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forget that there are coral reefs of a very different kind in deeper and colder waters. The featured paper in this issue of L&O draws our attention to these structures and presents vital clues as to how the many mouths of a deep-water coral community in the North Atlantic Ocean, dominated by the colonial scleractinian Lophelia pertusa, are maintained and fed. Deep water coral reefs are found on continental shelves and slopes at depths below 100 m, where there is not enough light to sustain algal symbionts, as is the case in tropical and subtropical coral reefs. Yet deep-water corals thrive: many reefs have been in existence over geological time-scales and have laid down carbonate mounds several hundreds of meters in thickness. An important question has been just how these deep-water corals obtain food. This is not an easy question to answer because their inaccessibility and the exposed nature of such sites has made direct observation for periods long enough to yield answers difficult.

Davies et al. used current meters and sensors on landers and moorings to obtain vital clues that address this question. Over two years, they studied currents, temperature, turbidity, and fluorescence at Mingulay Reef at a depth of 140 m in a relatively shallow strait between the Outer Hebridean Island chain and the Scottish mainland. This enabled them to determine particle supply to the coral community. They found that there are two major mechanisms for supplying organic particles to the hungry coral mouths. The first consists of a tidally-driven process that sucks surface water down to the coral community within an hour at the onset of ebb and flood tides. The second is the upwelling of deeper water, bringing with it a high load of suspended organic matter. These processes combine, usually at peak tides, to deliver particles to the reefs. Deep-water reefs exist on canyons, slopes, and seamounts and in much deeper waters than this one. This study provides, for the first time, important clues as to how such communities depend strongly on the interplay between water flow and bottom topography to supply the food particles and larvae on which these communities depend.

BOOK REVIEWS


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Kjørboe’s book offers an exciting tour through biological-physical interactions in the plankton. The book successfully demonstrates how basic knowledge of small-scale physical and chemical processes contributes to a better understanding of plankton ecology at the individual level. Expanding on these individual-level processes, the book produces new insights in community dynamics, and the structure and functioning of pelagic food webs. It is an outstanding overview of ongoing research on plankton encounter rates, and will be highly suitable for seminars and advanced student courses.
The first chapters present an invitation to think about notions at the core of plankton ecology. Kiørboe leads the reader through a variety of ideas and fundamental questions to develop an intuitive understanding of the everyday life of individual plankters. At the individual level, the life of planktonic organisms is all about encounters. They have to find food, they have to find mates, and they should stay away from predators. These might seem simple and familiar tasks. After all, human beings also enjoy a good dinner, like to find a good mate, and prefer to avoid any undesired encounters. Yet imagine yourself as a tiny little plankter in the middle of the endless ocean, mostly blind-folded. The surrounding fluid is three-dimensional, concentrations of food are extremely low, and the nearest mate can be thousands of body lengths away. In addition, the surrounding fluid feels like dense syrup as the viscosity of water dominates over inertial forces at these small scales. Swimming is demanding. Got the picture? How are you ever going to arrive at dinner in time, let alone find yourself a suitable mate in this unstructured, viscous and vast environment? The ocean environment as experienced from the perspective of a small plankter isn’t quite the same as our own world after all.

Natural selection has favored a multitude of adaptations in the individual behavior, morphology, and ecology of planktonic organisms to cope with these challenges. Take the copepods, which make up about 80% of the mesozooplankton in the oceans. As nicely illustrated on the front cover of the book, copepods have two huge antennules packed with sensory hairs sticking out in the water, aimed at chemical and hydromechanical signals in the environment. They put this sensory machinery into use to explore their surroundings. For instance, female copepods can leave a long trail of pheromones behind as they slowly swim through the endless ocean. Male copepods crossing this trail pick up the scent, and track the convoluted trail. During tracking, the male constantly checks the borders of the trail by chemoreceptive sensors on its antennules, and adjusts its chase accordingly, until he finally makes it to the female. Kiørboe discusses these spectacular stories in a very lucid style, and then moves on to derive equations that allow a quantitative evaluation of the implications. For instance, based on simple calculus, he shows that pheromone tracking increases the encounter rates of males and females substantially. Girls shouldn’t leave without a trace.

These analyses point to the issue of spatial scale. Do we observe plankton dynamics at scales relevant to the organisms? Much of our knowledge of aquatic ecosystems is based on “blind sampling,” where we simply scoop up a few liters of water, several meters apart along the vertical, and enumerate the organisms in our samples. However, these coarse methods only sample bulk properties of aquatic ecosystems. Kiørboe argues, convincingly, that these sampling methods exceed the spatial scale of individual plankters by orders of magnitude. The whole book builds up on this logic. It starts from descriptions of the spatial and temporal scales at which chemical signals and food particles are dispersed by diffusion and advection, and shows how these important transport processes affect the feeding rates and motility of individual organisms. Subsequently, Kiørboe discusses the emergence of global properties at larger scales, extrapolating the individual-based processes from preceding chapters to the population level. For instance, according to the coagulation theory developed with his colleague George Jackson, encounters between sticky particles can ultimately lead to the formation of large aggregates in the form of marine snow. Such aggregate formation has important implications for the dynamics of phytoplankton populations, which suffer large sedimentation losses by coagulation, and for the downward flux of organic carbon from surface waters into the deep ocean. Finally, in the last chapter of the book, the individual- and population-level processes are integrated to gain a more comprehensive understanding of the dynamics of entire pelagic food webs.

