

Preface

Toward an emerging consensus on the ecology of *Pfiesteria*

Only discovered in the late 1980s, *Pfiesteria* soon became linked to estuarine fish kills on the eastern seaboard of the U.S. by the early 1990s. It was considered to be an unusual cryptic, heterotrophic dinoflagellate with various traits, some of which are now known to be shared with other dinoflagellates including a group of “*Pfiesteria*-like” organisms that have since been described. Over the past 15 years, much has been learned regarding its physiology, ecology and toxicity. This issue is devoted to a synthesis of the ecology of *Pfiesteria*, findings based an ECOHAB regional grant, and associated collaborative projects. Some important aspects of the interactions with other components of the microbial web, such as bacteria and viruses, were not included here; however, the lack of inclusion of papers on these topics should not be taken as indicative of lack of importance. Emerging from this synthesis are many consistencies regarding its distribution, nutrient regulation and interactions of *Pfiesteria* species (*P. piscicida* and *P. shumwayae*) with other components of the food web. We highlight some of these consistencies in this preface, and hope that some of these ideas may find applicability in the yet unresolved issues of this fascinating organism.

One of the important facts to emerge in recent years about *Pfiesteria* spp. is that they are common estuarine organisms with widespread distribution. They generally occur in low abundance in the water column and often are found in or near the sediments. Although *Pfiesteria* originally was isolated from the Pamlico Estuary, North Carolina, USA, and soon thereafter in Chesapeake Bay, Maryland, it was the development of species-specific molecular probes that led to the finding that *Pfiesteria* is widely distributed. Here, Bowers et al. and Coyne et al. describe the distribution of *Pfiesteria* species in the sediments of Chesapeake Bay and Delaware Bay, and the relationship between distribution and water-column

characteristics. In these embayments *Pfiesteria* was shown to be common, with localized regions of higher populations or “seed beds” that may lead to potential blooms under suitable conditions. Rublee et al. extends the range of *Pfiesteria* north along the U.S. Atlantic Coast to the waters of Long Island in New York. While the more northern habitats are similar to those of the coastal bays of Maryland where *Pfiesteria* previously has been documented, these results also underscore the fact that *Pfiesteria* is more commonly observed in sites where nutrients, particularly organic nutrients, are enriched. The range of *Pfiesteria* now documented shows it to be most abundant in highly eutrophic waters, as was first reported in North Carolina estuaries. Collectively, the data show that *Pfiesteria* is common in estuaries along the U.S. Atlantic Coast.

Previous studies have shown that *Pfiesteria* can cause disease (for example, fish lesions) and death in finfish and shellfish through two interactive mechanisms: physical attack while feeding on prey, and toxin production. Early research in North Carolina estuaries showed that, while many incidents of ulcerative fish disease in juvenile Atlantic menhaden (*Brevoortia tyrannus*) have occurred in the absence of *Pfiesteria*, toxic outbreaks of this organism typically involved high incidence of ulcerations in menhaden. In Maryland waters, Tango et al.’s statistical analysis indicate that the incidence of fish lesions and presence *Pfiesteria* are associated, based on the multi-year data set from monitoring activities. The authors were careful to point out that the statistically detected association is not meant to infer a cause-and-effect relationship. Nevertheless, this association may prove to be a useful management tool as previously suggested, helping to guide the need for more targeted sampling of *Pfiesteria* spp.

Previous observations from field studies have indicated that low-turbulence environments are conducive

for toxic *Pfiesteria* activity. Stoecker et al. show that *Pfiesteria* is sensitive to small-scale shear, more so than other heterotrophic dinoflagellates studied to date, but within the same range as some auxotrophic dinoflagellates. Their results also show that strains of differing toxicity status vary in susceptibility to the effects of shear, with toxic strains being most sensitive.

