DINOFLAGELLATE CYST ASSEMBLAGES AND ENVIRONMENTAL FACTORS CONTROLLING THEIR DISTRIBUTION IN NEW ENGLAND (USA) ESTUARIES

by

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ABSTRACT

Extensive data sets of water quality and sediment chemistry as well as detailed historical records were used to analyze environmental factors controlling dinoflagellate cyst distribution in shallow estuaries (lagoons and embayments) of southern New England. Cyst abundance, species richness, the proportion of cysts produced by heterotrophic and autotrophic dinoflagellates, and the composition of cyst assemblages reflect spatial and temporal variation in environmental conditions.

The cyst record in sediment cores from two embayments, New Bedford Harbor and Apponagansett Bay, Massachusetts demonstrates cyst sensitivity to environmental change caused by anthropogenic activity in the watersheds. Intensive industrialization and urbanization occurred during the 20th century in New Bedford Harbor resulted in extreme eutrophication and toxic pollution (heavy metals and PCBs). These conditions are reflected in declining cyst diversity and wide fluctuation in total cyst production. At the same time, the proportion of certain heterotrophic taxa increases. As impacts of extreme eutrophication and toxic pollution cannot be separated, the cyst response must be interpreted as a cumulative «pollution signal». The spatial distribution of modern dinoflagellate cysts in the area supports this signal. Cysts vary along gradients of nutrient enrichment, corresponding to distance from sewage outfalls.

Dinoflagellate cysts in surface sediments from New England lagoons also were studied. A comparison of assemblages to water quality parameters, that are affected greatly by the degree of water exchange between lagoon and ocean, indicates that temperature and salinity are the main abiotic factors controlling cyst distribution in these estuaries.

A new species of dinoflagellate cyst, *Islandinium brevispinosum*, has been identified and described. This species was found within a narrow range of water temperature and salinity, and at elevated nutrient levels.

Dinoflagellate cysts reflect environmental conditions at the small spatial scales necessary to characterize variability within estuaries. However, the relative importance of abiotic factors controlling the spatial and temporal distribution of dinoflagellate cysts is likely to vary with the hydrological differences between lagoons and embayments.

Therefore, dinoflagellate cysts can be useful indicators of environmental conditions in and human impacts on shallow estuaries.

RÉSUMÉ

Des banques de données exhaustives sur la qualité de l'eau et sur la chimie des sédiments, ainsi que de nombreux documents historiques ont été utilisés pour l'analyse des facteurs contrôlant la distribution de kystes de dinoflagellés dans les estuaires peu profonds (lagons et embayments) du sud de la Nouvelle-Angleterre. L'abondance de kystes, la richesse en espèces, la proportion de kystes produite par les dinoflagellés hétérotrophiques et autotrophiques, et la composition des assemblages de kystes reflètent des variations spatiales et temporelles dans les conditions environnementales.

Les kystes dans les carottes de sédiments provenant de l'embayment du New Bedford Harbor et du Apponagansett Bay au Massachusetts, démontrent la sensibilité du kyste aux changements environnementaux causés par les activités anthropiques dans les basins hydrologiques. Au cours du dernier siècle, une industrialisation et urbanisation intense à New Bedford Harbor a causé une eutrophisation sévère et une pollution toxique (métaux lourds et BCP). Ces conditions se reflètent dans le déclin de la diversité des kystes et aussi à travers de larges fluctuations dans la production totale de kystes. En même temps, la proportion de certains taxa hétérotrophiques a augmenté. Puisque l'impact de l'industrialisation et de l'urbanisation ne peut être dissocié, la réponse des kystes doit être interprétée comme un «signal de pollution» cumulatif. La distribution spatiale des kystes de dinoflagellés dans les sédiments de surface supporte le signal. Les kystes varient sur des gradients d'enrichissement de nutriments, correspondant à leur proximité des sorties d'évacuations des vidanges.

Les kystes de dinoflagellés dans les sédiments de surface aux lagons de la Nouvelle-Angleterre ont aussi été étudiés. Une comparaison des assemblages de paramètres de la qualité de l'eau indique que la température et la salinité sont les principaux facteurs abiotiques contrôlant la distribution du kyste dans ces estuaires. Dans les lagons, ces paramètres de qualité de l'eau sont grandement affectés par le degré d'échange d'eau entre le lagon et l'océan.

Une nouvelle espèce de kystes de dinoflagellés, *Islandinium brevispinosum*, a été identifiée et décrite. Ces espèces ont été trouvé dans un intervalle de température et de salinité restreint et à des niveaux élevés de nutriments.

Les kystes de dinoflagellés reflètent les conditions environnementales à fine résolution spatiale qui caractérise les variabilités à travers un estuaire. Cependant, l'importance relative des facteurs abiotiques contrôlant la distribution spatiale et temporelle des kystes de dinoflagellés est susceptible de varier avec les différences hydrologiques entre les lagons et les embayments. Les kystes de dinoflagellés peuvent être des indicateurs utiles des conditions environnementales et des impacts anthropiques sur les estuaires peu profonds.

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I am indebted to my student colleagues, Z. Spasojevic and B. Beecher, for providing a stimulating and interesting environment. My dear friends, I thank you for helping me to get through joyful and difficult times, and for all the emotional support and caring you provided. I am also grateful to all my co-workers in the lab for keeping a good company and technical assistance, especially to R. Lam and L. Sun.

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TABLE OF CONTENTS

LIST OF TABLES

Chapter 2.

Chapter 3.

Chapter 4.

LIST OF FIGURES

Chapter 2.

Chapter 3.

Chapter 4.

Chapter 5.

Appendix.

CHAPTER 1. GENERAL INTRODUCTION

This thesis focuses on the distribution of modern dinoflagellate cysts in relation to environmental conditions in estuaries. Dinoflagellates are single-celled organisms (kingdom Protista), one of the major components of the phytoplankton in aquatic environments. Dinoflagellates have two flagella and occur typically as motile cells, capable of maintaining an optimal position in the water column. About half of the dinoflagellates are heterotrophic and half are autotrophic, but some dinoflagellates can feed both ways, termed mixotrophic (Dale, 1996; Jacobson and Anderson, 1996). The distribution of heterotrophic dinoflagellates is controlled, in part, by availability of prey (diatoms and small flagellates), whereas the distribution of autotrophic species depends on the availability of light and dissolved nutrients. Approximately 13% to 16% of extant species of dinoflagellates produce resting cysts during their life cycle (Head, 1996). The organic (dinosporin) nature of walls of many cysts makes them resistant to degradation (Fensome et al., 1993), providing a good fossil record. Assemblages of dinoflagellate cysts accumulated in sediments can encode information about dinoflagellates in the upper water column (Dale, 1976; Reid & Harland, 1978), thus reflect the ecology of living dinoflagellates (Taylor, 1987).

Over the last three decades dinoflagellate cysts have been studied increasingly in modern marine and oceanic systems, where they reflect environmental conditions with considerable sensitivity. The distribution of dinoflagellate cysts in surface sediments has been correlated with conditions of overlying surface water masses in marine and oceanic environments. A number of studies showed that the composition of cyst assemblages depends on environmental conditions such as temperature, salinity, ice-cover, offshore/inshore proximity and upwelling zones (Wall et al., 1977; Harland, 1983; Turon, 1984; Mudie and Short, 1985; de Vernal and Giroux, 1991; Edwards and Andrle, 1992; Edwards, 1992; Dale, 1996; de Vernal et al., 1997; Marret and de Vernal, 1997; Rochon et al., 1999). Northern North Atlantic and Arctic cyst distributions are now well documented (Rochon et al. 1999, de Vernal et al. 2001) and have provided the foundation for detailed quantitative reconstructions of the Quaternary oceanic record in this region (e.g., de Vernal et al. 2000, de Vernal and Hillaire-Marcel 2000, Hillaire-Marcel et al. 2001).

In contrast to oceanic and marine systems where at least 2,000 surface samples have been analyzed, our understanding of the biogeography of dinoflagellate cysts in more variable coastal and estuarine environments is minimal. Studies on dinoflagellate cysts solely from estuarine environments include a maximum of 200 surface samples. The distribution of dinoflagellate cysts was studied within estuaries of sub-polar and polar regions of Europe (Dale, 1976; Saetre et al., 1997; Thorsen and Dale, 1997; Dale et al., 1999; Dale, 2001) and Canada (Miller et al., 1982; Mudie and Short, 1985; de Vernal and Giroux, 1991), as well as temperate regions of Europe (Blanco, 1995) and Australia (McMinn, 1989; 1990; 1991; Sonneman and Hill, 1997). Some samples from estuaries were also analyzed in surveys by Wall et al. (1977), Reid (1974, 1977), Harland (1977), Nehring (1997), and Rochon et al. (1999). Most investigators concluded that the composition of dinoflagellate cyst assemblages in estuaries reflects water temperature and salinity. However, to date direct comparison or calibration of environmental parameters to modern dinoflagellate cyst assemblages in estuarine systems is minimal.

Only one estuary on the east coast of North America, the river-dominated estuary and Gulf of St. Lawrence, has been studied in detail in order to relate modern dinoflagellate cysts to known water quality parameters (de Vernal and Giroux, 1991; Rochon et al., 1999). Other studies have been cursory in nature (Wall et al., 1977, Dale 1996) or targeted at selected toxic species (Anderson et al. 1994, Anderson, 1998). The lack of comprehensive surveys limits our geographical knowledge of the dinoflagellate cysts in temperate estuarine systems. We do not know yet what the general characteristics of dinoflagellate cyst assemblages in temperate estuarine systems of eastern North America (cyst abundance, diversity, and composition) are and how these characteristics change spatially and over time.

The spatial and temporal scales of environmental variability are smaller in estuaries than in the marine and oceanic environments. This is due to the relatively small size of estuarine water bodies, which makes them sensitive to external influences. In marine and oceanic environments, that are usually sampled on temporal scales of

~10-1000 yr and spatial scales of ~10-1000 km, the distribution of dinoflagellate cyst assemblages reflects abiotic environmental conditions, temperature and salinity in particular. Can we find correlations between dinoflagellate cyst distributions and environmental parameters in shallow estuaries where temporal and spatial scales are order(s) of magnitude smaller than in marine and oceanic systems? At the current stage of knowledge it is difficult to make any predictions as to what environmental parameter or group of parameters would play a dominant role in dinoflagellate cyst distribution. Are there any particular characteristics of assemblages that are the most sensitive to the change of environmental conditions? The answers to these questions will test the central hypothesis of my research: "Dinoflagellate cysts serve as indicators of abiotic environmental conditions in estuarine systems."

Pritchard's (1967) general definition of an estuary (a semi-enclosed coastal body of water, which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage) does not recognize the high degree of variability amongst estuaries. Estuaries come in different sizes and shapes, and can be classified according to tidal range or stratification. In this research, I use the estuarine classification system of Boynton et al. (1982) which is based upon physical circulation and geomorphology. These characteristics directly or indirectly affect the primary mechanisms known to influence phytoplankton production: flushing rate, nutrient input, salinity and light regime. Boynton's classification divides estuaries into four groups: fjord, lagoon, embayment and river-dominated. A shallow sill; deep stratified waters; and a slow exchange with ocean waters are characteristics of fjords. Lagoons are characterized by shallow depth, a well-mixed water column (not stratified), slow flushing and minimal input of freshwater. Embayments are deeper than lagoons, often stratified, only slightly influenced by riverine inputs, and have good exchange with the coastal ocean. The river-dominated category includes estuarine systems with seasonal changes in salinity due to river inputs and variable degrees of stratification. Lagoons, embayments and river-dominated systems are the most common features of the temperate northwest Atlantic coast.

Estuaries are complex systems where, in addition to natural variability of environmental parameters, anthropogenic input of nutrients and pollutants are likely be important. Human activity over past few hundred years has altered environmental conditions in estuaries. The clearance of vegetation, development of farms and cities has led to the changes in landscape, hydrology and water quality. These impacts include increasing nutrient and toxin loads, changes of salinity and oxygen regimes, and changes in sediment accumulation rates.

Palynological studies of Norwegian fjords (Dale and Fjellså, 1994; Sætre et al., 1997; Thorsen and Dale, 1997; Dale et al., 1999; Dale, 2001) and Tokyo Bay (Matsuoka, 1999; Matsuoka, 2001) have shown the potential of dinoflagellate cysts as indicators of eutrophication and industrial pollution in those estuaries. Dale and co-workers have investigated the dinoflagellate cyst record from several fjords which differ in the degree of industrial and nutrient pollution. A significant increase in total dinoflagellate cyst concentrations in the Oslofjord in the 19th-20th centuries was interpreted as a consequence of the increase of production due to anthropogenic nutrient enrichment (Dale and Fjellså, 1994; Dale et al., 1999). Investigators suggested that *Lingulodinium machaerophorum* is an indicator of cultural eutrophication, as its number increased with increasing nutrient enrichment. Industrially polluted Frierfjord showed a different pattern of dinoflagellate cyst occurrence over time (Sætre et al., 1997). The decrease in total dinoflagellate cyst concentrations since the mid-19th century was interpreted as a possible consequence of reduced dinoflagellate production caused by industrial pollution. This reduction was accompanied by an increase of the relative proportion of cysts of the heterotrophic species *Selenopemphix quanta* (the paleontological name for the cyst of *Protoperidinium conicum*). The cyst signal from Nordåsvannet Fjord (Thorsen and Dale, 1997) was similar to that observed in Frierfjord, although the Nordåsvannet Fjord was mostly subjected to eutrophication with little industrial waste. Thorsen and Dale (1997) proposed that an increase in the cysts of heterotrophic dinoflagellates may represent an “alternative” eutrophication signal.

Study of dinoflagellate cyst records in Tokyo Bay (Matsuoka, 1999; 2001) has shown dinoflagellate cyst sensitivity to eutrophication. Matsuoka reported an increased number of cysts of heterotrophic dinoflagellates as well as a sharp increase in the abundance of *Gyrodinium instriatum* cysts, caused by a large bloom of this species.

However, a large increase in absolute cyst abundance (observed in some Norwegian studies) corresponding to eutrophication was not observed in Tokyo Bay.

Studies in Japan and Norway showed that the dinoflagellate cyst record reflects anthropogenic activity in an estuary, but the response was encoded in different ways. To date there is no universally accepted parameter of cyst assemblages or set of parameters that reflects nutrient enrichment and/or industrial pollution in an estuary. Thus, it is not clear to what extent dinoflagellate cysts can be used to assess the status and trends of ecological change in estuarine systems.

Research strategy and thesis structure

This dissertation is the first comprehensive study of the dinoflagellate cyst records from the temperate estuaries along the southern coast of New England, USA. It documents cyst abundance, diversity, composition and temporal and spatial distributions of dinoflagellate cyst assemblages in a number of New England estuaries. By examining two types of estuaries, embayments and lagoons, within a single climatic zone, variability is expected to be due to differences in hydrology and levels of anthropogenic activity in the watersheds.

New Bedford Harbor, Apponagansett Bay and Clarks Cove (Buzzards Bay embayments) were studied. The most developed is New Bedford Harbor with a history of intensive industrial activity in the watershed and highly urbanized shorelines. Neighboring Apponagansett Bay and Clarks Cove were not subjected to the same high degree of industrial development. The history of this area is well documented and has been reviewed to assess the human impact on these embayments (Voyer et al., 2000; Pesch and Garber, 1994). Extensive chemical analyses of sediments have been performed by the Environmental Protection Agency (USA). Thus study of dinoflagellate cyst assemblages from these embayments provides an excellent opportunity to learn how different degrees of human impact on estuarine environments are reflected in the cyst records.

In order to assess the applicability of dinoflagellate cysts as indicators of environmental conditions, both temporal and spatial dinoflagellate cyst records must be studied. Multiple sites in 11 back-barrier lagoons located along the southern coasts of

Rhode Island and Massachusetts were sampled because of the availability of a high quality data set, providing multi-year water temperature, salinity and chemistry coverage. Physical and chemical parameters of estuarine waters have been measured over the last decade (Lee et al., 1997; WBNERR, 1996) as part of a water quality monitoring program. Water quality monitoring data can be used to relate dinoflagellate cyst distribution in surface sediments to environmental parameters.

The following four chapters present results of my research. Chapter 2 reports the study of sedimentary records of dinoflagellate cysts from two neighboring embayments and compares these records with the historical data of human activity in the watersheds over the past 500 years. The observed "signals" of eutrophication and pollution are compared with the observations from previous studies in Norway and Japan. Chapter 3 incorporates and expands the results of the Chapter 2 by describing the spatial distribution of dinoflagellate cyst assemblages in this region in response to different degrees of anthropogenic activity. The focus is on the distribution of dinoflagellate cysts along environmental gradients such as nutrient enrichment and toxic pollution. Chapter 4 reports analysis of the spatial variability and pattern of the dinoflagellate cyst distribution in coastal lagoons of Rhode Island and Massachusetts. A comparison of cyst assemblages to multi-year water quality measurements from 24 sites shows correlations between dinoflagellate cyst distribution and environmental parameters at small spatial scales. The environmental parameters controlling dinoflagellate cyst distribution in these ecosystems are discussed. Chapter 5 describes a new species of organic-walled dinoflagellate cyst, *Islandinium brevispinosum*, and its geographical distribution.