Emphasis is clearly set on processes at the organism scale. Hence, the chapters on community processes and ecosystem dynamics are relatively brief, and the book does not cover all aspects of plankton ecology. In particular, the title of the book may suggest that it covers mechanistic approaches to competition theory, which is textbook material in many undergraduate ecology courses, and has been extensively tested in plankton competition studies (e.g., papers by Tilman, Sommer, Grover, Rothhaupt, Lampert, and several others). However, although the book contains many useful references to competition studies, the book does not review resource competition theory, and also doesn’t tackle several other hot topics in plankton ecology such as ecological stoichiometry, inducible defenses, biogeochemical processes, and regime shifts in aquatic ecosystems. The book is more limited in scope than the title suggests. Clearly, dealing with all these topics would have been a tremendous task, and would have diluted the original message of the book in a mass of information. The book may thus present a starting point for plankton ecologists, to inspire further research linking the small-scale physical processes that are so important in the everyday life of the plankton with other important themes in plankton ecology. The intended audience of the book consists of graduate students and postdocs as well as senior researchers. Some understanding of biological oceanography and/or aquatic ecology, at the undergraduate level, is recommended. Many of the conceptual ideas build on earlier books on physical-biological interactions by Denny (1993), Berg (1993), and Vogel (1994). However, none of these earlier books focused specifically on the plankton. The author makes extensive use of simple fluid dynamics and diffusion theory to understand and evaluate the adaptations of planktonic organisms to their physical and chemical surroundings. Hence, mathematical equations are presented throughout the book. Yet, the math never becomes really complicated. A basic knowledge of high school calculus is required, and is often (but not always) sufficient to follow the arguments. It is clear from the careful explanations that much of the material has been developed as teaching material for courses. The writing style is very pleasant and reveals a passionate author, who offers his thoughts, and shares his experience, in a very didactic synthesis. Last but not least, the book is affordable (only US$ 39.50!). If you are interested in the state of the art on life at the scale of the individual plankter, then this book is definitely something for you!
REFERENCES


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Known for his seminal work on the functional response and resilience, C.S. Holling in 1992 published a paper (Holling 1992) that would again stir up the field of ecology. He showed that the distribution of body size in ecological communities might not follow the classical smooth power-law, but rather show a puzzling regular pattern of ‘lumps’ and ‘gaps.’ Analyzing data from birds and mammals he found that there were groups of species of roughly the same size (the lumps), whereas other sizes in the possible range were conspicuously missing (the gaps). While there was initial doubt about the statistical significance of the lumpy patterns, later studies in terrestrial but also in aquatic communities (e.g. Havlicek and Carpenter 2001) suggest that the lumpiness might actually be a quite common feature of size distributions.

Clearly, this pattern is fascinating as (unlike standard distributions) it might hint at underlying mechanisms that shape communities. The overall explanation suggested by the editors is introduced in the very first sentence of Chapter 1: “We describe the organization of ecological systems as […] hierarchically arranged, mutually reinforcing sets of processes that operate at different spatial and temporal scales, with all levels subject to an adaptive cycle of collapse and renewal, and with levels separated by discontinuities in key variables.” While the lumpy patterns were received with some reservation, this associated worldview has created perhaps more resistance in the ecological community. In an effort to push the field further a meeting of proponents and skeptics was organized at the Santa Fe Institute in 2001, providing the foundations for most of the chapters in the book, highlighting the issue from diverse angles.

One of the most fascinating reads is the synthesis chapter by Donald Ludwig in which he ponders the evidence, but also allows the reader a rare look behind the screens. Ludwig interviewed some of the participants to the meeting, amongst those one of the most outspoken critics, Jim Brown, who in an email quoted in the chapter wrote: “I am concerned that Buzz [Holling] wants the community to buy into his complete worldview.” Another participant, Brian Maurer, wrote after the meeting: “The lack of mechanistic explanations […] I think limits the usefulness of the lump/gap concept […] As yet, I have not seen many, if any, general synthetic theories that can be used to predict the existence of hierarchical structure in ecosystems.”

I think it is wonderful that the editors made these doubts visible in the book. It more-or-less characterizes where the field is: There are intriguing lumpy patterns in various body-size distributions (as well as in other characteristics such as range sizes), but the explanation is still rather open. This points the reader to two kinds of follow-up efforts. Firstly, we should explore how common such lumpy patterns really are. For those interested in pursuing this track, the book points the reader towards useful approaches to scan for patterns and provides examples of applications. Secondly, the existence of a pattern with no obvious explanation is an exciting opportunity to test theories and invent new ones. Several potential explanations are evaluated in the book ranging from slow evolution and size specific predation to the central idea that landscape patterns somehow impose body-size patterns. My own favorite explanation is yet another one: the lumpy patterns may be caused by two alternative ways for species to co-exist: being sufficiently different (allowing niche separation) or being sufficiently similar (allowing neutral coexistence within the lumps) (Scheffer and Van Nes 2006). Perhaps there are other potential explanations that nobody thought of. Certainly we need inventive approaches to sort out between such ideas.

In summary, the book introduces the reader to a field in which there are puzzling patterns but no consensus on their explanation. Aren’t such fields of work the best places to be?

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