Two papers in this special issue describe processes by which *Pfiesteria* acquires nitrogen and phosphorus. Glibert et al. show that different culture conditions may lead to different rates of uptake and different preferences for nitrogenous nutrients. Overall, in the strains examined, organic forms of nitrogen were consistently preferred over inorganic forms. Further, the data suggest that organic nutrients can contribute significantly to the nutrition of *Pfiesteria*, especially of actively toxic strains. Skelton et al. demonstrate that acid phosphatases predominate in *P. shumwayae*, as in various other heterotrophic protists that have been examined. Both papers underscore the premise that *Pfiesteria*, a heterotroph that can become mixotrophic through retention of kleptochloroplasts, has multiple mechanisms for acquiring nutrients, utilizing both dissolved organic and inorganic nutrient forms, as well as particulate nutrients.

A wide range of physiological and cellular properties is manifested among the strains within each *Pfiesteria* species, and their behavior and toxicity are strongly influenced by the culture conditions. As examples, strains can range from nontoxic (producing negligible toxin) to highly toxic, and their response to nutrients depends upon the strain and the history of feeding. *Pfiesteria* strains, like those of other toxigenic algae, also lose toxicity over time in culture, often rapidly, and change in other important characteristics as well (e.g. attraction to fish). *Pfiesteria* can be grown in bacteria-free conditions (e.g. with a sterile fish cell line), but the presence of a bacterial consortium previously has been shown to stimulate *Pfiesteria* toxicity, similarly as for certain other toxigenic algae. Nevertheless, not all species of bacteria would be expected to enhance growth and toxin production in *Pfiesteria*; accordingly, Coyne et al. suggest, based on low and patchy abundance of *Pfiesteria piscicida* cysts in Delaware Bay, a potential role for an algicidal bacterium with deleterious effects on *Pfiesteria*.

Three papers in this issue examined phagotrophy by *Pfiesteria*. In addition to the differences in nutrient uptake found between different strains and toxicity status of *Pfiesteria*, differences in phagotrophy of algal prey by toxic versus non-inducible strains were also

observed. The study by Lewitus et al. found that rates of phagotrophy were higher in cells with low or negligible toxicity, whereas grazing of algae was much lower by actively toxic cells. Egerton and Marshall show that rates of feeding by *Pfiesteria* also depend on total prey abundance and prey type, with strongest preference for fish blood cells among the prey provided. Shumway et al. document an aggressive predatory response toward larval shellfish species by most, but not all, strains of algal- and fish-fed *P. shumwayae* tested. Assays conducted with versus without direct contact between *P. shumwayae* and shellfish larvae indicated that larval mortality resulted primarily from damage inflicted by *Pfiesteria* physical attack, and secondarily from *Pfiesteria* toxin. Survival of adult shellfish was species-specific, and also depended upon the *P. shumwayae* strain.

Two papers herein examined responses of grazers (predators) toward *Pfiesteria*. Lewitus et al. show that the response of microfaunal grazers depends upon the species of grazer and the toxicity of the strain, responses not unlike those of many other harmful algae. Grazing by two benthic ciliates on *Pfiesteria* was significantly lower on cells that were actively toxic than cells that displayed low or negligible toxicity. Roman et al. studied non-inducible versus weakly toxic *Pfiesteria* strains and found that ingestion rates by copepods did not differ substantially for cells of varying toxicity status. Based on their data, they hypothesize that overall biological control of *Pfiesteria* by copepods would be likely only if copepods were present in high abundance.

Hood et al. synthesized measurements of nitrogen uptake, responses to turbulence, and grazing interactions from these and other studies in constructing the first available model of *Pfiesteria* population dynamics. This model supports the generalization that nontoxic blooms are more likely to occur under more turbulent, inorganic-nutrient rich conditions, but toxic blooms are more likely in calm, organic-nutrient rich conditions when grazing pressure is relatively low.

Although great strides have been made in the understanding of this fascinating organism, and many relationships, previously viewed with skepticism (e.g. intraspecific variation, varying nutritional mechanisms, association with nutrients, varying toxicity levels, and impacts and interactions with other trophic levels), have now been documented by multiple investigators, there is still much to be learned. Unlike most species that are considered to be “harmful algae,” *Pfiesteria* is not an alga according to the classical definition (primitive plant-like organisms). Thus, its

complicated role in the ecosystem is, in many ways, different from that of “traditional” algae. Nevertheless, there are many commonalities with factors such as high nutrient loadings that we associate with various HAB species. Overall, we hope that this special issue is of use to researchers studying these interesting, heterotrophic, harmful species.

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