Two chapters of this thesis have been published, one has been accepted for publication, and one will be submitted for publication. Chapter 2 (Pospelova, V., Chmura, G.L. Boothman, W.S. and Latimer, J.S. Dinoflagellate cyst records and human disturbance in two neighboring estuaries, New Bedford Harbor and Apponagansett Bay, Massachusetts, USA) has been published in *The Science of the Total Environment* 2002, 298(1-3):81-102. Chapter 3 (Pospelova, V., Chmura, G.L. Boothman, W.S. and Latimer, J.S. Spatial distribution of modern dinoflagellate cysts in polluted estuarine sediments from Buzzards Bay (Massachusetts, USA) embayments) will be submitted to *Marine Pollution Bulletin*. Chapter 4 (Pospelova, V., Chmura, G.L. and Walker, H.A. Environmental factors influencing spatial distribution of dinoflagellate cyst assemblages in shallow lagoons of southern New England, USA) has been accepted for publication in *Review of Paleobotany and Palynology*. Chapter 5 (Pospelova, V. and Head, M.J. *Islandinium brevispinosum* sp. nov. (Dinoflagellata), a new organic-walled dinoflagellate cyst from modern estuarine sediments of New England, USA) has been published in the *Journal of Phycology* 2002, 38(3):593-601.

Contributions of authors

I have written all parts of the thesis, including four main chapters (2, 3, 4 and 5). I contributed to the collection of samples from Rhode Island lagoons and prepared all sediment samples for microscope analysis. The latter was done solely by me and produced the dinoflagellate cyst data presented in this thesis, including the discovery of a new species, *Islandinium brevispinosum*. I also performed all analysis of the data, including statistical treatment, evaluated the results, made the interpretations and formulated the conclusions. My supervisor G.L. Chmura, who initiated this study, selected the sites and collected most of the samples from the Rhode Island and Massachusetts lagoons. She assisted in an editorial and advisory capacity and provided partial funding. G.L. Chmura is the second author for the papers that constitute the content of Chapters 2, 3 and 4. J.S. Latimer and W.S. Boothman provided sediment samples from Buzzards Bay embayments and the data on physical and chemical characteristics of sediments. They appear as the third and fourth authors in the manuscripts corresponding to Chapter 2 and 3. H.A. Walker contributed by suggesting the project and by helping access and collect sediment samples from Rhode Island lagoons. M.J. Head provided data on previously assigned species of genus *Islandinium* in order to compare and establish new species of *Islandinium brevispinosum*. He helped with the interpretation of its morphological features and editing the manuscript corresponding to Chapter 5.

CHAPTER 2. DINOFLAGELLATE CYST RECORDS AND HUMAN DISTURBANCE IN TWO NEIGHBORING ESTUARIES, NEW BEDFORD HARBOR AND APPONAGANSETT BAY, MASSACHUSETTS (USA)

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ABSTRACT

The dinoflagellate cyst records in sediments from New Bedford Harbor and Apponagansett Bay demonstrate sensitivity to environmental change caused by human activity in the watersheds over the last 500 yr. Changes in the species richness, as well as absolute and relative abundance of dinoflagellate cyst taxa reflect recent periods of development around the estuaries. Cyst taxa sensitive to these changes include *Dubridinium* spp., *Polykrikos schwartzii, Lingulodinium machaerophorum, Operculodinium israelianum* and *Selenopemphix quanta*. The greatest changes in the dinoflagellate cyst record occur during the 20th century, when New Bedford Harbor was exposed to both toxic pollution and heavy nutrient loading from point and non-point sources. Apponagansett Bay was not subject to industrial pollution and nutrient enrichment has been lower (from non-point sources). In Apponagansett Bay there is an increase in the dinoflagellate cyst species richness while species richness first increased, then declined in New Bedford Harbor. During the same period, the total dinoflagellate cyst concentration in New Bedford Harbor fluctuated over a wide range. The decline of species richness and the large fluctuations in the total cyst abundances signal the intensified anthropogenic disturbance in the watershed, notably a high degree of eutrophication and toxic pollution.

INTRODUCTION

As a site to many of the world's major ports, estuaries have a significant economic importance. Not surprisingly, they often suffer from inputs of sewage and other contamination. Over history, estuarine watersheds have been subjected to vegetation clearance, agricultural development, urbanization and industrialization, and their waters to dredging and other physical alterations. These factors have led to problematic changes in hydrological regimes and water quality.

One of the most acute problems in estuarine systems is nutrient over-enrichment, resulting in eutrophication. Human activity has accelerated nutrient enrichment during the last century with increased inputs of mostly nitrogen and phosphorus, stimulating the greater production and standing crops of phytoplankton. Comparative studies on Waquoit Bay, Massachusetts have shown that the size of the total dinoflagellate population increased with the level of nitrogen loading in an estuary (Evgenidou et al., 1999). High nitrogen loading, accompanied by other factors, such as water column stratification and high allochthonous organic matter loading, may lead to nuisance blooms of dinoflagellate species (Paerl, 1988). High levels of nutrient loading can also change the nature of the estuarine ecosystem as shifts in phytoplankton communities from diatoms to greater importance of nanoplankton (Eppley and Weiler, 1979). A decrease of species diversity (Cooper and Brush, 1993; Sullivan, 1999) also has been observed in highly eutrophic systems.

Within the last few decades a concern has emerged about eutrophication caused by continued human population growth and urbanization around North American estuaries (Neilson and Cronin, 1981; Nixon, 1995). However, the character and extent of eutrophication can vary from one estuary to another depending on the intensity of the anthropogenic activity within the watershed, the basic nutrient level of the system and the characteristics of the system itself.

Although there are many qualitative observations, long-term, empirical measurements (decades and beyond) of estuarine water quality are rarely available. Historical photographs can be used to document changes in indicators of eutrophication, such as the loss of eelgrass, *Zostera marina* (McCleland and Valiela, 1996), but are limited to the availability of the photographic record.

Paleoecological studies can provide critical information on the timing and magnitude of ecological change in estuaries caused by anthropogenic activity. Microfossils, those of phytoplankton in particular, are useful tools in paleoecological studies due to their ubiquity and abundance. For example, sedimentary records of diatoms showed changes in their populations coincident with human disturbance in Chesapeake Bay, particularly nutrient enrichment of the estuary (Brush and Davis, 1984; Cooper and Brush, 1993; Cooper, 1995).

Dinoflagellate cysts are an important group of microfossils with potential as biological indicators of the timing and degree of environmental change in estuaries. Paleoecological studies of Norwegian fjords (Dale and Fjellså, 1994; Sætre et al., 1997; Thorsen and Dale, 1997; Dale et al., 1999; Dale, 2001) have examined dinoflagellate cysts as indicators of cultural eutrophication and industrial pollution, investigating the record from several fjords, which differ in the degree of industrial and nutrient pollution (for the most recent discussion, see Dale, 2001). Investigators concluded that increased concentrations of cysts were a consequence of the increase of dinoflagellate production due to anthropogenic nutrient enrichment, but suggested that where nutrient enrichment was accompanied by industrial pollution cyst production might actually decrease.

The Norwegian studies have provided evidence that some cyst taxa may show a positive response to cultural eutrophication. For example, in some fjords the number of *Lingulodinium machaerophorum* increased with increasing nutrient enrichment. In other fjords an increase of the relative proportion of cysts of the heterotrophic species *Selenopemphix quanta* (the paleontological name for the cyst of *Protoperidinium conicum*) also was reported. Thus Thorsen and Dale (1997) have proposed that the increase in the cysts of heterotrophic dinoflagellates may represent an eutrophication signal.

Matsuoka (1999; 2001) examined the cyst record over a period of increasing nutrient enrichment and industrial pollution in Tokyo Bay. He observed an increased number of cysts of heterotrophic dinoflagellates and an isolated peak in the abundance of *Gyrodinium instriatum* cysts that he assumed was caused by a bloom of this species of dinoflagellate. However, Matsuoka reported neither large increase in absolute cyst abundance nor an increase in *Lingulodinium machaerophorum* and *Selenopemphix quanta*, as suggested by researchers on Oslofjord (Dale and Fjellså, 1994; Dale et al., 1999).

Although studies in Japan and Norway show that the dinoflagellate cyst record reflects anthropogenic activity in an estuary, the response was encoded in different ways. Presently, there is no universally accepted cyst assemblage parameter or set of parameters that reflect nutrient over-enrichment and/or industrial pollution in an estuary. Because the primary mechanisms that influence phytoplankton production such as flushing rate, salinity and light regime, vary with estuarine hydrography, dinoflagellate cyst distributions may differ with the type of estuary (based on Boynton's et al., 1982 classification: fjords, embayments, lagoons, river-dominated estuaries). The signs of eutrophication encoded in dinoflagellate cyst records may vary with estuarine type but more research is needed to establish this.

The geographical application of dinoflagellate cyst studies is limited and there is no literature documenting the utility of dinoflagellate cysts as bio-indicators of anthropogenic changes in North American estuaries. We present the first such study for North American estuaries. Our research examines the sedimentary record of dinoflagellate cysts from two shallow embayments, New Bedford Harbor and Apponagansett Bay (Massachusetts), and compares it to detailed historical records of anthropogenic activity over the past 450 yr. These embayments are located within 10 km of each other, minimizing climatic variation, but have distinct watersheds and different histories. Intensive urban and industrial development in the watershed of New Bedford Harbor created a number of stimulating (nutrient enrichment) and suppressing (toxic pollution) influences, which we expect to be reflected in dinoflagellate cyst records. Apponagansett Bay serves as our control site as it is subject to lower levels of nutrient loading and no industrial pollution. We compare our results to those from dinoflagellate cyst studies in estuaries outside North America to determine if there are common signals of eutrophication and industrial pollution and how they might vary with differences in estuarine hydrography.

STUDY AREA

History

New Bedford Harbor, also known as the Acushnet River estuary, and Apponagansett Bay are side embayments of the northwestern part of Buzzards Bay, Massachusetts (Fig. 1). Europeans first settled the estuarine watersheds approximately 350 yr ago and from that time until the present day this region has been extensively exploited (Voyer et al., 2000).

Development and urbanization of the New Bedford area has had dramatic effects on the estuarine environment. New Bedford's history can be divided into four main periods (Pesch and Garber, 2001). The agricultural period spans the 1670s to the 1780s (Table 1). Forest clearance and land cultivation characterize this period. The second period is marked by the rise of the whaling industry and in the mid 19th century,

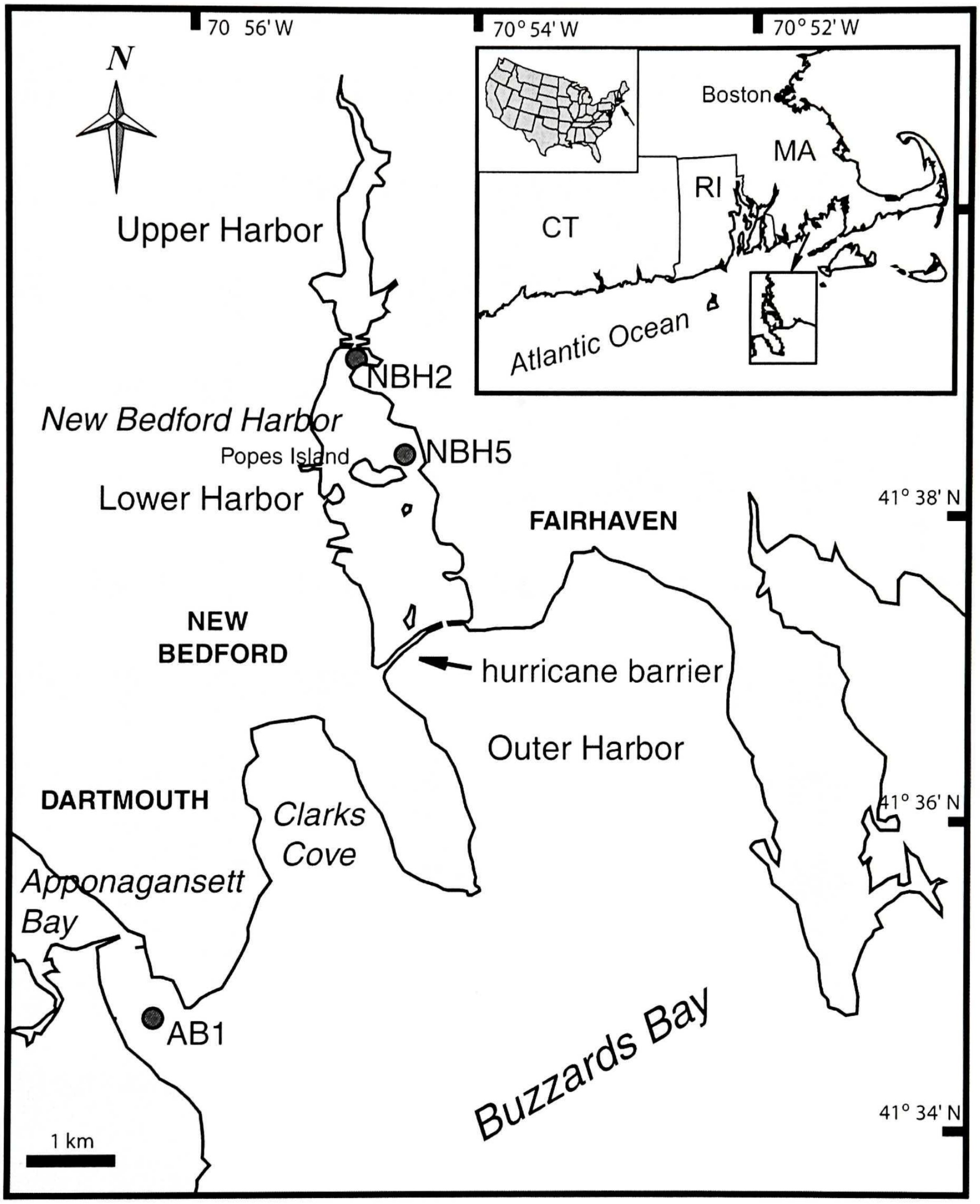

Figure 1. Map of New Bedford Harbor and Apponagansett Bay showing core locations.

Table 1. Summary of assumed ecological effects of development around New Bedford Harbor (adopted from Pesch and Garber 2001).

Time	Development	Consequence
Agricultural (1676-1780)	Cleared land, farmed	Minimal effect
Whaling (1750-1900)	Built wharfs	Altered currents and sedimentation
	New Bedford-Fairhaven Bridge	Altered currents and sedimentation
	Industries	Contaminated sediments in harbor
	Cleared more land for building	Erosion, input sediment and nutrient to estuary
Textile (1880-1940)	Built mills on wetlands	Loss of habitat and filtering capability
	Dramatic population increase led to increase sewage input	Increased organic matter, low species diversity, closed shellfish beds, Typhoid fever
	Industries	Contaminated sediments in harbor
Post-textile (1940-present)	Electronics industries	PCB contamination in harbor
	Other industries	Contaminated sediments in harbor
	Hurricane barrier 1964	Altered circulation patterns

whaling vessels from New Bedford Harbor numbered over 300 (Nelson et al., 1996). The boom in the textile industry, which began around the 1880s, marks the third period that lasted until the 1940s. This period was related with a significant increase of the population in the watershed (Fig. 2). Municipal sewage from the City of New Bedford was directed into the harbor, and in the early 1900s sewage discharged into the harbor from ~30 sewage outfalls (Voyer et al., 2000). Voyer et al. (2000) propose that nutrient enrichment resulted in an increase of algal production in the 1910s, suggesting a shift in the trophic status of the estuary from mesotrophic to eutrophic. During the fourth, post-textile period, industry shifted towards production of electronic components and xenobiotic chemicals were discharged into the harbor (Summerhayes et al., 1977; Pruell et al., 1990). Finally, a hurricane barrier across the mouth of the harbor constructed in the 1960s, reduced flushing rates in the inner part of New Bedford Harbor by as much as 30% (Abdelrhman, 2002), further degrading water quality. Eelgrass began disappearing during the 1960s and now is largely absent in New Bedford Harbor. Loss of eelgrass in estuaries is considered a signal of deteriorating water quality due to nutrient over-enrichment (Costa et al., 1996). In 1982, New Bedford Harbor was added to the Environmental Protection Agency (EPA) National Priority List for cleanup due to extreme levels of PCB sediment contamination (Nelson et al., 1996).

In contrast, Apponagansett Bay has experienced much lower levels of industrialization and population growth in its watershed. This bay can be considered as an example of an estuary affected mostly by nutrient enrichment, thus a control to which we contrast the impact of industrial pollution.

Modern and historical climatic conditions

The 30-year (1951-1980) average annual monthly air temperature at New Bedford is 11.3°C (Environmental Data and Information Service, 1983). Mean monthly temperatures are above 0°C 12 months of the year, but minimum temperatures are below 0°C from December to February, with the lowest monthly mean in January (-4.0°C).

