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Edited by Craig D. Sandgren
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Chapter 1

GENERAL INTRODUCTION

CRAIG D. SANDGREN

There is hardly a lack of published information concerning the ecology of freshwater phytoplankton. The growth in numbers of journals, journal articles, and published symposia in this research area since the appearance of Hutchinson's seminal thesis (Hutchinson 1967) and Lund's review paper (Lund 1965) is impressive. A number of recent works have attempted to synthesize the topic from various viewpoints (e.g., Morris 1980; Moss 1980; Platt 1981; Round 1981; Meyers & Strickler 1984; Reynolds 1984a; Harris 1986; Sommer et al. 1986; Munawar & Talling 1986).

One important trend during this recent surge of interest in freshwater phytoplankton ecology has been the simultaneous emphasis on *both* growth and loss processes as mediated through resource supply, trophic exchange, and physical mixing of the system (Crumpton & Wetzel 1982; Reynolds et al. 1982; Lehman & Sandgren 1985). Related topics of particular interest have been the role of limiting nutrient supply ratios in competitive interactions (Rhee & Gotham 1980; Tilman 1982; Tilman, Kilham & Kilham 1982; Smith 1983; Kilham & Kilham 1984; Terry, Laws, & Burns 1985); mixotrophic nutrition of algae and heterotrophic flagellates, with associated food web complexities (Paerl 1982; Hobbie & Williams 1984; Porter et al. 1985; Bird & Kalff 1986,

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1987; Fenchel 1986a,b; Sherr & Sherr 1987); zooplankton feeding mechanisms and nutrient remineralization (Porter 1976, 1977; Lehman 1980a,b; Lehman & Scavia 1982a,b; Koehl 1984; Strickler 1984; Sterner 1986; Fryer 1987); the role of turbulence in phytoplankton periodicity (Knoechel & Kalff 1975; Reynolds 1980, 1984b; Reynolds, Wiseman, & Clark 1984; Sommer 1984; Paerl, Chapter 7, this volume); organism morphology and size as scaling factors (Lewis 1976; Margalef 1978; Reynolds 1980, 1984b; Werner & Gilliam 1984); and "cascading" effects of changes within individual trophic levels on whole system structure and production (Carpenter & Kitchell 1984; Neill 1984; Bergquist, Carpenter, & Latino 1985; Carpenter, Kitchell, & Hodgson 1985; Drenner, Threkeld, & McCracken 1986; Mills, Furney, & Wagner 1987; Siegfrield 1987; Threkeld 1987). One outgrowth of these many studies has been increasing emphasis on the physiological and behavioral attributes of the *individual organisms* – the algae, protozoa, zooplankton, and fish species – and renewed recognition of the importance of the actual species mix for determining plankton dynamics and response to perturbations. It has become increasingly clear that individual species may constitute important keystone predators or may act as critical "bottlenecks" to the flow of information and resources through planktonic food webs. Planktonic species are certainly more than bits of carbon and chlorophyll that may be freely substituted one for another without affecting planktonic food web dynamics and productivity.

Much insight into the dynamics of planktonic ecosystems has been gained from careful study of the reproductive and feeding ecology of individual fish and zooplankton species (e.g., King 1977; Dumont & Green 1980; Kerfoot 1980; Zaret 1980; Werner & Gilliam 1984; Lampert 1985; Kerfoot & Sih 1987). However, understanding of the ecology or "life history strategies" of phytoplankton species remains a formidable task because of the comparatively great diversity of species and the frustratingly great interannual and interlake variability in seasonal distribution patterns. The problem has been intensified in the modern literature by a tendency to emphasize short-term data sets and only dominant species in publication. Despite these inconsistencies and shortcomings in the data, limnologists have long recognized general trends suggesting that taxonomic groups of phytoplankton and morphological types of cells characteristically predominate the plankton of lakes at only certain times of the year. As common examples, we can cite the spring diatom blooms and the summer succession of coccoid green algae, cyanobacteria, and dinoflagellates so typical of moderately productive dimictic lakes. These general distributional trends likely represent strong interactions between species and both biotic and abiotic components of aquatic ecosystems. Attempts at

