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## The Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton

Edited by John R. Dolan, David J.S. Montagnes, Sabine Agatha, Wayne Coats, and Diane K. Stoecker, 2013, Wiley-Blackwell, 304 pages, ISBN 978-0-470-6715-1, Hardcover \$149.95 US, E-book \$119.99 US

REVIEWED BY EVELYN SHERR

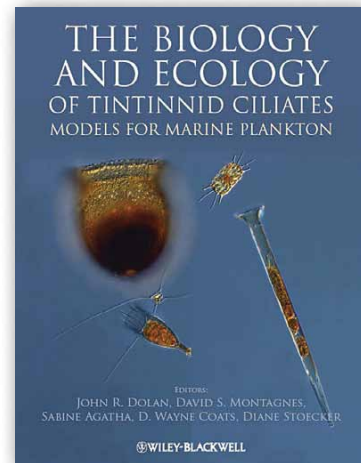
Single-celled eukaryotes called protists are vitally important to marine ecosystems. Protists with chloroplasts (algae) carry out most of the primary production in the sea. What feeds on this algal production? Mainly predatory protists such as ciliates in the microzooplankton, organisms that are 20 to 200 microns in size. This fact is well supported by empirical data. Still, predatory protists remain the Rodney Dangerfield “I don’t get no respect” of planktonic organisms. Compared to the amount of investigative effort devoted to bacteria, phytoplankton, and crustacean zooplankton, these protists, while unquestionably the dominant consumers of other microbial cells in plankton food webs, just don’t seem to get the research interest they deserve.

A notable exception to the lack of study of phagotrophic protists, as thoroughly explicated in this book, is the tintinnid ciliate group. The euphonious name of this group stems from the implied ringing of the bell-shaped shell, or lorica, of the type species. The loricae of these curious ciliates are also the chief reason they have piqued the interest of marine biologists for over 200 years. Attributes of the lorica can be used to identify individual tintinnid species, and

lorica-inhabiting ciliates are easily collected in plankton nets. Some tintinnid species are amenable to laboratory culture and experimentation. These characteristics are desirable for a model group of organisms, hence the wealth of knowledge about tintinnids presented here.

And wealth it is. The editors, Dolan, Montagnes, Agatha, Coats, and Stoecker, all highly respected plankton ecologists, have combined their deep knowledge of marine protists with that of other scientists to produce a delightfully comprehensive treatise. From an overview of tintinnids (Chapter 1 by Dolan) to the formation and composition of tintinnid loricae (Chapter 2 by Agatha, Michèle Laval-Peuto, and Paul Simon), to tintinnid systematics based on both lorica characteristics and molecular genetics (Chapter 3 by Agatha and Michaela Strüder-Kypke), to tintinnid physiology and ecological roles as predator and prey (Chapter 4 by Montagnes; Chapter 5 by Stoecker; Chapter 9 by George McManus and Luciana Santoferrara), and the rest, the chapters are uniformly informative and readable. The text is beautifully enhanced by images of the diversity of tintinnid loricae that range from Ernst Haeckel’s precise drawings of 1873 to modern light microscopy and scanning electron micrographs.

Dolan begins the book with a general description of tintinnid ciliates, and then summarizes the long history of research on these protists. The first known observations are from 1776, and detailed morphological descriptions of tintinnids by Haeckel and other natural historians



were published throughout the 1800s. An interesting tidbit: the term “lorica” used for the tintinnid shell was adopted from a Latin word for protective armor worn by Roman soldiers.

The chapters following the introduction provide in-depth reviews of work done on tintinnids since the initial descriptive reports. The amount of information just on the structure, composition, and formation of the tintinnid lorica (Chapter 2) is formidable. Chapter 3 on tintinnid evolution and systematics reveals not only the complicated story of how tintinnids split from the ancestral, naked ciliate but also how systematics based on morphology of the lorica does not always agree with more recent molecular genetic trees of relationships between tintinnid species. Apparently, few tintinnids have managed to colonize freshwater habitats; virtually all species are marine. Later chapters on tintinnid fossils (Chapter 8 by Jere Lipps, Thorsten Stoeck, and Micah Dunthorn) and on biogeography of tintinnid species in the global ocean (Chapter 10 by Dolan and Richard Pierce) complement the evolutionary history based on relationships of extant ciliates. Because tintinnid species are easily distinguished by lorica

characteristics, abundant data on the distribution of these ciliates have revealed much endemism and variation in species richness in different habitats.

A cautionary note that McManus and Santoferrara (Chapter 9) make clear is that tintinnids, although a fascinating group and a useful model for marine herbivorous protists, represent only a small fraction of marine ciliates. So far, only about 1,000 species of marine tintinnids have been described, and tintinnids usually comprise only a few percent of the total number of ciliates in the microzooplankton.

The most useful chapters for ecosystem modelers are those on the roles of tintinnids in marine food webs. In Chapter 4, Montagnes presents general background on the mathematical predator-prey functional responses used in modeling before delving into specifics of tintinnid prey selectivity, growth, swimming behavior, and effects of abiotic factors such as temperature and salinity. Stoecker's review (Chapter 5) of tintinnid predators is also impressive. There is abundant documentation of tintinnids as prey based on recognizable loricae in protist food vacuoles and in zooplankter guts and fecal pellets. Feeding experiments have also quantified ingestion of tintinnids by protists, including by other tintinnids, by copepods, and by jellyfish.

An unexpected body of work involves the microbial parasites of tintinnid ciliates. D. Wayne Coats and Tsvetan Bachvaroff (Chapter 6) summarize known ciliate parasites, then provide details on the most studied of them: dinoflagellates that parasitize tintinnids. They cover morphology, infection cycles, host specificity, evolutionary relationships based on molecular genetics, and

global distribution of dinoflagellate parasites of tintinnids. The inclusion of tintinnid parasites is significant, as there is as yet little understanding of how parasitism by eukaryotic microbes affects the functioning of marine food webs.

Chapter 7 (Takashi Kamiyama) is devoted to another underappreciated aspect of protists: formation of resting cysts. Although most marine ciliates do not form cysts, a few, including species of tintinnids, do. Kamiyama reviews the dynamics of cyst formation and excystment in tintinnids and other ciliates, and the potential importance of this strategy for dispersal and survival.

This well-produced, well-referenced book provides a great resource for both protozoologists and marine plankton ecologists. Each chapter concludes with a list of key points for a quick summary of the contents. However, even with the information gained over decades of study, it is also clear that gaps remain in understanding of tintinnid biology and ecology. For instance, why tintinnids evolved loricae, and what advantage these shells confer, is still not resolved. The book should stimulate much thought and future research not only on tintinnids, but also on marine protists in general. 📖

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