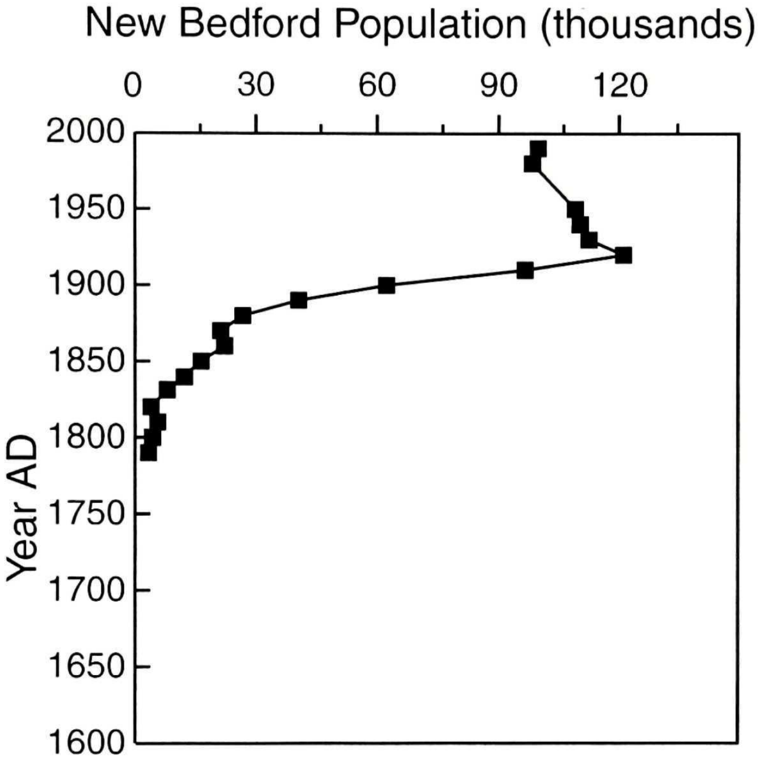

Figure 2. Historical data on population growth in New Bedford Harbor (modified from Latimer et al., in press).

Baron and Gordon (1985) used a combination of historical and instrumental records to reconstruct climate parameters in eastern Massachusetts over the period 1600-1980. They provide a reconstruction of winter air temperatures for 1742-1980, but the record is incomplete, missing the period 1780-1825. From 1742-1895 average winter temperatures were below 0ºC. After this period winter temperatures were more variable, but remained above 0ºC for 19 years of their record. Baron and Gordon (1985) also reconstructed the length of the growing season in eastern Massachusetts for the years 1750-1980. Growing season length shows a different pattern than average winter temperatures. Periods of the longest growing seasons occurred from 1800-1830, 1865-1895, and 1945-1980.

Modern estuarine conditions

The Acushnet River flows into the northern part of New Bedford Harbor providing a small freshwater input (Nelson et al., 1996). Average salinity in the estuary ranges from 28 ppt to 31 ppt and mean summer water temperature is about 21-23°C (Howes et al., 1999). Water depth varies from 1 to 12 m with a tidal range of 1.2 m. New Bedford Harbor is highly industrialized and has the heaviest nitrogen-loading in Buzzards Bay (Howes et al., 1999). Modern sediment concentrations are as high as 700 $\mu g \cdot g^{-1}$ PCBs, 1500 $\mu g \cdot g^{-1}$ Cu, 600 $\mu g \cdot g^{-1}$ Pb, and 1200 $\mu g \cdot g^{-1}$ Zn (Latimer, personal communications). Mean summer concentrations of nitrate and phosphorus in harbor waters are 11 and 1.8 μM, respectively, resulting in average summer concentrations of chlorophyll *a* of 8.5 $\mu g \cdot l^{-1}$ (ranging from 1.1 to 67.8 $\mu g \cdot l^{-1}$). The trophic status of New Bedford Harbor is considered to be eutrophic to hypertrophic (Howes et al., 1999).

As Apponagansett Bay has not been subjected to industrial pollution sediment concentrations of xenobiotics are relatively low: 0.6 $\mu g \cdot g^{-1}$ PCBs, 50 $\mu g \cdot g^{-1}$ Cu, 30 $\mu g \cdot g^{-1}$ Pb, and 100 $\mu g \cdot g^{-1}$ Zn (Latimer, personal communications). Absence of intense urbanization of its watershed means that nutrients come from non-point sources and concentrations in its waters are also lower. Nitrate and phosphorus concentrations are 5.2 μM and 1.7 μM, respectively, resulting in 3.5 $\mu g \cdot l^{-1}$ of chlorophyll *a*. Nitrate and chlorophyll *a* concentrations are less than half that recorded in New Bedford Harbor and the trophic status of Apponagansett Bay is considered to be only mesotrophic to eutrophic (Howes et al., 1999).

MATERIAL AND METHODS

Two sediment cores were collected in the fall of 1996 and one in the summer of 1998. Cores were collected at sites not affected by dredging or reclamation work. Two hand piston cores, NBH5 and NBH2, were obtained from the lower part of New Bedford Harbor in water depths of 2.3 and 3 m, respectively (Fig. 1). One gravity core, AB1, was collected from neighboring Apponagansett Bay, where the water depth was 4.6 m (Fig. 1). Sediments in all three cores are generally characterized as silt and sandy silt (Table 2) reflecting the generally coarse-grained character of the watershed's soils (Roffinoli and Fletcher, 1981). The mean grain size is shown in Figures 3, 4, and 5.

Sediments were dated using radiometric (^{210}Pb and ^{137}Cs) and palynological methods. Radiometric dating of two cores, AB1 (Apponagansett Bay) and NBH2 (New Bedford Harbor), was performed at the University of Liverpool's Environmental Radioactivity Centre, and core NBH5 (New Bedford Harbor) by OceanChem, Narragansett, Rhode Island. The palynological analysis was performed in the Paleoenvironmental Laboratory, Department of Geography, McGill University. Sedimentary concentrations of heavy metals and PCBs as well as the organic carbon content and δ^{13}C of sediments were measured by EPA and are reported by Latimer et al. (in press).

Samples for dinoflagellate cyst analyses were taken at 10 cm intervals, and at additional depths where required. Sampling intervals correspond to 4 - 40 yr of deposition, with an average of 15 yr during the 20th century.

Samples were treated according to a standardized protocol: dried at 40°C, weighed, sieved through a 125-μm and retained on a 10-μm mesh to eliminate coarse and fine material, treated with warm HF (40%) to dissolve silicates, and HCl (10%) to remove carbonates and silicoflourides. Calibrated tablets of *Lycopodium* spores (Stockmarr, 1977), added during processing, allowed for calculation of dinoflagellate cyst concentrations based on the dry weight of sediments.

Table 2. General sediment characteristics, as well as dinoflagellate cyst total counts, relative abundance, and species richness in cores from Apponagansett Bay (AB1) and New Bedford Harbor (NBH2 and NBH5). Asterisks denote taxa not counted for cyst richness, including the freshwater *Protoperidinium wisconsinense* .

Core depth (cm)	Date (year AD)	Sediment color	Lithology	Numbers of counted cysts	Species richness	*Alexandrium tamarense*	*Ataxiodinium choane*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* spp.	*Dubridinium* spp.	*Impagidinium* spp.	*Islandinium brevispinosum*	*Islandinium? cezare*	*Islandinium minutum*	*Lejeunecysta sabrina*	*Lingulodinium machaerophorum*	*Nematosphaeropsis* spp.
Core AB1																		
0-1	1993	brownish-black	sandy silt	309	23	0.0	0.0	0.0	1.6	1.9	2.3	0.3	5.5	1.3	2.6	0.3	0.3	1.3
5-6	1976	brownish-black	sandy silt	220	21	0.0	0.0	0.0	0.9	0.5	6.4	0.5	1.8	1.4	2.3	0.0	0.5	0.0
10-11	1957	brownish-black	sandy silt	267	20	0.0	0.0	0.0	1.5	3.4	6.0	0.0	0.0	1.5	3.4	0.4	0.0	0.7
14-15	1939	olive gray	sandy silt	241	19	0.0	0.0	0.0	0.4	0.8	8.7	0.0	1.2	0.4	1.7	0.0	0.0	0.4
20-21	1901	olive gray	sandy silt	308	19	0.0	0.0	0.0	0.6	1.9	10.4	0.0	1.9	0.3	0.3	0.0	0.3	0.3
30-31	1826	olive gray	sandy silt	354	19	0.0	0.0	0.0	1.7	0.6	4.0	0.6	0.0	0.0	0.8	0.3	1.1	0.8
40-41	1750	olive gray	sandy silt	321	19	0.0	0.0	0.3	0.6	1.2	3.1	0.0	0.9	0.3	0.3	0.0	0.0	0.6
50-51	1675	olive gray	sandy silt	329	17	0.0	0.0	0.0	0.6	0.6	2.1	0.6	0.0	0.0	0.6	0.3	0.9	1.8
60-61	1600	olive gray	sandy silt	392	19	0.0	0.0	0.0	1.0	2.3	4.3	0.3	0.0	0.3	0.3	0.5	1.8	1.3
70-71	1525	olive gray	sandy silt	286	17	0.0	0.0	0.0	0.0	2.4	3.1	0.0	0.0	0.0	1.0	1.4	1.4	0.3
75-76	1487	olive gray	sandy silt	329	20	0.0	0.0	0.0	0.3	0.0	1.8	0.0	0.6	0.3	0.3	0.3	0.9	0.3
Core NBH2																		
1-2	1996	olive black	sandy silt	106	17	0.9	0.0	0.0	0.9	2.8	0.9	0.9	0.9	1.9	3.8	0.0	2.8	0.9
10-11	1992	olive black	sandy silt	209	15	0.0	0.0	0.5	1.0	5.7	7.2	0.0	0.0	0.5	2.4	0.0	0.5	2.4
20-21	1983	olive black	sandy silt	222	15	0.0	0.0	0.0	0.9	2.3	11.3	0.0	1.8	0.0	0.5	0.0	0.9	1.4
30-31	1972	olive black	sandy silt	221	15	0.0	0.0	0.0	1.4	4.1	23.5	0.0	0.0	1.8	1.8	0.0	1.4	1.4
40-41	1959	grayish black	sandy silt	217	15	0.0	0.0	0.0	0.5	3.2	14.7	0.0	1.4	0.9	0.0	0.0	0.0	2.3
Core NBH5																		
0-1	1972	olive black	silt	149	15	0.7	0.0	0.0	0.0	2.0	7.4	0.0	2.7	0.0	0.7	0.0	0.7	2.0
5-6	1957	olive black	silt	210	15	0.0	0.0	0.0	0.0	1.4	3.3	0.0	0.5	0.5	1.9	0.0	0.5	2.4
10-11	1943	olive black	silt	385	16	0.3	0.0	0.0	0.3	0.8	1.0	0.3	0.3	0.8	1.6	0.0	0.3	1.0
15-16	1928	olive black	silt	235	15	0.0	0.0	0.0	0.9	0.4	0.9	0.4	0.0	0.4	0.9	0.0	1.3	0.4
20-21	1911	olive gray	silt	349	18	0.0	0.0	0.0	2.0	2.9	2.6	0.3	0.3	1.4	3.7	0.3	1.4	1.4
30-31	1877	olive gray	silt	305	21	0.0	0.0	0.0	3.3	4.3	3.0	0.3	1.0	0.7	3.3	1.0	0.7	2.6
40-41	1843	olive gray	silt	304	20	0.7	0.0	0.0	0.3	3.9	2.0	0.3	3.9	1.0	3.0	0.0	0.7	3.6
50-51	1808	olive gray	silt	345	22	0.0	0.0	0.0	0.3	4.9	4.6	0.6	3.8	0.3	2.6	0.6	1.4	2.9
60-61	1774	olive gray	silt	264	19	0.0	0.0	0.0	0.0	5.3	3.8	0.8	1.1	0.8	1.5	0.4	1.1	3.4
70-71	1740	olive gray	silt	344	22	0.0	0.0	0.0	2.9	1.7	4.4	0.3	0.9	0.0	0.6	0.6	1.7	3.2
80-81	1706	olive gray	silt	374	21	0.3	0.0	0.0	1.6	4.0	5.9	0.3	1.3	0.3	1.9	0.5	0.5	3.2
90-91	1672	olive gray	silt	375	18	0.0	0.0	0.0	0.5	2.4	5.1	0.5	0.3	0.0	0.5	0.8	1.3	2.7
100-101	1638	olive gray	silt	450	22	0.4	0.0	0.0	1.6	2.9	2.7	0.4	1.1	0.7	1.6	0.9	2.0	2.4
110-111	1605	olive gray	silt	341	19	0.0	0.0	0.0	0.3	2.3	2.3	0.0	0.3	0.0	0.3	1.5	4.4	5.3
120-121	1570	olive gray	silt	324	18	0.0	0.3	0.0	0.3	2.8	0.6	0.3	0.3	0.3	0.6	0.9	2.8	5.6

Table 2 (Continued)

Core depth (cm)	*Operculodinium centrocarpum* sensu Wall & Dale 1966	*Operculodinium centrocarpum* var. *truncatum*	*Operculodinium israelianum*	*Pentapharsodinium dalei*	*Polykrikos schwartzii* & *P. kofoidii*	*Protoperidinium oblongum*	*Protoperidinium type*	*Protoperidinium wisconsinense**	*Quinquecuspis concreta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Spiniferites* cf. *bentorii*	*Spiniferites elongatus*	*Spiniferites* spp.	*Stelladinium stellatum*	*Tectatodinium pellitum*	*Votadinium calvum*	*Votadinium spinosum*	Cyst type E	*Protoperidinium minutum*	Unknown cysts*
Core AB1																					
0-1	33.3	0.3	1.0	1.6	5.8	0.0	4.5	0.0	0.3	0.6	0.3	1.9	2.3	28.5	0.3	0.0	0.0	0.0	0.0	0.0	1.6
5-6	30.0	0.5	0.5	0.9	2.7	0.0	8.2	0.0	0.0	0.0	1.4	3.2	1.8	34.1	0.5	0.0	0.0	0.9	0.0	0.5	0.9
10-11	18.4	0.4	1.9	1.1	0.4	0.0	13.1	0.0	1.1	0.0	0.4	4.1	2.2	37.1	0.7	0.7	0.0	0.0	0.0	0.0	1.5
14-15	30.3	0.8	1.2	0.4	0.8	0.0	7.5	0.0	0.4	0.0	0.0	4.6	2.9	34.9	0.4	0.0	0.0	0.4	0.0	0.0	1.7
20-21	32.5	0.3	1.3	0.0	0.0	0.0	6.8	0.3	0.3	0.0	0.3	6.2	1.6	32.1	0.0	0.3	0.3	0.0	0.0	0.0	1.3
30-31	43.2	0.3	0.6	1.1	0.0	0.0	7.3	0.0	0.6	0.6	0.3	2.3	2.3	30.2	0.0	0.0	0.0	0.0	0.0	0.0	1.4
40-41	40.2	0.3	0.0	1.6	0.0	0.0	9.3	0.0	0.3	0.3	1.2	2.2	0.9	35.2	0.3	0.0	0.0	0.0	0.0	0.0	0.6
50-51	33.4	0.3	3.0	2.1	0.0	0.0	6.1	0.0	0.3	0.0	1.2	0.0	0.0	45.3	0.0	0.0	0.0	0.0	0.3	0.0	0.3
60-61	34.7	0.0	2.0	1.0	0.0	0.0	8.9	0.0	0.5	0.0	2.8	1.3	0.8	33.9	0.3	0.0	0.0	0.0	0.0	0.0	1.8
70-71	30.4	0.3	1.4	1.4	0.0	0.0	11.2	0.0	0.0	0.3	2.1	1.4	0.3	39.5	0.3	0.0	0.0	0.0	0.0	0.0	1.4
75-76	39.8	0.3	3.0	1.2	0.0	0.0	3.6	0.0	0.9	0.0	2.1	1.5	0.9	40.4	0.3	0.0	0.3	0.0	0.0	0.0	0.6
Core NBH2																					
1-2	15.1	0.0	0.0	3.8	0.0	0.0	15.1	0.0	0.0	0.0	0.0	0.9	0.9	37.7	0.9	0.0	0.0	0.0	0.0	0.0	8.5
10-11	12.9	0.0	0.0	0.5	0.5	0.0	14.4	0.5	0.0	0.0	0.0	1.4	1.4	45.5	0.0	0.0	0.0	0.0	0.0	0.0	2.9
20-21	13.1	0.0	0.0	0.5	0.9	0.0	15.8	0.0	0.5	0.0	0.0	2.3	0.0	46.4	0.0	0.0	0.0	0.0	0.0	0.5	1.4
30-31	6.8	0.5	0.0	0.0	1.8	0.0	15.8	0.0	0.5	0.0	0.0	2.3	1.4	33.5	0.0	0.0	0.0	0.0	0.0	0.0	2.3
40-41	9.2	0.0	0.0	0.9	4.1	0.0	15.2	0.0	2.8	0.0	0.0	3.2	0.5	38.7	0.0	0.5	0.0	0.0	0.0	0.0	1.8
Core NBH5																					
0-1	6.7	0.7	0.0	3.4	0.0	0.0	8.1	0.0	0.0	0.0	0.0	4.0	2.7	55.0	0.0	0.0	0.0	0.0	2.7	0.0	0.7
5-6	14.8	0.0	0.0	2.4	0.0	0.0	9.0	0.0	0.0	0.0	0.0	3.3	0.5	55.2	1.0	0.0	0.0	0.0	0.5	0.0	2.9
10-11	7.0	0.0	0.0	1.8	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.8	0.3	79.7	0.0	0.0	0.0	0.0	0.0	0.0	0.5
15-16	10.6	0.4	0.0	0.9	0.0	0.0	5.1	0.0	0.0	0.0	0.0	2.1	0.9	71.5	0.0	0.0	0.0	0.0	0.0	0.0	3.0
20-21	16.6	0.0	0.0	2.6	0.9	0.0	10.0	0.3	0.3	0.0	0.0	0.6	2.0	49.3	0.0	0.0	0.0	0.0	0.0	0.0	1.1
30-31	15.4	0.0	0.0	2.3	0.0	0.3	6.9	0.3	0.0	0.0	0.3	1.3	0.3	50.8	0.3	0.3	0.0	0.3	0.0	0.0	1.0
40-41	21.4	0.0	0.3	3.6	0.0	0.0	8.2	0.3	0.3	0.0	0.0	1.6	1.6	41.4	0.7	0.7	0.0	0.0	0.0	0.0	0.3
50-51	14.8	0.3	0.0	1.7	0.0	0.0	9.3	0.0	0.3	0.0	0.6	1.7	0.6	47.0	0.6	0.0	0.0	0.3	0.3	0.0	0.6
60-61	18.9	1.5	0.0	4.9	0.0	0.0	7.6	0.4	0.8	0.4	0.4	3.0	1.9	42.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
70-71	11.6	0.3	0.6	1.5	0.6	0.0	5.5	0.0	2.0	0.3	0.0	0.6	0.3	56.7	0.6	1.2	0.0	0.0	0.0	0.0	2.0
80-81	14.7	0.3	0.0	1.6	0.0	0.0	7.8	0.3	1.1	0.0	0.3	1.3	0.5	51.1	0.5	0.0	0.0	0.0	0.0	0.0	0.8
90-91	19.2	0.0	0.3	1.3	0.0	0.0	6.1	0.8	0.8	0.0	1.1	1.3	0.8	54.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
100-101	17.3	0.0	0.2	2.9	0.0	0.0	8.9	0.0	0.4	0.0	0.9	1.3	0.4	50.0	0.4	0.2	0.0	0.0	0.0	0.0	0.2
110-111	16.1	0.3	0.0	1.8	0.0	0.0	5.3	0.9	0.3	0.0	0.9	0.6	0.6	53.1	1.8	0.0	0.0	0.0	0.3	0.0	1.5
120-121	16.0	0.0	0.0	1.5	0.0	0.0	6.5	0.6	0.0	0.0	0.0	0.0	0.9	57.7	0.0	0.9	0.3	0.0	0.0	0.0	0.6

