



## Preface

### *A tribute to Professor Bruce W. Frost*

This volume is dedicated to Professor Bruce W. Frost, for his service as a mentor and colleague to the authors of this volume and for his contributions to the marine science community at large. This volume is based on a series of talks presented at the symposium held in honor of Professor Frost's sixtieth birthday at the School of Oceanography, University of Washington on March 17, 2001, entitled "Progress in Zooplankton Biology: Ecology, Systematics and Behavior". The broad scope of this volume reflects the enormous breadth of Professor Frost's career, which includes population, community, and ecosystem ecology (Part II), systematics and evolution (Part III), and sensory biology and behavior (Part IV). This compilation contains historical essays, synthetic reviews, and research articles, some which aim to challenge current paradigms and identify areas for future research.

This volume begins with a biographical sketch of Professor Frost, where Karl Banse describes his multifaceted contributions to biological oceanography and zooplankton biology. Part II of this volume focuses largely on marine ecosystems, on which Professor Frost has devoted much of his career, particularly on the role of zooplankton grazing on phytoplankton abundance. In the first paper of Part II, Karl Banse presents a historical note on Steeman Nielsen's contributions to zooplankton ecology, focusing on his recognition of the impact of grazing on phytoplankton abundance. In doing so, Banse alludes to the importance of Professor Frost's research on grazers in marine ecosystems. Michael Landry's essay discusses major new insights that have emerged from the microbial loop concept and related discoveries, the iron limitation hypothesis, and ocean time series. Focusing mainly on the tropical and subtropical Pacific Ocean, he reviews the influences of these new perspectives on classical views of food web complexity, phytoplankton regulation and diversity, and temporal dynamics. Suzanne Strom discusses the importance of examining effects of individual behavior and physiology on the coupling between rates of phytoplankton growth and microzooplankton grazing. She further emphasizes the necessity of characterizing the nature of this coupling for understanding stability of ecosystem dynamics.

Mark Ohman, Jeffrey Runge and colleagues present a comparative analysis of mortality patterns of two sympatric copepod genera, the free-spawning *Calanus* and the egg-brooding *Pseudocalanus*. Based on extensive field studies, they report divergent patterns of stage-specific mortality and a fundamental life-history tradeoff in these copepods. Wendy Gentleman documents the history of the application of computer models for exploring plankton dynamics in marine ecosystems. She describes major insights revealed by some of the important models and outlines areas for future research within a historical context. While the previous papers addressed issues regarding intact communities and ecosystems, Bollens and colleagues focus on disruptions caused by invasive zooplankton species, providing the first comprehensive review on zooplankton invasions in marine, estuarine, and freshwater systems. In addition, they present field and experimental data on community impacts and trophic interactions for two Asian copepod species invading the west coast of North America.

Throughout his career, Professor Frost has emphasized the importance of individual-based research for understanding large-scale processes in the sea. Consequently, Professor Frost's research has frequently delved into the physiology, systematics, and behavior of individual organisms. His contributions to the systematics of copepod species have consisted of detailed morphological studies, which resulted in splitting of copepod 'species' into sibling-species complexes. The following three studies in Part III highlight difficulties of copepod systematics caused by the problem of stasis in morphology, and emphasize the importance of combining multiple approaches, such as morphometrics, genetics, and mating experiments to identify species boundaries and evolutionary relationships among populations.

The first paper in Part III, by Carol Lee and Bruce Frost, focuses on the problem of morphological stasis in copepods. Their study shows that for the copepod species complex *Eurytemora affinis*, systematic relationships

based on morphology, molecular markers, and reproductive isolation are discordant, partly because morphological evolution occurs very slowly. Charlie Miller's study exemplifies the difficulty of identifying copepod species from detailed morphological analysis. He tackles the problem of evaluating the taxonomic significance of a single salient character found in a regionally restricted population of *Megacalanus*, and describes remarkable structures of uncertain function. Through a detailed morphometric analysis of closely-related species, Gayle Heron describes a new species of *Oncaea* of intermediate size, which she dedicates to Bruce Frost with the name *Oncaea frosti*.

As evident from numerous ecological studies, distributions of zooplankton in the sea are far from homogeneous. Patchiness in distribution often results from complex individual behaviors, in response to food resources or predators. Such behaviors are often difficult to observe or characterize, requiring measurements of sensory perception, detailed field observations, and mathematical models, as illustrated by the papers in Part IV. Jeannette Yen and Akira Okubo's paper focuses on thresholds of perception by individual copepods. They use a mathematical approach to evaluate whether a copepod, using mechanoreception, could detect a variety of signals in its environment. Julie Ambler reviews the topic of naturally occurring zooplankton swarms. She discusses characteristics of swarms in different species, experiments that investigate proximal cues for inducing swarm formation, and evidence for possible ecological advantages. Daniel Grünbaum presents a non-dimensional index, the 'Frost number,' which provides a simple prediction of availability to consumers of spatially and temporally varying resource concentrations. This index incorporates characteristics of both resource distributions and consumer movement behaviors. In the paper by Andrew Leising and Peter Franks, they quantify the behavioral response of a marine copepod to the presence of food, a response that is consistent with an area-restricted search foraging strategy. They argue that such information on a copepod's functional response to food could aid predictions on patchiness of its food source.

Together, these papers represent efforts of those that have collaborated with or have been influenced by Professor Frost. They reflect his approach of examining multiple hierarchical levels and employing numerous techniques and conceptual frameworks for solving problems. Thus, Professor Frost has passed on a legacy of conducting integrative and individual-based research, with the aim of making larger-scale inferences.

I would like to thank Laurie Bryan, Administrator at the School of Oceanography, University of Washington, for assistance with logistics and finances for this symposium. Drs Wendy Gentleman and Andy Leising, former postdocs of Dr Frost, procured the audiovisual equipment for the presentations and assisted with preparation for the reception and dinner banquet at the Burke Museum.

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