large-scale organised structures well beyond the occupants' direct influence. Ecological spatial patterns can arise naturally through individual interactions, independent of the surrounding landscape. However, Johan van de Koppel, from the Royal Dutch Institute for Sea Research, challenges the scope of this assertion in his review of three estuarine ecosystems, suggesting that landscape-scale factors also contribute to the development of self-organised spatial patterns (p. 962). Describing estuarine mussel beds, mudflats and salt marshes, Van de Koppel, Tjeerd Bouma and Peter Herman outline the interaction between physical and ecological processes that shape all three systems; for example, the interplay between mussel attachment strength, filter feeding and tidal flows that produce the banding often found in mussel beds, or the ecological factors that produce the feathery, fractal drainage patterns found in salt marshes. The trio say, 'We argue that to explain the patterns observed in self-organized ecosystems, both processes occurring at small spatial scales and processes occurring at the landscape scale need to be considered'.

Moving further out to sea, Joshua Madin from Macquarie University, Australia, considers the physiological and mechanical effect of water flowing over delicate coral reef structures (p. 968). Explaining how flows can affect corals on a number of different levels – physiological (photosynthesis, calcification and respiration) and mechanical (physical storm damage) – Madin and colleagues Mia Hoogenboom and Sean Connolly construct a model that integrates the biochemical and biomechanical impacts of wave exposure on individual corals. They then scale the effects up to the population level to predict the performance and distribution of scleractinian reef corals. The trio confirms their model by showing that their predictions for the distribution of *Acropora hyacinthus* corals agree well with the distribution found throughout the Indo-Pacific region. Ultimately, they intend to use their model to make predictions about coral distributions in response to anthropogenic climate change.

Another ecosystem that is vulnerable to the climatic effects of human activity is that of canopy algae, which offer shelter to a wide range of understory algae and invertebrates. Lisandro Benedetti-Cecchi and colleagues from Italy and the USA explain that canopy algae are being replaced by less productive turf algae (p. 977). Using scale-transition theory applied to small-scale observations of the local density of turf and canopy algae, the team successfully predicted the short- and long-term development of turf algae populations on the rocky shore of Capraia Island, Italy. The team concludes, 'Scale-transition theory will provide a powerful tool to connect individual-, population- and community-level dynamical processes across ecological scales, fostering our understanding of natural and anthropogenically induced large-scale biodiversity changes'.

Roi Harel

While many of the processes previously outlined have influenced the evolution of visible ecological patterns, Ran Nathan and an international team of collaborators describe their work with free-ranging animals to understand the processes shaping animal movements (p. 986). Nathan explains that there are four basic components that are common to all movement phenomena. He hopes to build a new understanding of the factors governing movement in an ecological context and create a novel general theory of whole-organism movement. Using GPS tracking coupled with tri-axial acceleration recordings made on free-ranging animals, the team describes how they identify behavioural modes using a variety of statistical methods. Appling these techniques to track the movements of 43 griffon vultures in the Middle East, the team found that the proportion of costly active flights is reduced in the summer. They also observed a tiny fraction of costly long-range flights where the birds strayed well beyond their home range. The team suspects that the vultures' high energetic investment in these exceptionally long flights is justified by the benefits of exploring new resources or maintaining genetic diversity by mating with distant populations.

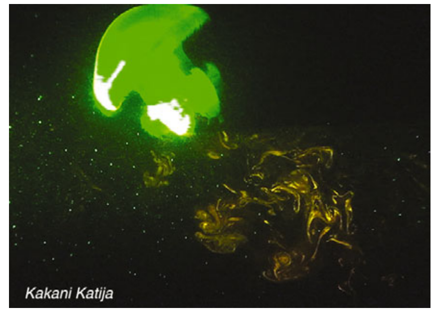
MIXING AT MULTIPLE SCALES

With just over 70% of the planet covered by salt water, many ecological and biological processes in the oceans are subject to the dynamics of fluid movement over a wide range of scales. Describing how traditional biomechanics analyses have mainly addressed the physical challenges faced by individual giant kelp (*Macrocystis pyrifera*) in their turbulent environment, Brian Gaylord and colleagues from the University of California at Davis explain that few studies have taken a broader ecomechanical perspective (p. 997). Explaining that kelp spore dispersal is fundamental to the turnover of kelp populations and that the majority of spores travel only a few meters, the team built a model of the physical processes that underlie spore dispersal and found that turbulent flows can carry a small percentage of spores over several thousand metres. Using this approach, the team showed how important population-level patterns could be inferred from analyses grounded in fluid dynamics.