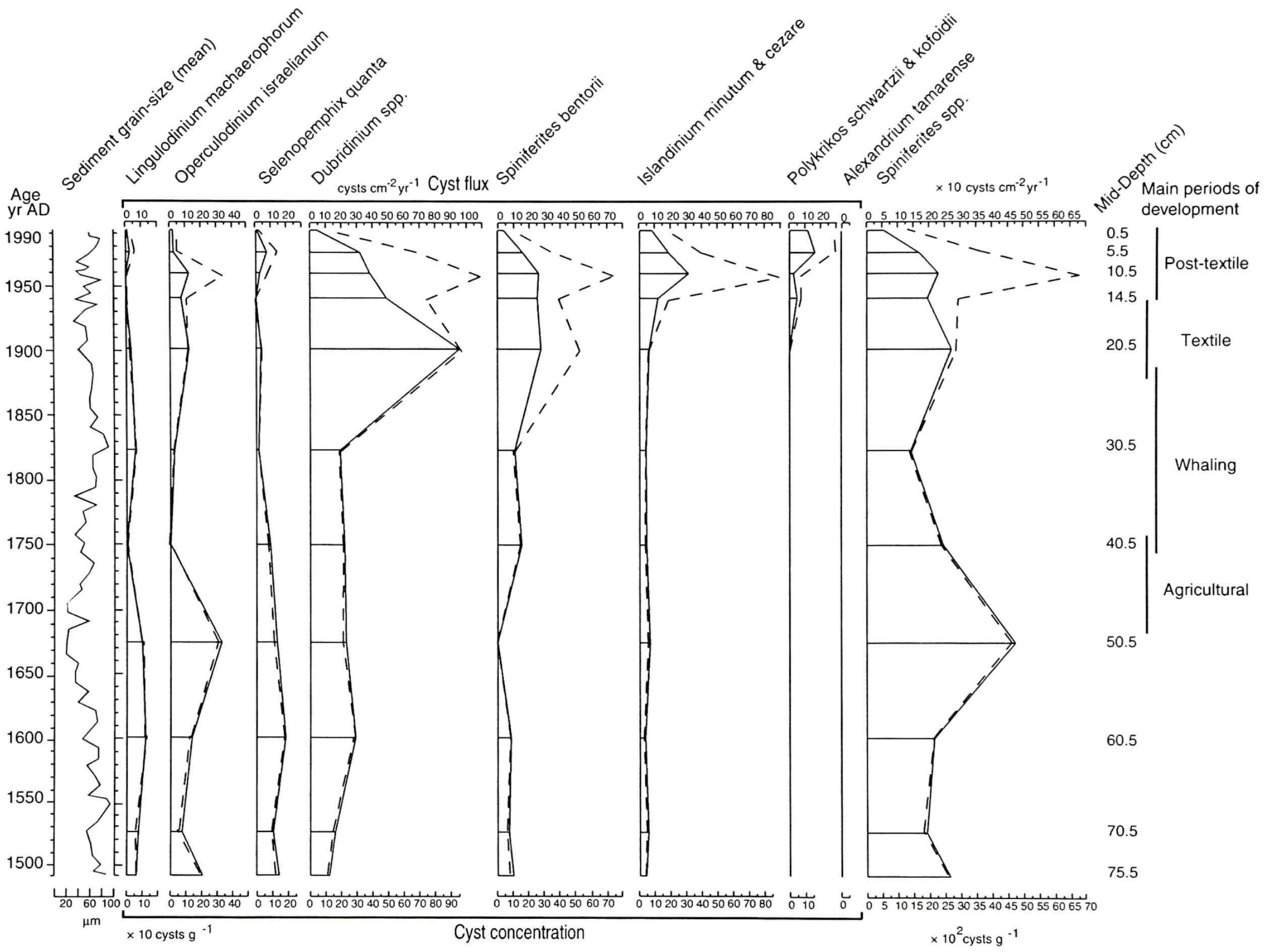

Figure 3. Concentrations and estimated fluxes of selected dinoflagellate cyst taxa in core AB1, Apponagansett Bay.

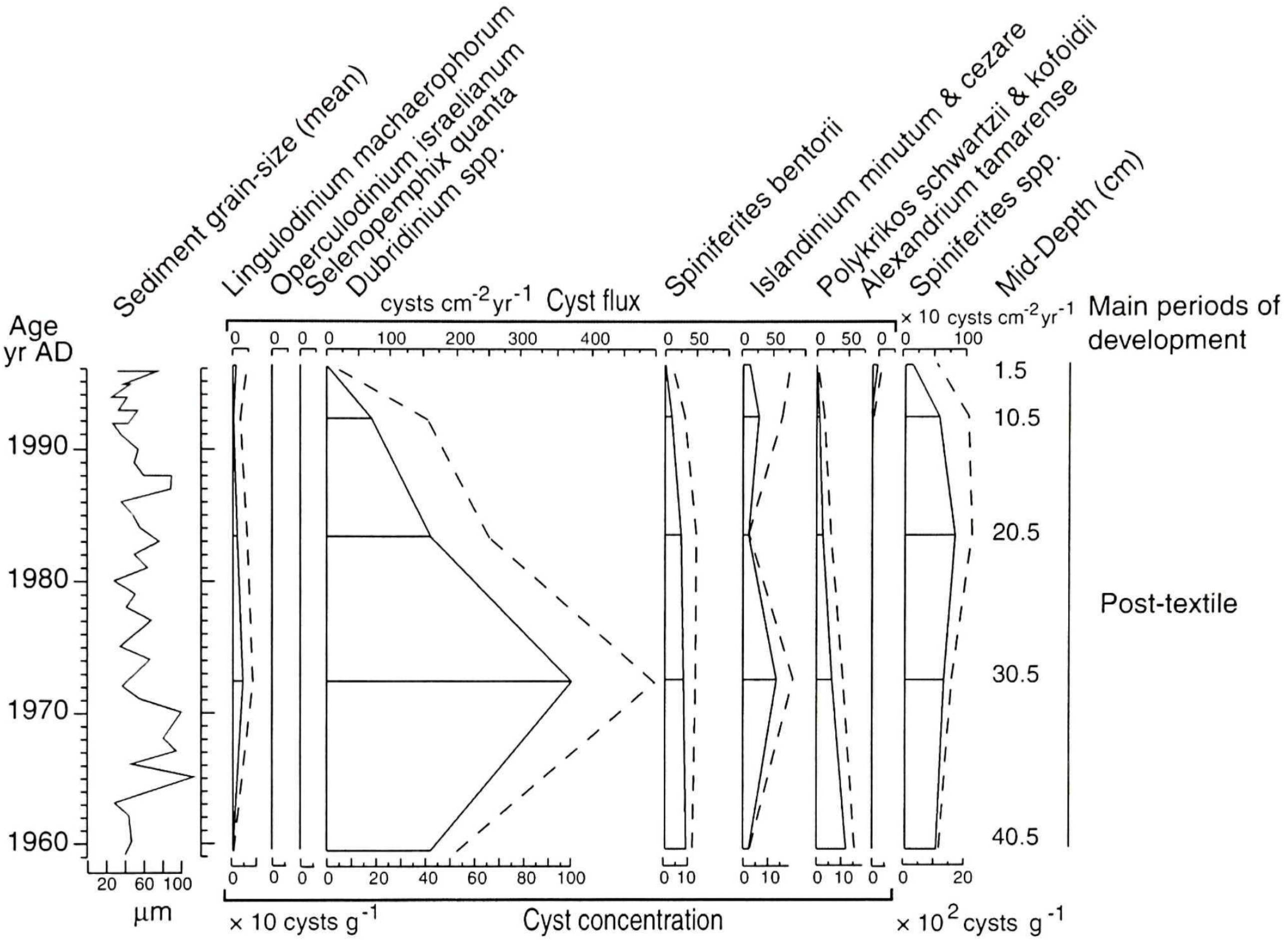

Figure 4. Concentrations and estimated fluxes of selected dinoflagellate cyst taxa in core NBH2, New Bedford Harbor.

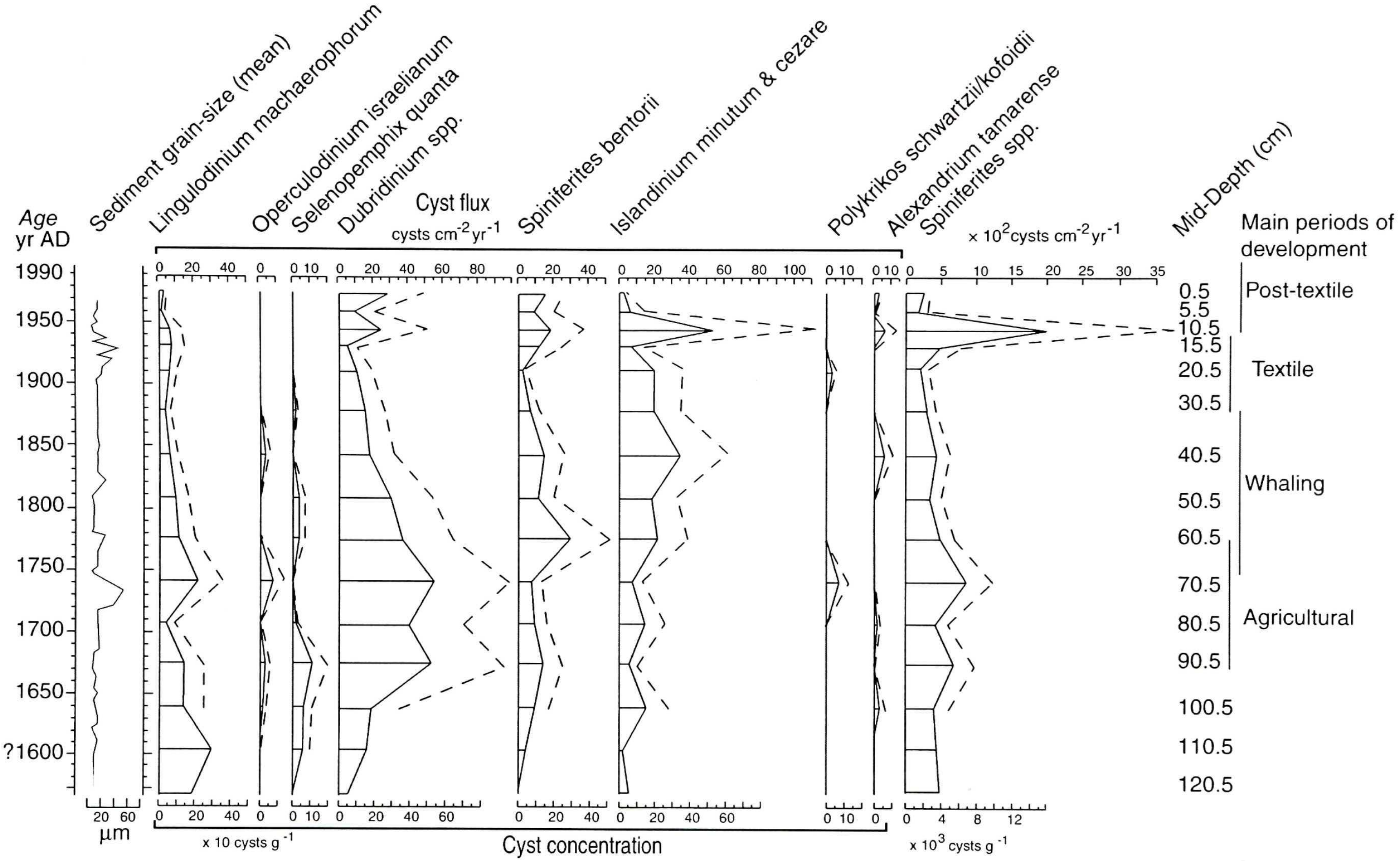

Figure 5. Concentrations and estimated fluxes of selected dinoflagellate cyst taxa in core NBH5, New Bedford Harbor.

Aliquots were mounted on microscope slides with glycerin jelly. Identification of dinoflagellate cysts was made on the basis of published descriptions in accordance with taxonomy given in Lentin and Williams (1993). However, when species-level identification was not possible, identification was done at the genus level. There are different taxonomic systematics for cysts and thecal stages of dinoflagellates because paleontological studies of cysts originally were carried out independently from biological studies of the motile forms. Here we use the paleontological nomenclature according to Head (1996), Head et al. (2001), and Pospelova and Head (2002). A list of the dinoflagellate cysts counted and their known biological name or thecal equivalent is provided in Table 3.

Temporal changes in dinoflagellate cyst assemblages were analyzed by determining the total cyst concentrations, total cyst fluxes (or cyst accumulation rates), species richness, the proportions of cysts of heterotrophic and autotrophic dinoflagellates, as well as certain species-indicators. Species richness (or number of taxa) was preferred over other diversity indices as it has been found to be the most sensitive indicator of the response of phytoplankton to changes in aquatic ecosystems induced by nutrient enrichment, pollution or environmental stress (Sommer, 1995; Tsirtsis and Karydis, 1998).

An average of 293 cysts and a minimum of 106 were counted in each sample. More than 34 dinoflagellate cyst taxa were identified and counted in sediments from the three cores (Tables 2, 4). We observed no reworked pre-Quaternary dinoflagellate cysts or pollen in this study. Microphotographs of selected taxa are shown in Figure 6.

Total cyst flux, or accumulation rate of cysts (cysts cm^{-2} yr^{-1}), is the product of the total cyst concentration (cysts g^{-1}), the sedimentation rate (cm yr^{-1}), and the dry bulk density (g cm^{-3}). Because it accounts for variable sedimentation rates, cyst flux is the preferable indicator of changes in cyst production (Dale, 2001). The total cyst fluxes were calculated for the upper parts of cores AB1, NBH5 and for the whole section of NBH2, that is for the sediment samples deposited during the 20th century where the sedimentation rates were determined directly from the radiometric dating. For lower parts of cores AB1 and NBH5 only approximate dinoflagellate cyst flux can be

Table 3. Taxonomic citation of dinoflagellate cysts used in this study. Thecal equivalents are taken from Head (1996), [1]Pospelova and Head (2002), and [2]Head et al. (2001).