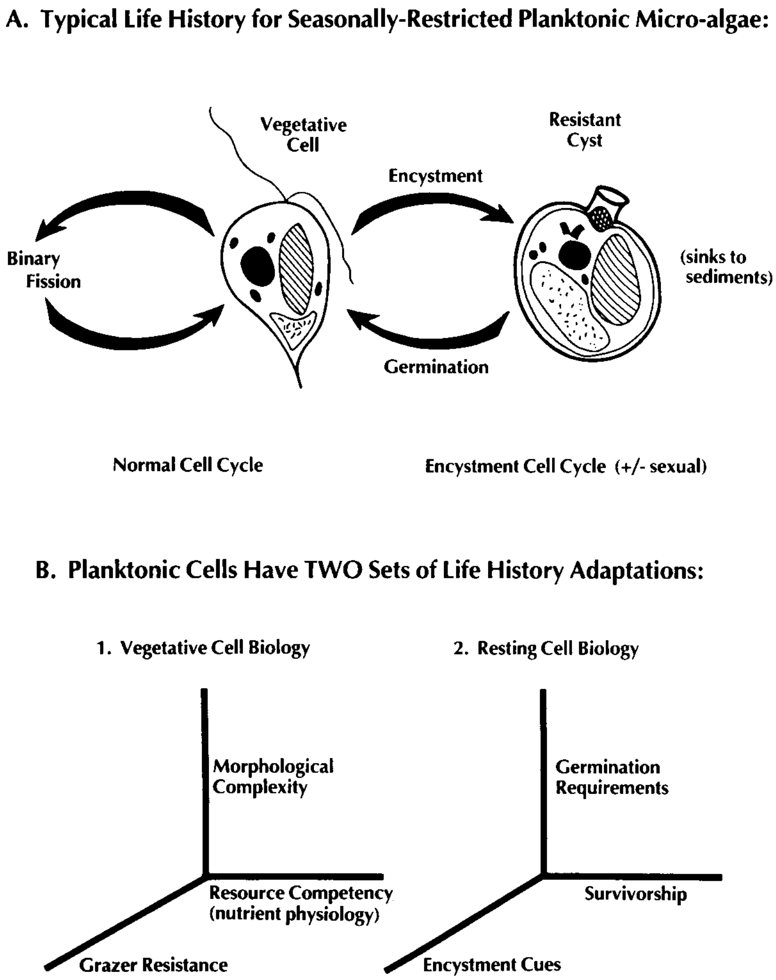

Fig. 1-1. Interacting aspects of phytoplankton population and reproductive ecology that compose the elements of a planktonic alga's life history strategy. (A) Typical life history for many phytoplankton species exhibiting an alternation between vegetative cells and resting cells (resting cyst in this example). (B) Axes representing the characteristics by which microalgae diversify and adapt for persistence in stressful, heterogeneous planktonic habitats.

understanding the nature of these strong interactions have occupied much of the modern autecological literature on freshwater phytoplankton.

The chapters in this book contribute to an understanding of the mechanisms generating phytoplankton distributional patterns by summarizing (1) the morphological, nutritional, and physiological characteristics of the algae, and (2) the competitive and trophic interactions affecting members of the major taxonomic classes of freshwater phytoplankton. A relatively unique feature of these contributions is that the authors have also attempted to integrate information about the reproductive biology of species with the ecology of the vegetative cell populations. Adopting this integrative approach has permitted a great deal of both limnological and phycological literature to be synthesized, in some instances for the first time. Such integration is an important consideration because, though some planktonic algae seemingly perennate via small refuge populations of vegetative cells in the plankton (e.g., araphid pennate diatoms such as *Asterionella*), the majority of freshwater phytoplankton incorporate resistant benthic resting stages into their life history strategies (Fig. 1-1a). Attempts have also been made here to recognize distinctive "packaging plans" of physiological, morphological, and reproductive features among freshwater phytoplankton that represent evolutionary solutions to the problems of persistence in stressful and periodic planktonic habitats (Fig. 1-1b). This evolutionary consideration is a second relatively unique feature of the book. It is hoped that the combination of organismal and evolutionary approaches to freshwater phytoplankton ecology emphasized here will provide new insights into the interplay of both proximate (short-term) and ultimate (evolutionary) factors influencing phytoplankton dynamics.

