MIXOTROPHY IN MARINE PLANKTONIC CILIATES: PHYSIOLOGICAL AND ECOLOGICAL ASPECTS OF PLASTID-RETENTION BY OLIGOTRICHES

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INTRODUCTION

Although oligotrichous ciliates (subclass Choreotrichia, order Choreotrichida) are often regarded as strict phagotrophs, deriving their nutrition from the ingestion of other cells, many species contain pigmented bodies which have long been thought to be residues of digestion of algal cells and only recently have been shown to be algal chloroplasts (Kahl 1932, Burkholder et al. 1967, Taylor 1982, McManus and Fuhrman 1986). Transmission electron microscopy has demonstrated that many marine oligotrichs retain isolated chloroplasts derived from phytoplankton (Blackbourn et al. 1973, Laval-Peuto and Febvre 1986, Jonsson 1987, Stoecker and Silver 1987). A substantial proportion of the planktonic oligotrich fauna contains chloroplasts and is probably mixotrophic, deriving nutrition from both phagocytosis and photosynthesis (Laval-Peuto et al. 1986, Stoecker et al. 1987, Laval-Peuto and Rassoulzadegan 1988).

These data suggest that the role of planktonic oligotrichs in marine processes is more varied and complex than we once thought. Physiological and ecological data are needed to understand the role of plastidic ciliates in trophodynamics, particle transformation, and nutrient cycling in the oceans. In addition, chloroplast-retention in oligotrichs, although this phenomenon is not unique to this taxon (Trench 1975, Lopez 1979, Patterson and Dürrschmidt 1987), is a model system in which organelle-cell interactions can be experimentally investigated from ecological, cellular and molecular viewpoints. Presently, our interest in, and knowledge of, plastidic ciliates is increasing rapidly. In the
following sections, I will describe the current status of our knowledge of plastidic oligotrichous ciliates, discuss their possible roles in marine processes, and when possible, suggest potentially fruitful areas for future research.

FREQUENCY AND ABUNDANCE

Various criteria have been used to identify plastidic ciliates. Epifluorescence microscopy is a convenient and reliable technique for categorizing ciliates as potentially photosynthetic (due to isolated chloroplasts or algal endosymbionts) or strictly heterotrophic (McManus and Fuhrman 1986, Stoecker et al. 1987, Laval-Peuto and Rassoulzadegan 1988). Based on light microscopy alone, it is difficult to distinguish between small algal endosymbionts and isolated algal plastids. With electron microscopy, isolated algal chloroplasts have been observed in *Laboea strobila* (Blackbourn et al. 1973, Jonsson 1987, Stoecker et al. 1988), several *Strombidium* species (Blackbourn et al. 1973, Stoecker and Silver 1987, Stoecker et al. submitted), and in *Tontonia appendiculariformis* (Laval-Peuto and Febvre 1986, Laval-Peuto et al. 1986). Based on light microscopy, some marine and freshwater oligotrich species have been reported to contain whole algal cells (Burkholder et al. 1967, Hecky and Kling 1981, Jonsson 1987). The freshwater oligotrich, *Strombidium viride*, had been thought to contain zoochlorellae (Hecky and Kling 1981) but recently transmission electron micrographs have revealed that isolated chloroplasts are present rather than algal cells (Rogerson et al. in press). Algal endosymbiosis and plastid-retention are physiologically and ecologically quite different and transmission electron microscopy should be used, whenever possible, to differentiate between them.

The term 'plastidic' was proposed by Laval-Peuto and Rassoulzadegan (1988) for all ciliates that contain intact plastids, either isolated or in algal endosymbionts. I use this definition because most studies employ epifluorescence microscopy and thus cannot always distinguish between small