Cyst species (paleontological name)	Dinoflagellate thecate name or affinity (biological name)
AUTOTROPHIC	
Gonyaulacaceae	
—	*Alexandrium tamarense*
Ataxiodinium choane	*Gonyaulax spinifera complex*
Impagidinium spp.	? *Gonyaulax* sp. indet.
Lingulodinium machaerophorum	*Lingulodinium polyedrum*
Nematosphaeropsis spp.	*Gonyaulax spinifera* complex
Operculodinium centrocarpum sensu Wall & Dale 1966	*Protoceratium reticulatum*
Operculodinium israelianum	? *Protoceratium reticulatum*
Spiniferites bentorii	*Gonyaulax digitalis*
Spiniferites elongatus	*Gonyaulax spinifera* complex
Spiniferites spp.	*Gonyaulax spinifera* complex
Tectatodinium pellitum	*Gonyaulax spinifera* complex
Protoperidiniaceae	
—	*Pentapharsodinium dalei*
HETEROTROPHIC	
Protoperidiniaceae	
Brigantedinium cariacoense	*Protoperidinium avellanum*
Brigantedinium simplex	*Protoperidinium conicoides*
Brigantedinium spp.	? *Protoperidinium* spp.
[1]*Islandinium brevispinosum*	*Protoperidinium* sp. indet.
[2]*Islandinium? cezare*	*Protoperidinium* sp. indet.
[2]*Islandinium minutum*	*Protoperidinium* sp. indet.
Lejeunecysta sabrina	*Protoperidinium leonis*
—	*Protoperidinium minutum*
Protoperidinium oblongum	*Protoperidinium oblongum*
Protoperidinium type	*Protoperidinium* group
Protoperidinium wisconsinense	*Protoperidinium wisconsinense*
Quinquecuspis concreta	*Protoperidinium leonis*
Selenopemphix nephroides	*Protoperidinium subinerme*
Selenopemphix quanta	*Protoperidinium conicum*
Stelladinium stellatum	*Protoperidinium stellatum*
Votadinium calvum	*Protoperidinium oblongum*
Votadinium spinosun	*Protoperidinium claudicans*
Diplopsalidaceae	
Dubridinium spp.	Diplopsalid group
Polykrikaceae	
—	*Polykrikos schwartzii*
—	*Polykrikos kofoidii*

Table 4. Concentrations of dinoflagellate cysts (cysts per gram of dry sediments) in cores from Apponagansett Bay (AB1) and New Bedford Harbor (NBH5 and NBH2).

Core depth (cm)	Date (year AD)	Total cyst concentrations (cysts gr^{-1})	*Alexandrium tamarense*	*Ataxiodinium choane*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* spp.	*Dubridinium* spp.	*Impagidinium* spp.	*Islandinium brevispinosum*	*Islandinium? cezare*	*Islandinium minutum*	*Lejeunecysta sabrina*	*Lingulodinium machaerophorum*	*Nematosphaeropsis* spp.	*Operculodinium centrocarpum* sensu Wall & Dale 1966	*Operculodinium centrocarpum* var. *truncatum*	*Operculodinium israelianum*
Core AB1																		
0-1	1993	1973	0	0	0	32	38	45	6	109	26	51	6	6	26	658	6	19
5-6	1976	5051	0	0	0	46	23	321	23	92	69	115	0	23	0	1515	23	23
10-11	1957	6427	0	0	0	96	217	385	0	0	96	217	24	0	48	1179	24	120
14-15	1939	5627	0	0	0	23	47	490	0	70	23	93	0	0	23	1704	47	70
20-21	1901	9204	0	0	0	60	179	956	0	179	30	30	0	30	30	2988	30	120
30-31	1826	4866	0	0	0	82	27	192	27	0	0	41	14	55	41	2103	14	27
40-41	1750	7102	0	0	22	44	88	221	0	66	22	22	0	0	44	2854	22	0
50-51	1675	10774	0	0	0	65	65	229	65	0	0	65	33	98	196	3602	33	327
60-61	1600	6681	0	0	0	68	153	290	17	0	17	17	34	119	85	2318	0	136
70-71	1525	5120	0	0	0	0	125	161	0	0	0	54	72	72	18	1557	18	72
75-76	1487	6720	0	0	0	20	0	123	0	41	20	20	20	61	20	2676	20	204
Core NBH2																		
1-2	1996	703	25	0	0	6	19	6	6	6	13	26	0	19	6	103	0	0
10-11	1992	2629	0	0	13	25	151	189	0	0	13	63	0	13	63	340	0	0
20-21	1983	3787	0	0	0	34	85	426	0	68	0	17	0	34	51	495	0	0
30-31	1972	4075	0	0	0	55	166	959	0	0	74	74	0	55	55	277	18	0
40-41	1959	2924	0	0	0	13	94	431	0	40	27	0	0	0	67	270	0	0
Core NBH5																		
0-1	1972	3712	25	0	0	0	75	274	0	100	0	25	0	25	75	249	25	0
5-6	1957	2572	0	0	0	0	37	86	0	12	12	49	0	12	61	380	0	0
10-11	1943	22678	59	0	0	59	177	236	59	59	177	353	0	59	236	1590	0	0
15-16	1928	5349	0	0	0	46	23	46	23	0	23	46	0	68	23	569	23	0
20-21	1911	3828	0	0	0	77	110	99	11	11	55	143	11	55	55	636	0	0
30-31	1877	4952	0	0	0	162	211	146	16	49	32	162	49	32	130	763	0	0
40-41	1843	8680	57	0	0	29	343	171	29	343	86	257	0	57	314	1856	0	29
50-51	1808	6312	0	0	0	18	310	292	36	237	18	164	36	91	182	930	18	0
60-61	1774	9526	0	0	0	0	505	361	72	108	72	144	36	108	325	1804	144	0
70-71	1740	12310	0	0	0	358	215	537	36	107	0	72	72	215	394	1431	36	72
80-81	1706	6722	18	0	0	108	270	395	18	90	18	126	36	36	216	988	18	0
90-91	1672	10269	0	0	0	55	246	520	55	27	0	55	82	137	274	1972	0	27
100-101	1638	6769	30	0	0	105	196	181	30	75	45	105	60	135	165	1173	0	15
110-111	1605	6640	0	0	0	19	156	156	0	19	0	19	97	292	350	1071	19	0
120-121	1570	7112	0	22	0	22	198	44	22	22	22	44	66	198	395	1141	0	0

Table 4 (Continued)

Core depth (cm)	*Pentapharsodinium dalei*	*Polykrikos schwartzii & P. kofoidii*	*Protoperidinium oblongum*	*Protoperidinium type*	*Protoperidinium wisconsinense**	*Quinquecuspis concreta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Spiniferites* cf. *bentorii*	*Spiniferites elongatus*	*Spiniferites* spp.	*Stelladinium stellatum*	*Tectatodinium pellitum*	*Votadinium calvum*	*Votadinium spinosum*	Cyst type E	*Protoperidinium minutum*	Unknown cysts*
Core AB1																		
0-1	32	115	0	89	0	6	13	6	38	45	562	6	0	0	0	0	0	32
5-6	46	138	0	413	0	0	0	69	161	92	1722	23	0	0	46	0	23	46
10-11	72	24	0	842	0	72	0	24	265	144	2383	48	48	0	0	0	0	96
14-15	23	47	0	420	0	23	0	0	257	163	1961	23	0	0	23	0	0	93
20-21	0	0	0	628	30	30	0	30	568	149	2959	0	30	30	0	0	0	120
30-31	55	0	0	357	0	27	27	14	110	110	1471	0	0	0	0	0	0	69
40-41	111	0	0	664	0	22	22	88	155	66	2500	22	0	0	0	0	0	44
50-51	229	0	0	655	0	33	0	131	0	0	4879	0	0	0	0	33	0	33
60-61	68	0	0	597	0	34	0	187	85	51	2267	17	0	0	0	0	0	119
70-71	72	0	0	573	0	0	18	107	72	18	2023	18	0	0	0	0	0	72
75-76	82	0	0	245	0	61	0	143	102	61	2717	20	0	20	0	0	0	41
Core NBH2																		
1-2	26	0	0	103	0	0	0	0	6	6	258	6	0	0	0	0	0	58
10-11	13	13	0	377	13	0	0	0	38	38	1195	0	0	0	0	0	0	75
20-21	17	34	0	597	0	17	0	0	85	0	1757	0	0	0	0	0	17	51
30-31	0	74	0	645	0	18	0	0	92	55	1364	0	0	0	0	0	0	92
40-41	27	121	0	445	0	81	0	0	94	13	1132	0	13	0	0	0	0	54
Core NBH5																		
0-1	125	0	0	299	0	0	0	0	149	100	2043	0	0	0	0	100	0	25
5-6	61	0	0	233	0	0	0	0	86	12	1421	24	0	0	0	12	0	73
10-11	412	0	0	766	0	0	0	0	177	59	18084	0	0	0	0	0	0	118
15-16	46	0	0	273	0	0	0	0	114	46	3824	0	0	0	0	0	0	159
20-21	99	33	0	384	11	11	0	0	22	77	1887	0	0	0	0	0	0	44
30-31	114	0	16	341	16	0	0	16	65	16	2516	16	16	0	16	0	0	49
40-41	314	0	0	714	29	29	0	0	143	143	3598	57	57	0	0	0	0	29
50-51	109	0	0	584	0	18	0	36	109	36	2955	36	0	0	18	18	0	36
60-61	469	0	0	722	36	72	36	36	289	180	4005	0	0	0	0	0	0	0
70-71	179	72	0	680	0	250	36	0	72	36	6978	72	143	0	0	0	0	250
80-81	108	0	0	521	18	72	0	18	90	36	3433	36	0	0	0	0	0	54
90-91	137	0	0	630	82	82	0	110	137	82	5559	0	0	0	0	0	0	0
100-101	196	0	0	602	0	30	0	60	90	30	3385	30	15	0	0	0	0	15
110-111	117	0	0	350	58	19	0	58	39	39	3524	117	0	0	0	19	0	97
120-121	110	0	0	461	44	0	0	0	0	66	4105	0	66	22	0	0	0	44

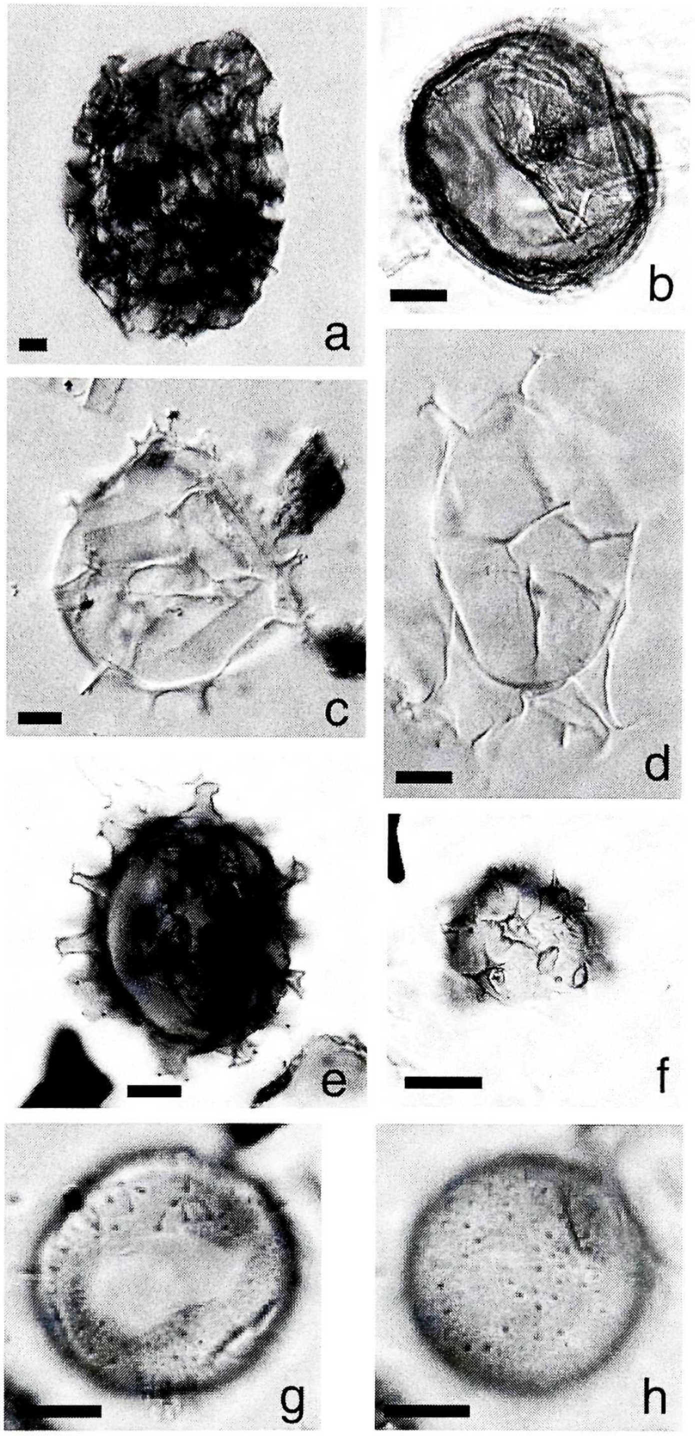

Figure 6. Microphotographs of selected dinoflagellate cysts found in sediments of New Bedford Harbor and Apponagansett Bay: a) *Polykrikos schwartzii,* b) *Dubridinium* spp., c) *Spiniferites bentorii,* d) *Spiniferites elongatus,* e) and f) *Protoperidinium minutum,* g) and h) Cyst type E. Scale bar = 10 µm.

calculated. As bulk densities were not available for all samples, some values were estimated based upon the available data. Our minimum values of total dinoflagellate cyst flux are on the order of 100 times higher that those reported from oceanic sediments (e.g., Höll et al., 2000).

RESULTS

Core chronologies

The combined results of the radiometric and palynological dating of the three cores are presented in Figure 7. A detailed account of the dating will be reported elsewhere (Latimer et al., in press).

Core AB1, from Apponagansett Bay, is 0.76 m deep and represents more than 500 years of deposition. At 11.5 ±2 cm traces of ^{137}Cs signal the onset of fallout of radionuclide due to the nuclear weapon testing in 1954. Peak concentration of ^{137}Cs at 5.5 ±1.5 cm indicates the maximum fallout in 1963. The ^{210}Pb profile interpreted with the constant rate of supply (CRS) model (Appleby and Oldfield, 1978) dates the upper 16.5 cm of the core to 1931-1996. The sedimentation rate increases from ~0.23 cm yr^{-1} in the 1930-1950s to 0.35 cm yr^{-1} and greater in the following 20 yr. Palynological analysis shows that ragweed pollen increases at ~51.5 cm indicating initial land clearance by European settlers (Brugam, 1978).

The sedimentation rate in core NBH2, from Lower New Bedford Harbor, was about three times higher than in Apponagansett Bay, and the upper 45 cm of this core represents approximately 40 yr of deposition. The dating based on ^{137}Cs activity is in a broad agreement with the CRS interpretation of the ^{210}Pb profile. The sedimentation rate varies from 0.59 cm yr^{-1} at the bottom of the core (1956) to 1.8 cm yr^{-1} at the top.

The dating of core NBH5, from Lower New Bedford Harbor, was more problematic. The maximum of ^{137}Cs activity occurs within the top 6 cm of the core. Together with sedimentation rates determined by the CRS ^{210}Pb method, it dates the top of the core as ~1973, suggesting that the part of this core was lost during core collection. The ^{210}Pb-dating is supported by PCB concentrations that first occur in trace amounts at 11 cm. This should correspond to the 1930-40s, when PCBs were first

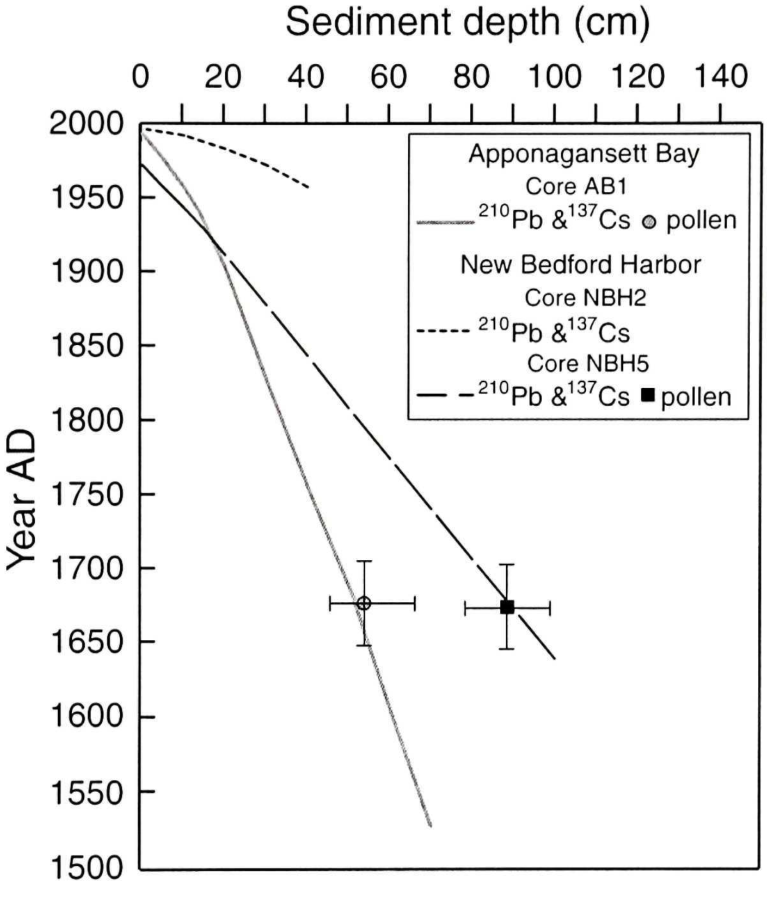

Figure 7. Age/depth plots for sediments from Apponagansett Bay and New Bedford Harbor based on the radionuclide (^{210}Pb and ^{137}Cs) and palynological analyses.

synthesized. A mean sedimentation rate of 0.29 cm yr^{-1} was extrapolated to the depth of 90.5 cm. This extrapolation was confirmed by pollen analysis. At 90-91 cm ragweed comprises >1% of the total pollen assemblages, corresponding to the time of the first European settlement in the area around the 1670s (Brugam, 1978). Dating below this point is uncertain.