Scaling down from giant kelp to some of the smallest organisms in the biosphere – plankton – Margaret McManus and Brock Woodson, from the University of Hawaii at Manoa, discuss the physics of interactions between the hydrodynamic structures in the water column and movements of the oceans' plankton (p. 1008). Describing plankton aggregations that occur at coastal ocean fronts and thin plankton layers that form at the lower boundary of stratified regions near the ocean surface, the duo explain that these thin layers are thought to be home to up to 75% of the water column's total biomass. Outlining the interaction between plankton behaviour and fluid mixing that produces these remarkably stable structures, the duo say, 'We now have a mechanistic understanding of how organism behavior in response to the physical environment produces fine-scale and mesoscale planktonic aggregations, which has a direct impact on the way marine ecosystems function'.

Continuing the theme of mixing, George Jackson, from Texas A&M University, USA, describes the physical nature of the ocean environment at the microscopic level of bacteria and other single-celled organisms (p. 1017). Building a strong formal mathematical representation of the distribution and diffusion of nutrient plumes over a range of scales, Jackson describes how even at this small scale, organisms create structure in the marine environment that affects rates of primary production and predation. These in turn contribute strongly to the control of marine ecology.

Moving on from the hydrodynamic processes that produce chemical and physical structure in the ocean, John Crimaldi, from the University of Colorado, USA, addresses the problem of broadcast fertilization (p. 1031). The vast majority of marine invertebrates reproduce by shedding sperm and eggs into the water. Crimaldi explains that, 'The instantaneous turbulent structure of the gamete fields is fundamental to the process', having the potential both to bring gametes together and to dilute them. Developing a simulation of interactions between gamete plumes during broadcast fertilization, Crimaldi shows that the detailed structure of turbulent eddies is essential, allowing gametes to interact for a sufficient length of time to ensure successful fertilization. Backing up the theory with experimental observations that reveal the extent of plume mixing in a turbulent environment, Crimaldi hopes to refine his simulation with the inclusion of gamete buoyancy and sperm motility to develop a better understanding of the mechanisms behind this fundamental process.



Kakani Katija

Finally, Kakani Katija, from the Woods Hole Oceanographic Institution, USA, suggests that vertically migrating marine populations could be responsible for a significant portion of the mixing in the upper ocean strata (p. 1040). Physical oceanographers have traditionally attributed ocean mixing to physical factors, such as winds and tides. However, Katija presents evidence that swimming animals generate fluid mixing through a process called 'drift' in which fluid is dragged into motion by the pressure field surrounding the swimmer and thereafter drifts with the moving creature. Analyzing this phenomenon in jellyfish, Katija reports that biogenic mixing could account for 1 TW of mixing energy in the ocean and points out that this could be a key mechanism that is currently absent from global climate models.

ECOMECHANICS AND THE COLLABORATION BETWEEN ECOLOGISTS AND PHYSIOLOGISTS

Reflecting on the diverse range of topics covered in this overview of the burgeoning field of echomechanics, Denny anticipates that it will 'provide an entrée into the field for people from both the physiological and the ecological sides'. He hopes that the collection will inspire ecologists to employ the wealth of physiological and biomechanical information and theory that underlies ecological phenomena, while he hopes that physiologists and biomechanicists will be motivated to apply their mechanistic approach to fundamental ecological issues. Considering the role of ecomechanics in the context of climate change, Denny predicts direct applications for several of the studies cited in the review.

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