The book is organized into two sections. Chapters 2–7 concern the ecology of important taxonomic classes of phytoplankton. Authors were asked to consider the validity and utility of the interactions outlined in Fig. 1-1 for the group of algae in which they have special interest and expertise. Each of the last three chapters (8–10) constitutes a more detailed discussion of one of the axes in the left-hand panel of Fig. 1-1b in regard to its effects on phytoplankton in general.

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Chapter 2

THE ECOLOGY OF CHRYSOPHYTE FLAGELLATES: THEIR GROWTH AND PERENNATION STRATEGIES AS FRESHWATER PHYTOPLANKTON

CRAIG D. SANDGREN

INTRODUCTION

The goal of this volume as stated in the general introduction is to integrate information about growth and reproduction of groups of phytoplankton into identifiable suites of characteristics that can be considered successful adaptive "strategies" for survival. Chrysophytes are a most intriguing group of freshwater algae for which to consider sets of adaptations for persistence in heterogeneous planktonic habitats. Most members of the class Chrysophyceae are unicellular and colonial flagellates that have apparently evolved in, and are restricted to, freshwater planktonic habitats. Among common species there exists a broad diversity in the size, shape, and surface ornamentation of cells as well as in the morphology and complexity of colonies. These algae are nutritionally opportunistic, many species apparently being capable of switching among autotrophic, heterotrophic, and phagotrophic mechanisms for energy acquisition in response to changes in the planktonic environment. They commonly exhibit markedly seasonal

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growth cycles in lakes with one or two restricted population maxima observed during a year, thus suggesting strong interactions with periodic physical, chemical, and biotic components of lakes. Such demographic patterns would appear to require effective strategies for successful perennation from one growth season to the next, and chrysophyte populations are indeed often observed to produce resistant resting cysts during conditions of intolerable stress for the vegetative cells. As a group, then, chrysophyceaen algae would seem to be particularly well adapted for survival in the plankton of lakes. Combinations of characteristics relating to algal form, reproduction, nutrition, and biotic or abiotic interactions with the environment that can be summarized as life history strategies may be most easily documented for these algae.

Chrysophytes are among the most poorly known freshwater phytoplankton with regard to their reproductive biology, nutrition, and ecology. Although a number of genera are very common planktonic constituents of low or moderately productive lakes, chrysophytes, for a number of reasons, have seldom been the subject of limnological or laboratory study. First, they do not typically form dense blooms or create the water quality problems that have stimulated research on freshwater cyanobacteria and diatoms. Second, chrysophyte importance has undoubtedly been underestimated in many lake studies owing to difficulties in adequately preserving cells by standard limnological sampling methodology as well as the specialized techniques required for accurate identification of species in even common genera. Finally, difficulties experienced in culturing these algae have long discouraged attempts at critical in vitro study of life history, physiology, or nutritional requirements for all but a few "weed" species. To a large extent, then, chrysophytes have been ignored during the growth of quantitative phytoplankton ecology that has occurred in the last 25 years. Reviews concerning freshwater phytoplankton have often continued to rely on classical observational and correlative studies for chrysophyte information. A specific review of the ecology of freshwater chrysophytes has never been published, although Kristiansen has published a review of chrysophytes as environmental indicators (Kristiansen 1986a,b).

There is currently increased interest in planktonic chrysophytes stimulated primarily by three recent developments. The first is the tremendous increase since approximately 1970 in limnological studies of the myriad small, softwater, and largely oligotrophic lakes of the north temperate regions of North America and Scandinavia. These lakes, frequently dominated by flagellate chrysophytes and cryptomonads, have proven to be very sensitive to acidification by atmospheric pollutants, and an understanding of their biota and chemistry has been a primary