Dinoflagellate cyst assemblages

Apponagansett Bay, Core AB1

The dinoflagellate cyst record in core AB1 generally can be divided into two stages. The first stage spans the 1480s to the 1900s. This stage is characterized by dinoflagellate cyst assemblages with <22% heterotrophic (Protoperidiniaceae, Diplopsalidaceae, and Polykrikaceae) taxa (Fig. 8), while the group of Diplopsalidaceae and Polykrikaceae comprises <5% of total assemblages. The total cyst concentration increases from 5,120 cysts g^{-1} in the 16th century to a maximum of 10,774 cysts g^{-1} in the 1670s, then decreases to a minimum 4,866 cysts g^{-1} at the end of 1820s (Fig. 9a). The estimated average cyst flux during this stage is ~650 cysts cm^{-2} yr^{-1} (Fig 9b). The number of dinoflagellate cyst taxa during the first stage ranges from 17 to 20 (Fig. 10). In the 17th century the maximum concentration and flux of all dinoflagellate cysts is coincident with increases in autotrophic *Operculodinium israelianum* and *Spiniferites* spp. (Fig. 3). The 17th century is also characterized by relatively high levels of the autotrophic *Lingulodinium machaerophorum* and heterotrophic *Selenopemphix quanta* (Fig. 3).

The second stage in Apponagansett Bay extends from 1900 to the present. The total cyst flux varies from ~500 to 1800 cysts cm^{-2} yr^{-1} (Fig 9b). Total concentrations of dinoflagellate cysts reach a maximum of 9,204 cysts g^{-1} in ~1901, while total flux peaks in the 1950s (Fig. 9a).

The 20th century assemblages are characterized by higher proportions of cysts of the heterotrophic taxa Diplopsalidaceae and Polykrikaceae (Fig. 8). Around 1901, concentrations of both *Dubridinium* spp. (956 cysts g^{-1}, 86 cysts cm^{-2} yr^{-1}) and *Spiniferites bentorii* (568 cysts g^{-1}, 51 cysts cm^{-2} yr^{-1}) reach a maximum (Fig. 3). As

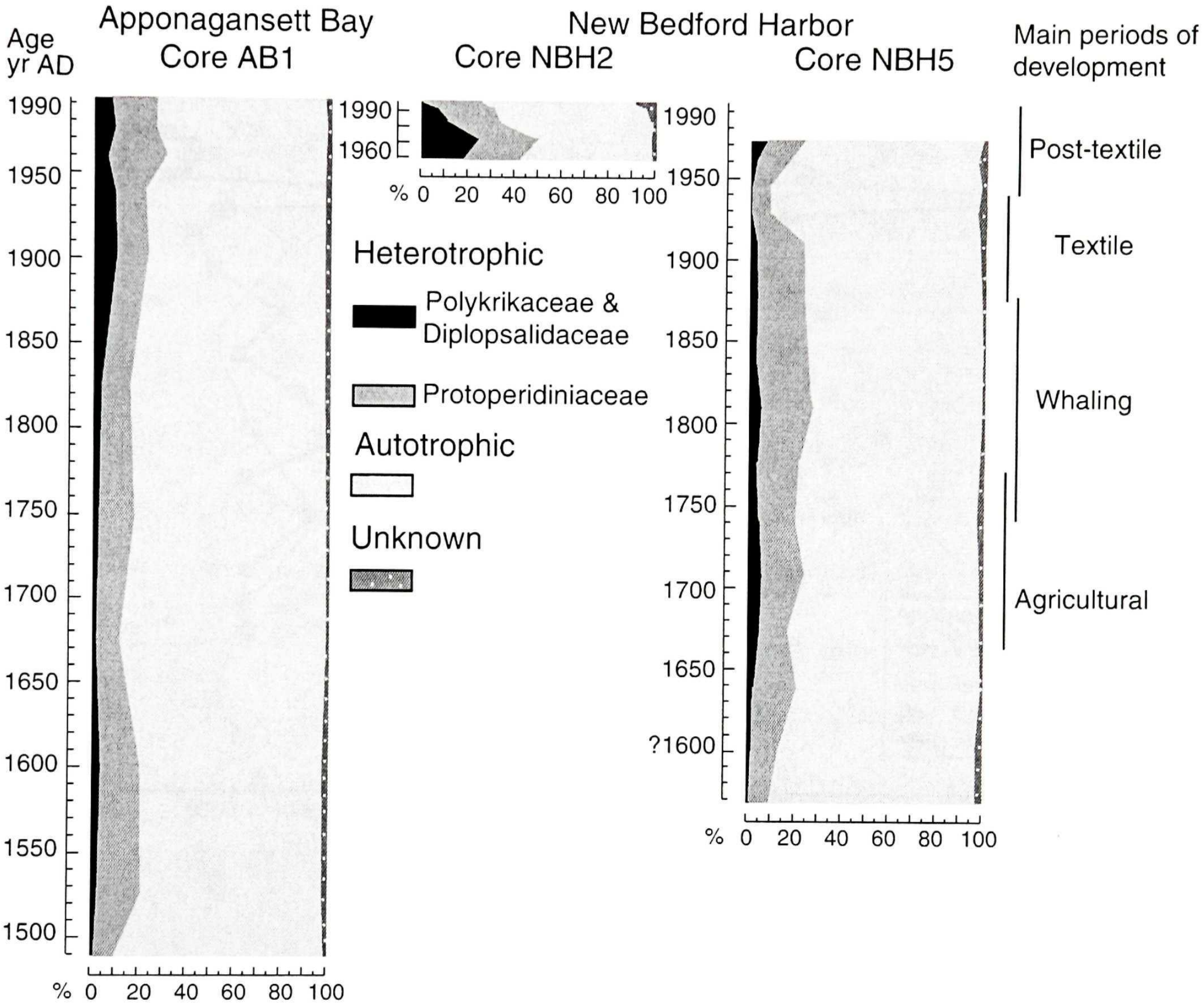

Figure 8. Relative abundance (%) of heterotrophic (Protoperidiniaceae, Polykrikaceae and Diplopsalidaceae) and autotrophic taxa in dinoflagellate cyst assemblages in cores from Apponagansett Bay and New Bedford Harbor.

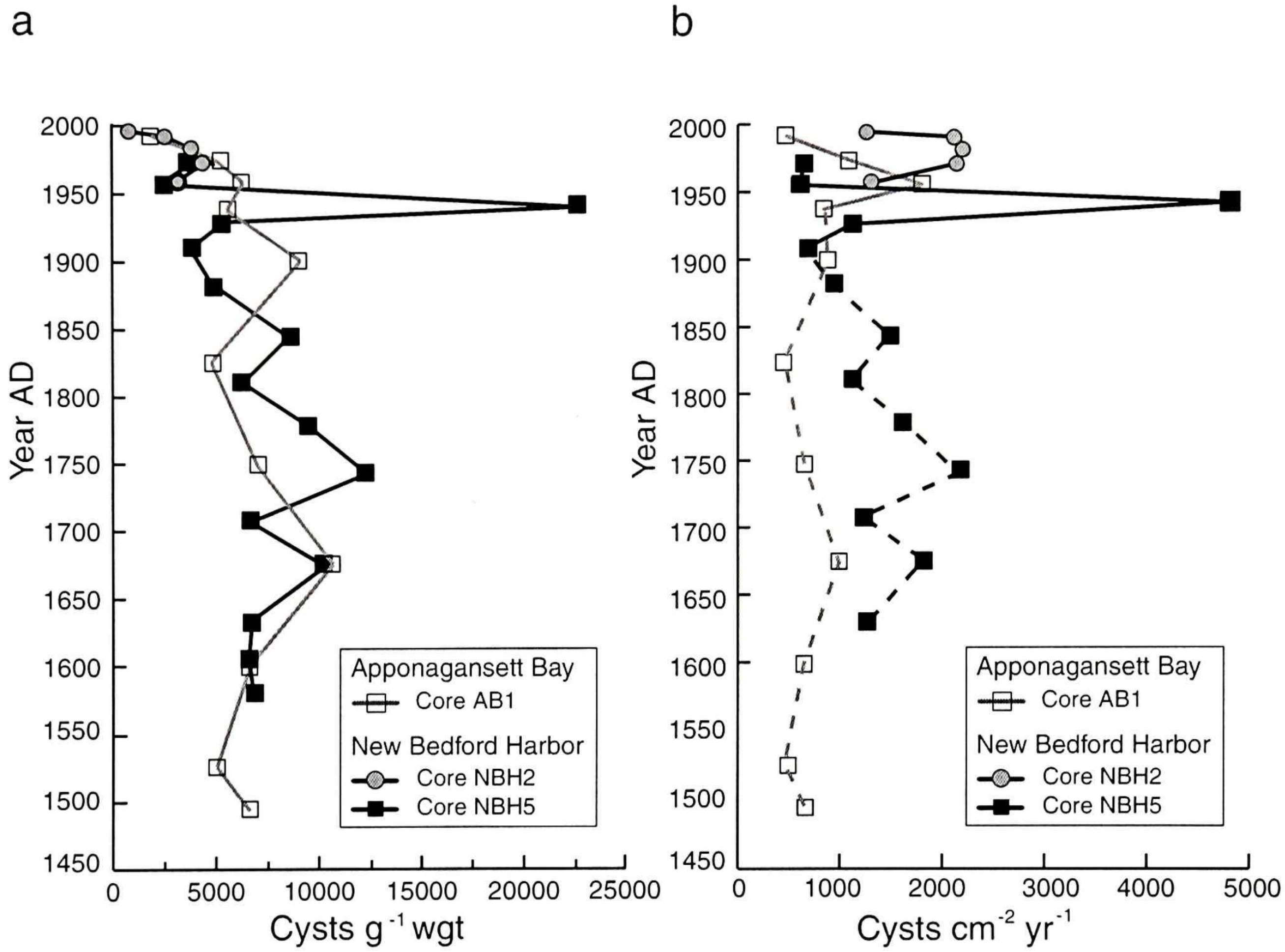

Figure 9. Changes in the total dinoflagellate cyst concentrations (a) and fluxes (b) over time in cores from Apponagansett Bay and New Bedford Harbor. Dashed lines show the approximate dinoflagellate cyst fluxes in cores AB1 (gray) and NBH5 (black) prior to 20th century.

Dubridinium spp. and *Spiniferites bentorii* gradually decrease to the surface, cysts of Polykrikaceae appear for the first time in the record and persist to the surface. The abundances of *Islandinium minutum & cezare* are < 65 cysts g^{-1} and 6 cysts cm^{-2} yr^{-1} until ~1901 and increases to 313 cysts g^{-1} or 88 cysts cm^{-2} yr^{-1} in the late 1950s. The second half of the 20th century is characterized by an increase in the number of dinoflagellate cyst taxa, from 19 to 23 (Fig. 10).

New Bedford Harbor, Core NBH2

The total concentration of dinoflagellate cysts ranges from 685 to 4,075 cysts g^{-1} (Fig. 9a). The total flux of dinoflagellate cysts in this core ranges from ~1300 to 2200 cysts cm^{-2} yr^{-1} (Fig. 9b). Both parameters reach a maximum in the 1970s.

The main characteristics of core NBH2 are the low number of dinoflagellate cyst taxa in assemblages, which ranges from 15 to 17 (Fig. 10), and the high proportion (27-51%) of cysts of heterotrophic dinoflagellates (Fig. 8). The proportion of Diplopsalidaceae and Polykrikaceae ranges from 25% to 1%, and reaches its maximum in the early 1970s (Fig. 8). The maximum abundances of *Dubridinium* spp. (984 cysts g^{-1}, 499 cysts cm^{-2} yr^{-1},) occur in the early 1970s (Fig. 4). The abundances of *Lingulodinium machaerophorum* are low (≤55 cysts g^{-1}, 37 cysts cm^{-2} yr^{-1}) (Fig. 4). *Operculodinium israelianum* and *Selenopemphix quanta* were not observed in this core.

New Bedford Harbor, Core NBH5

The dinoflagellate cyst record in core NBH5 reflects changes in the history of the Harbor, but the most distinctive changes occur in the 20th century. In the 1940s both concentration and flux show an isolated peak (22,678 cysts g^{-1} and 4,786 cysts cm^{-2} yr^{-1}), approximately twice that of the next highest value. Otherwise, the total concentration of dinoflagellate cysts ranges from 12,310 to 2,572 cysts g^{-1} and flux from 2,219 to 601 cm^{-2} yr^{-1} (Fig. 9a). The species richness ranges from 18 to 22 until the 1880s, when it declines to 15 in the 1990s (Fig. 10). In the 16th century the maximum % of heterotrophic taxa is 15%, then ranges from 18 to 28% until the present, with an exception of the late 1920-40s when relative abundance of cysts of heterotrophic

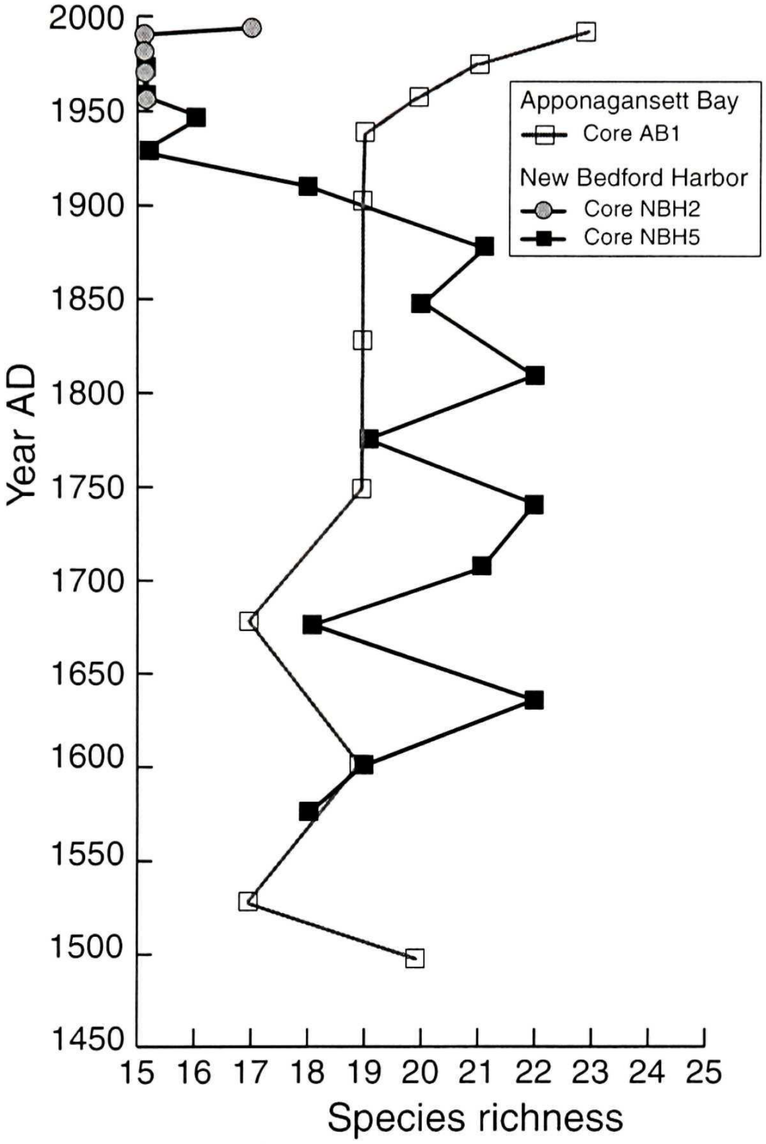

Figure 10. Changes in the number of dinoflagellate cyst taxa over time in cores from Apponagansett Bay and New Bedford Harbor.

dinoflagellates in assemblages is ~8% (Fig. 8). Higher abundances of *Dubridinium* spp. and *Lingulodinium machaerophorum*, as well as the presence of *Selenopemphix quanta* and *Operculodinium israelianum*, characterize the cyst record from the late 17th until the mid 19th century (Fig. 5). In contrast, abrupt, but distinctively brief increases in abundance of *Spiniferites* spp. (18,084 cysts g^{-1} and 3,817 cysts cm^{-2} yr^{-1}) and *Islandinium minutum & cezare* (530 cysts g^{-1}, 112 cysts cm^{-2} yr^{-1}) occur in the early 1940s (Fig. 5). Cysts of *Operculodinium israelianum* and *Selenopemphix quanta* were not observed in the sediment record of the last century.

DISCUSSION

General observations

Dinoflagellate cyst records show no detectable response to climate warming as indicated by winter low temperatures or extended growing seasons reported by Baron and Gordon (1985). The greatest change occurs with the intense human activity of the 20th century. Our results support Pesch and Garber's (2001) conclusion that the intensification of human activity and population growth in the watershed during the textile and post-textile periods caused the major degradation of New Bedford Harbor in the 20th century.

Total cyst concentrations and fluxes

Dale and Fjellså (1994), studying Norwegian fjords, suggested that an increase in total cyst concentration is an informative signal of eutrophication within an estuary. Our results (Fig. 9a) show no overall increase in total cyst concentration either in New Bedford Harbor or Apponagansett Bay. One could use the argument of Sætre et al. (1997) that industrial pollution can counterbalance the stimulating effects of nutrient enrichment so that the total cyst concentration remains constant or declines. We can exclude this explanation, as Apponagansett Bay was subject only to nutrient enrichment during the last century.

We suspect that increasing amplitude in the fluctuation of total cyst abundances may be a strong indicator of stressed environments. In the 16th-19th centuries, the total abundance of cysts in sediments from New Bedford Harbor varies by a factor of 2

(6,000 to 12,000 cysts g^{-1}, 900 to 2,200 cysts cm^{-2} yr^{-1}) compared to a much larger range, by a factor of 9 (2,600 to 23,000 cysts g^{-1}, 600 to 4,800 cysts cm^{-2} yr^{-1}) in the 20th century. This large magnitude of change in absolute cyst abundance occurs over a relatively short time interval. To some extent, this effect is caused by an abrupt increase of *Spiniferites* spp. around 1940s and by the increase in the sedimentation rate during the past 70 yr. In the 20th century New Bedford Harbor received the direct discharge of municipal sewage and organic pollutants (PAHs and PCBs) released from textile (during the third period) and electrical (during post-textile or the fourth period) industries (Latimer et al., in press). Changes in the production of dinoflagellate cyst in the 20th century in New Bedford Harbor is likely a response to this variety of new environmental influences that both suppress and stimulate dinoflagellate production. We assume that absence of large fluctuations in Apponagansett Bay total cyst abundances reflects lower environmental stress than in New Bedford Harbor.

Species richness

Although the lower level nutrient enrichment associated with early urbanization and population growth in New Bedford Harbor, and more recently in Apponagansett Bay, may have had positive effects on species richness, industrialization and final stages of urbanization had detrimental effects on species richness of dinoflagellates in New Bedford Harbor. Dinoflagellate cyst species richness in New Bedford Harbor is highest from the 17-19th centuries, when the system was shifting from an oligotrophic to mesotrophic condition. Through the same period, the species richness in Apponagansett Bay was generally lower than in New Bedford Harbor. However, during the 20th century, a period of population growth (and presumably, nutrient enrichment) around Apponagansett Bay, species richness increased from 19 to 23. In New Bedford Harbor this period was characterized by far greater population growth in addition to point source discharge of sewage and industrial pollutants. Species richness declined from 21 to 15. Such a magnitude of change (~5 taxa) at this level of diversity is notable, as similar changes in phytoplankton species richness indicate major changes in trophic status (Tsirtsis and Karydis, 1998). The differences in timing of the responses in New

Bedford Harbor and Apponagansett Bay allow us to exclude impacts of external factors such as climate change on the cyst record.

Our observations from Apponagansett Bay and the early history of New Bedford Harbor are consistent with those from studies reporting increasing species richness of estuarine phytoplankton subject to moderate nutrient enrichment, that is when the system shifts from oligotrophic to eutrophic conditions (Tsirtsis and Karydis, 1998). The record from the last century of New Bedford Harbor (decreasing cyst species richness) is consistent with those from highly eutrophic conditions. Studies of diatoms have shown that when the system is highly polluted with toxins or over-enriched with nutrients, diversity declines (Cooper and Brush, 1993, Sullivan, 1999). It seems appropriate to link the decline in dinoflagellate cyst species richness with the onset of hypertrophic and industrially polluted conditions in New Bedford Harbor in the 20th century.

We can compare this change in species richness, to two indicators of industrialization and urbanization, the latter being a major cause of eutrophication in an estuary. Heavy metals come from non-point as well as point sources of industrial and municipal sewage. As the toxicity of Cu to phytoplankton is well established (Taylor, 1987), we use its concentration in the sediments as a proxy for the stress of industrialization. Our second indicator is sedimentary organic carbon, which increases in both Apponagansett Bay and New Bedford Harbor after 1850. The carbon could come from increased pelagic production stimulated by nutrient inputs or directly from sewage outfalls in the case of New Bedford Harbor. (As the input of freshwater to these systems is minor it is unlikely that natural inputs from the watershed are detectable.) Both higher water column production and inputs of allochthonous carbon can be a stress by reducing light available to phytoplankton.

The source of sedimentary carbon can be deduced by examination of the $\delta^{13}C$ signature (e.g., Chmura and Aharon, 1995) which can indicate terrestrial (-26‰, PDB), saltmarsh (-16‰, PDB), eelgrass (-10‰, PDB), or marine (phytoplankton) sources (-20‰, PDB). We assume that human sewage carries the signal of terrestrial carbon. From about 1850 onwards there is a decline (from -18 to -24‰) in the $\delta^{13}C$ of sedimentary carbon in New Bedford Harbour (Fig. 11). The decline is probably due to

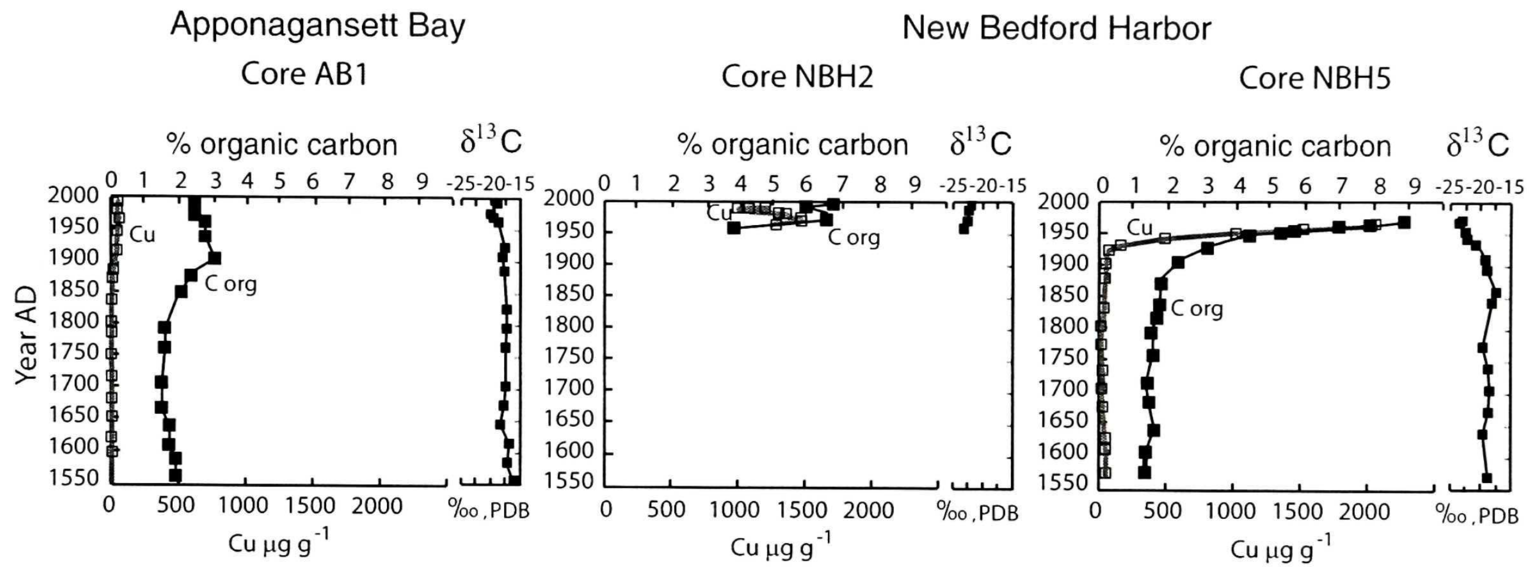

Figure 11. Changes in % organic carbon, $\delta^{13}C$ and copper concentrations over time in Apponagansett Bay and New Bedford Harbor.

the saltmarsh loss documented during this period, as well as the loss of eelgrass beds, presumed to have been once extensive in the Harbor. During the same period carbon concentration increases, probably due in part to increased phytoplankton production, but the low $\delta^{13}C$ indicates that terrestrial carbon sources are clearly increasing. The terrestrial component likely is from human sewage, a problem recognized throughout the history of the City (Pesch and Garber, 2001). The higher $\delta^{13}C$ ($\geq$-20‰) of sedimentary carbon in Apponagansett Bay indicates that terrestrial carbon sources are minor. (There are no municipal sewage outfalls in the Bay.) The minor decrease in the $\delta^{13}C$ over that last ~150 yr probably reflects declines in eelgrass beds and increased inputs of carbon from phytoplankton production.

The timing of the greatest changes in dinoflagellate cyst assemblages, species richness, total cyst concentrations and flux in New Bedford Harbor coincide with the increase in the concentrations of sedimentary carbon and copper (Fig. 11). In fact the decline of cyst species richness can be predicted by the two parameters (Fig. 12a, b). Linear regression analysis shows that sedimentary carbon concentration alone explains 70% of the variability in species richness, copper 72% - and both together (as independent variables in a linear regression) explain 73% of the variability in cyst species richness.

A comparable study, where both parameters are available, is that from Frierfjord and Brevikfjord reported by Sætre et al. (1997). Extracting the species richness from their Appendix 1 and 2 and the organic carbon content and copper concentrations from Fig. 2 and 4, we observe a strikingly similar inverse relationships between both sedimentary carbon (R=0.78) and Cu (R=0.73) with species richness (Fig. 12c, d). Together these two variables explain 79% of the variability in cyst species richness of the Norwegian fjords.

Proportion of heterotrophic taxa

An increase in the proportion of cysts of heterotrophic dinoflagellates has been suggested (Sætre et al. 1997; Matsuoka, 1999, 2001) as a signal of eutrophication and industrial pollution. The cause of this increase is disputed. Matsuoka (1999) suggests

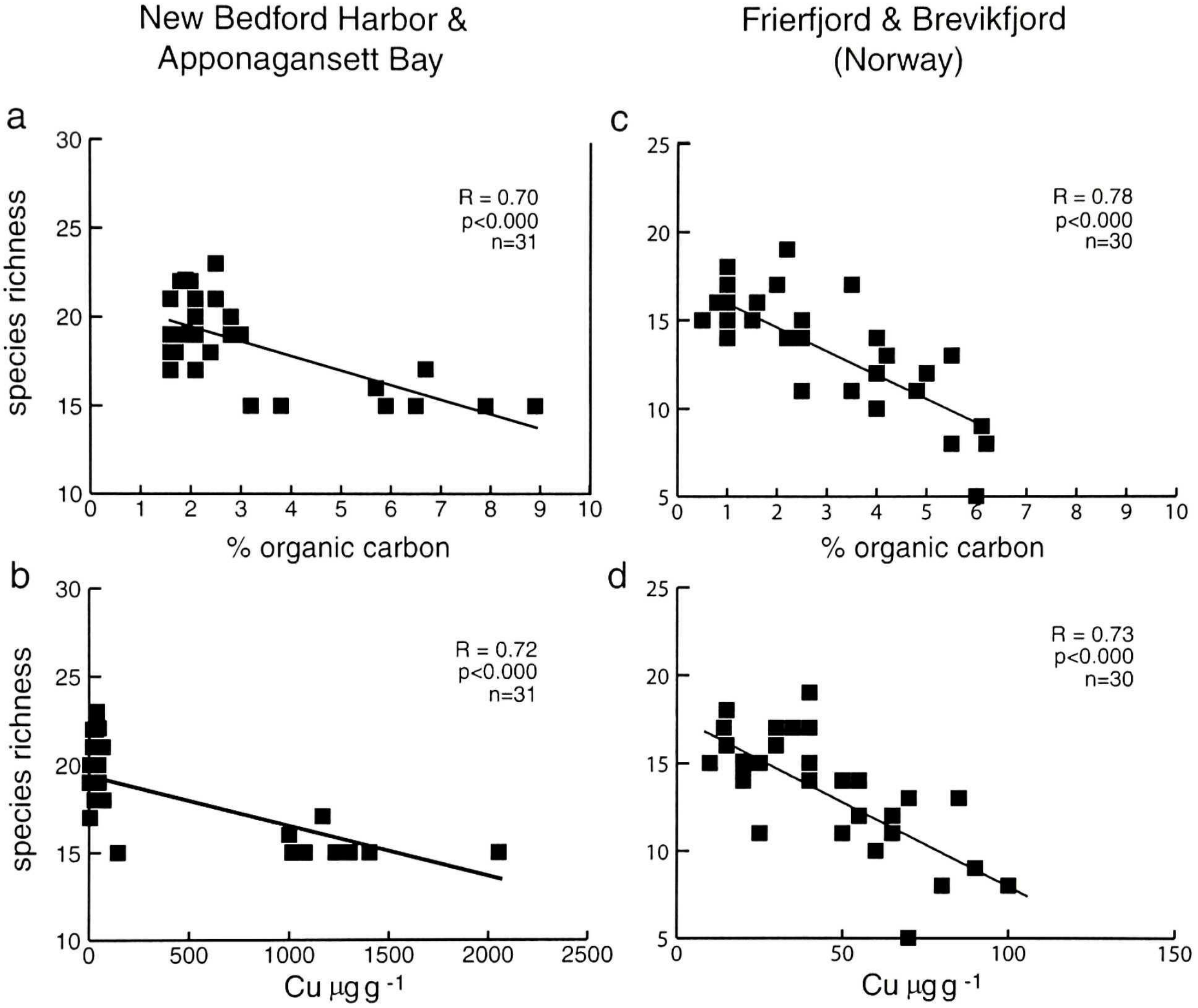

Figure 12. Relationship between dinoflagellate cyst species richness and % organic carbon and copper concentrations based on samples from cores from Apponagansett Bay and New Bedford Harbor (a, b) and Norwegian data (c, d) published in Appendix 1 and 2 and Fig. 1 and 2 by Sætre et al. (1997).

increasing diatom production as the main cause, whereas Dale (2001) links the increase to the reduced production of autotrophic dinoflagellates due to reduced light penetration.

Our results show a small increase in the proportion of cysts of heterotrophic taxa (particularly the Polykridaceae and Diplopsalidaceae) as nutrient enrichment increased in the 20th century at our control site, Apponagansett Bay. However, in New Bedford Harbor where both nutrient and inorganic pollutants increased over the 19th and 20th century, the proportion of cysts of heterotrophic dinoflagellates is variable (Fig. 8).

Individual species-indicators

Individual taxa respond to water quality changes in different ways. The cysts of *Spiniferites* spp. dominate the cyst assemblages. This group seems to be tolerant of extreme environmental conditions as they are the most abundant in cyst assemblages from low salinity (5 to 15 ppt) environments (Pospelova and Chmura, 1998) as well as in highly eutrophic conditions in New Bedford Harbor. Abundances of subdominant taxa, such as cysts of *Dubridinium* spp., *Islandinium minutum & cezare*, and *Polykrikos schwartzii* produced by heterotrophic dinoflagellates, as well as the cysts of *Spiniferites bentorii*, produced by autotrophic dinoflagellates, appear to increase with nutrient enrichment. In fact, the cysts of *Dubridinium* spp. and *Polykrikos schwartzii* are commonly recorded in nutrient-rich waters (Dale 1996; Matsuoka, personal communication). On the other hand, cysts of autotrophic dinoflagellates such as *Lingulodinium machaerophorum*, *Operculodinium israelianum* and heterotrophic *Selenopemphix quanta* tend to have negative response to eutrophication and inorganic pollution.

There are commonalties between species-indicators in the Massachusetts Bay and Tokyo Bay (Matsuoka, 1999, 2001). At Matsuoka's (2001) station 1 (his study site most subject to eutrophication) cysts of *Selenopemphix quanta* and *Lingulodinium machaerophorum* decrease over a period of increasing nutrient enrichment. The group of Diplopsalidaceae and Polykrikaceae increases in concentration during the same period, mostly because of increase in concentrations of *Polykrikos schwartzii* and *P.* cf. *kofoidii*.

The decreases in concentrations (and fluxes, in the case of Massachusetts estuaries) of *Lingulodinium machaerophorum* associated with nutrient enrichment in these shallow estuaries are not consistent with the observations from Norwegian fjords (Dale and Fjellså, 1994; Sætre et al. 1997; Dale et al., 1999). In the fjords *Lingulodinium machaerophorum* may not be responding to increases in nutrients, but to conditions associated with stratification and low oxygen concentrations characteristic of eutrophication in deep, stratified waters, such as Norwegian fjords. The shallow depths of Apponagansett Bay, New Bedford Harbor and Tokyo Bay mean they are generally unstratified and consequently do not suffer from severe oxygen depletion.

CONCLUSIONS

The study of dinoflagellate cysts from New Bedford Harbor and Apponagansett Bay over the last 500 years provides evidence that cyst assemblages contain a record of environmental changes induced by urbanization and industrial development. A number of parameters in the cyst record (species richness, concentrations, flux, and species abundances) can be used as indicators of environmental change.

Cyst species richness initially increases with nutrient level in an estuary, as observed in 17-19th century New Bedford Harbor and in 20th century Apponagansett Bay. However, in environments with extremely high levels of nutrients (hypertrophic conditions) and toxins, this trend is reversed and the number of dinoflagellate cyst taxa declines, as seen in 20th century New Bedford Harbor.

Another parameter possibly indicating human disturbance in an estuary is the variability in total dinoflagellate cyst concentrations and fluxes. We find that it is not a unidirectional change, but rather a great fluctuation in the cyst production that characterizes heavily disturbed estuarine systems. These fluctuations are amplified by abrupt increases of certain taxa, such as *Spiniferites* spp. in 1940s New Bedford Harbor.

The effects of recent pollution are clearest when species richness, abundances, and composition of the dinoflagellate cyst assemblages are considered together. The major changes in the dinoflagellate cyst record occur within the 20th century in New Bedford Harbor. These changes are coincident with an increase of organic carbon input, PAHs, PCBs, and heavy metal concentrations that may have antagonistic or cumulative effects.

We believe that the eutrophication signal seen in dinoflagellate cyst assemblages in fjords and shallow estuaries can be distinctly different. Under simple nutrient enrichment, increased concentrations of cysts may not be expected in shallow, well-mixed estuaries, yet appear to be a response in fjords. Species proposed as indicators of eutrophication in Norwegian fjords (Dale and Fjellså, 1994; Sætre et al., 1997; Dale et al., 1999) show different responses in the shallow estuaries of Massachusetts, the latter more similar to Tokyo Bay.

More research is needed to refine the use of dinoflagellate cysts as record of paleoenvironmental changes in estuaries. Some important research directions should include separation of the role of individual stressors such as nutrient over-enrichment and toxic pollution, as well as studies of dinoflagellate cyst assemblages from different types of estuaries with different degrees of human disturbance.

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CHAPTER 3. SPATIAL DISTRIBUTION OF MODERN DINOFLAGELLATE CYSTS IN POLLUTED ESTUARINE SEDIMENTS FROM BUZZARDS BAY EMBAYMENTS (MASSACHUSETTS, USA)

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ABSTRACT

Analysis of the spatial distribution of the dinoflagellate cyst assemblages in 19 surface sediment samples collected in three Buzzards Bay embayments (Massachusetts, USA) demonstrates the applicability of dinoflagellate cysts as biological indicators of environmental conditions in estuarine systems. There is a significant negative relationship between dinoflagellate cyst diversity and sediment concentrations of metals, PCBs and organic carbon. Sites with the highest levels of pollution are characterized by the lowest dinoflagellate cyst species richness and concentrations, which we interpret as a cumulative pollution signal. In these embayments salinity and temperature variability is low, thus the distribution of dinoflagellate cysts is controlled primarily by the nutrients and pollution. Principal component analysis, based on the proportions of cyst taxa, indicates that cyst assemblages gradually change when moving away from the sources of nutrient pollution, and sewage outfalls in particular.

INTRODUCTION

Human activities such as nutrient enrichment and toxic pollution cause water quality degradation and habitat loss. These activities are most intensive in estuaries with highly urbanized and industrialized watersheds. Concerns about water quality degradation in estuarine waters has stimulated a demand for development of indicators of nutrient enrichment and toxic contamination to examine paleo- and modern environmental conditions and trends caused by intensified anthropogenic activities in watersheds.

To be a useful biological indicator of environmental conditions, an organism has to satisfy certain criteria (Gibson et al., 2000). In general, a biological indicator should be ubiquitous, well preserved in sediments, numerous enough for statistical treatment, and reflect certain environmental parameters. Dinoflagellate cysts have proven to satisfy all of the above criteria (Fensome et al., 1996).

Dinoflagellates are single-celled organisms that constitute an important part of the phytoplankton population in aquatic ecosystems. During their life cycle some dinoflagellates produce hypnozygotes, or resting cysts, which can be preserved in sediments (Fensome et al., 1993). Assemblages of dinoflagellate cysts in sediments encode information on the dinoflagellates in the upper water column (Dale, 1976; Reid and Harland, 1978). In turn, the population of dinoflagellates is influenced by environmental factors, such as temperature, salinity, nutrients, turbidity, and pollution (Taylor, 1987). Dinoflagellate cysts recovered from coastal sediments have the potential to provide substantial information on biological processes and interactions within aquatic systems.

Several studies have examined the temporal development of estuarine eutrophication and pollution by analyzing the dinoflagellate cyst records in sediment cores (Dale and Fjellså, 1994; Sætre et al., 1997; Thorsen and Dale, 1997; Dale et al., 1999; Matsuoka, 1999; Dale, 2001; Matsuoka, 2001; Pospelova et al., 2002). A recent study of the historical records of dinoflagellate cysts from shallow unstratified embayments of Buzzards Bay (New Bedford Harbor and Apponagansett Bay, MA, USA) found that the species richness (number of taxa), total cyst concentrations and fluxes, proportions of some heterotrophic species, as well as abundance of indicator species changed as a result of eutrophication and toxic pollution (Pospelova et al., 2002). In oligotrophic systems, such as New Bedford Harbor in its early history (Pospelova et al., 2002), nutrient enrichment initially increases dinoflagellate cyst species richness. However, under highly eutrophic and polluted conditions, species richness declines, as seen during the 20th century in New Bedford Harbor. These extrime conditions are also characterized by large fluctuations in total cyst concentrations and fluxes. The proportion of cysts of heterotrophic dinoflagellates, Polykrikaceae and Diplopsalidaceae in particular, tends to increase with nutrient enrichment.

If the dinoflagellate cyst record reflects the temporal changes of the environmental conditions in an estuary, it must also show spatial change, as environmental conditions in an estuary are not-uniform. No previous studies have investigated spatial distributions of dinoflagellate cysts in relation to eutrophication and toxic pollution in estuarine systems. This work represents the first analysis of this kind.

In this study we document the dinoflagellate cyst assemblages on ~1 km scale in three side embayments of Buzzards Bay, Massachusetts. Comparison of these assemblages to known gradients of nutrient and toxic pollution allowes us to assess the utility of cysts as indicators of plankton response.

STUDY AREA

New Bedford Harbor, Clarks Cove and Apponagansett Bay are side embayments of the northwestern shore of Buzzards Bay, Massachusetts (Figure 1). The embayments are shallow with the water depths ranging from 1 to 12 m (mean 6 m), generally well mixed, and unstratified. Mean summer water salinity varies from 28 to 31 psu and summer temperatures from 21 to 23°C (Howes et al. 1999). Ammonium is the major form of inorganic nitrogen available throughout the Bay and its concentrations are heavily influenced by the sewage outfall (Borkman and Turner, 1993).

New Bedford Harbor

New Bedford Harbor, also known as the Acushnet River estuary, has a moderate freshwater input (median flow 0.54 $m^3 s^{-1}$) from the river flowing into the northern part of the harbor. This harbor is heavily urbanized as it is surrounded by 35% of the population of the entire Buzzards Bay watershed (Howes et al., 1999). As a result, ~20 combined sewer overflows (CSO) discharge to the inner part of New Bedford Harbor, in addition to outfall of the Fairhaven Wastewater Treatment Plant (Figure 1). From 1974 to 1996, the Fairhaven facility has continuously discharged primary-treated sewage to the harbor resulting in a load of 140 t N yr^{-1} (SAIC, 1991). A hurricane barrier greatly reduces water circulation relative to the rest of Buzzards Bay and affects water quality (Costa et al., 1996; Abdelrhman, 2002). Inner New Bedford Harbor is among the most eutrophic embayments in Buzzards Bay (Howes et al., 1999). Mean summer concentrations of nitrate, ammonium and phosphorus in the Harbor are 11, 5.7 and 1.8 μM, respectively. Average summer concentrations of chlorophyll *a* are 8.5 $\mu g \cdot l^{-1}$, but it ranges from 1.1 to 67.8 $\mu g \cdot l^{-1}$. New Bedford Harbor also is one of the most contaminated sites in the United States (Nelson et al., 1996) due to polychlorinated biphenyls (PCBs) used in the manufacture of electrical capacitors. Past discharges of PCBs and other pollutants in the upper harbor have resulted in modern sediment

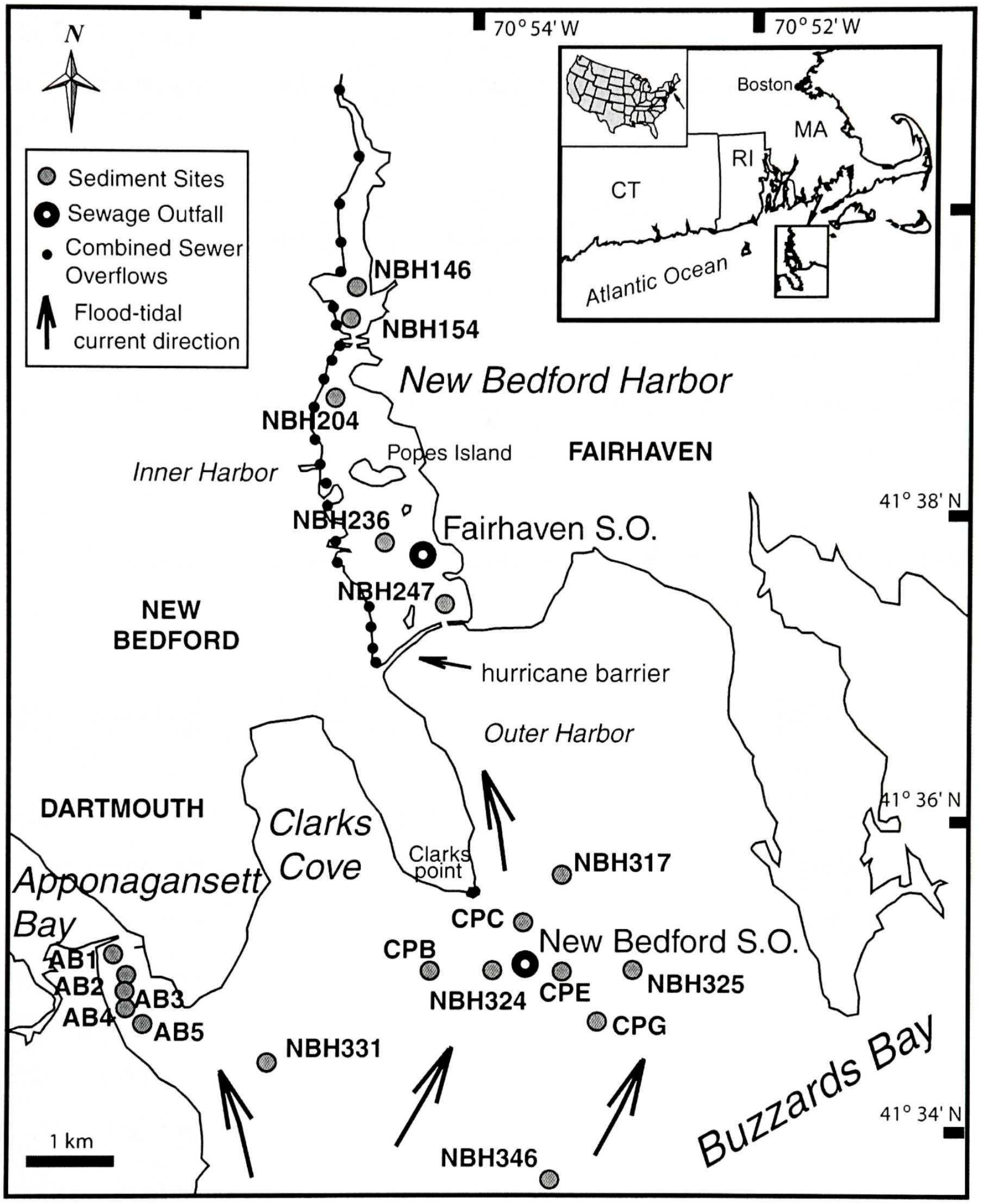

Figure 1. Map of New Bedford Harbor, Clarks Cove and Apponagansett Bay showing the location of surface sediment samples. Direction of flood-tidal current from Howes et al. (1996).

concentrations as high as 100 $\mu g \cdot g^{-1}$ PCBs, 1500 $\mu g \cdot g^{-1}$ Cu, 600 $\mu g \cdot g^{-1}$ Pb, and 1200 $\mu g \cdot g^{-1}$ Zn (Latimer, personal communications). In 1982 New Bedford Harbor was added to the EPA's Superfund Priority List for cleanup.

New Bedford's Outer Harbor, south of the hurricane barrier (Figure 1), is expansive and well flushed. The primary difference between the Outer and Inner Harbors is a lower sedimentary concentration of PCBs, heavy metals, and other industrial pollutants. However, the surface plume of effluent from the New Bedford Wastewater Treatment Facility, located off Clarks Point, influences local water quality conditions. The New Bedford Wastewater Treatment Plant discharges up to 962 $tN\ yr^{-1}$, into the system mostly in the form of ammonium (SAIC, 1991). Elevated concentrations of nitrate (1.2 μM), ammonium (16.4 μM), and phosphorus (3.0 μM) were measured near the outfall (Borkman and Turner, 1993). Despite the high sewage effluent input, effects of the discharge on water quality are detected only within 5 km of the outfall (Costa et al., 1999).

Apponagansett Bay

Inner Apponagansett Bay has been identified as one of the most eutrophic embayments of Buzzards Bay, similar to New Bedford Harbor, due to its restricted geomorphology and nutrient loading from watershed (Howes et al., 1999). The high nutrient load to the estuary is mostly due to its densely populated watershed followed by commercial and industrial development. In contrast to the Inner Bay, Outer Apponagansett Bay is better flushed and shows moderate nutrient levels (Howes et al., 1999). The mean summer nitrate concentration in the Outer Bay is 1.3 μM, ammonium 2.2 μM, phosphorus 1.6 μM and chlorophyll *a* 4.7 $\mu g \cdot l^{-1}$.

Clarks Cove

In contrast to New Bedford Harbor, neighboring Clarks Cove (Figure 1) has relatively good water quality due to the absence of major freshwater sources and a sewered watershed, with discharges located at Clarks Point (New Bedford Wastewater Treatment Plant). Clarks Cove water quality is maintained primarily by its tidal dynamics (Howes et al., 1999). Despite the fact that Clarks Cove is a comparatively deep (~9 m) and well-flushed embayment the total nitrogen level here is higher than the waters of outer Buzzards Bay. This enrichment of Clarks Cove waters comes from the Clarks Point outfall, when its waters enter the system during periodic shifts in the Outer Harbor circulation, and from the tidal waters of Apponagansett Bay to the west (Howes et al., 1999). In Clarks Cove average summer concentration of nitrate is 1.5 μM, ammonium 0.9 μM·, phosphorus 1.5 μM, and chlorophyll *a* 3.71 $\mu g \cdot l^{-1}$.

MATERIAL AND METHODS

Sample collection

Surface sediments were collected from 19 locations throughout New Bedford Harbor, Clarks Cove and Apponagansett Bay (Figure 1, Table 1). For the purpose of this study, we divide all samples into three groups (Table 1), based on their location. The first group (I) comprises 5 samples from the Inner part of New Bedford Harbor, the second group (II) includes 9 samples from Outer Harbor and Clarks Cove, and the third group (III) comprises five samples from the outer part of Apponagansett Bay. Sediments were collected with a van Veen or petite Ponar grab sampler during EPA cruises in October 1996. We assume that the top 2 cm of collected sediments represent ~10 yr deposition, based on the estimates of accumulation rates previously reported for the embayments (Summerhayes et al., 1985; Latimer et al., in press). Sediments are generally characterized as fine sands, silt and mud (Table 1). All samples were stored at ~4°C in the dark until processing.

Sediment chemistry

Sedimentary metal concentrations were measured by inductively coupled plasma atomic emission and graphite furnace atomic absorption spectrophotometry after digestion by microwave heating in a pressurized digestion vessels with a mixture of concentrated acids (Latimer et al., in press). PCBs were extracted using a microwave procedure and analyzed using gas chromatography with electron capture detector (Latimer et al. in press). The percent organic carbon was measured by continuous flow elemental analysis/isotope ratio mass spectrometry as described by Latimer et al. (in press).

Table 1. Surface sediment samples collection data

Group	Station site	Location	Latitude degrees N	Longitude degrees W	Water Depth (m)	Sediment Type	Sampling method
I	NBH146	Upper Part of New Bedford Harbor	41.660	-70.917	4.6	sandy silt	petite Ponar
I	NBH154	Upper Part of New Bedford Harbor	41.657	-70.918	7.3	sandy silt	petite Ponar
I	NBH204	Lower Part of New Bedford Harbor	41.652	-70.920	4	sandy silt	petite Ponar
I	NBH236	Lower Part of New Bedford Harbor	41.634	-70.913	9.8	mud	petite Ponar
I	NBH247	Lower Part of New Bedford Harbor	41.627	-70.905	3	sandy silt	petite Ponar
II	NBH324	Clarks Cove / Outer Part of New Bedford Harbor	41.582	-70.899	~9	sandy silt	petite Ponar
II	CPE	Clarks Cove / Outer Part of New Bedford Harbor	41.582	-70.890	9	silty mud	petite Ponar
II	CPC	Clarks Cove / Outer Part of New Bedford Harbor	41.588	-70.895	9	fine sand	petite Ponar
II	CPB	Clarks Cove / Outer Part of New Bedford Harbor	41.582	-70.907	9.6	sandy mud	petite Ponar
II	CPG	Clarks Cove / Outer Part of New Bedford Harbor	41.576	-70.886	8.8	silty mud	petite Ponar
II	NBH317	Outer Part of New Bedford Harbor	41.594	-70.890	9.8	sandy silt	petite Ponar
II	NBH325	Outer Part of New Bedford Harbor	41.582	-70.881	~10	sandy silt	petite Ponar
II	NBH346	Buzzards Bay	41.545	-70.891	~10	sandy mud	petite Ponar
II	NBH331	Clarks Cove / Apponagansett Bay	41.570	-70.928	7.5	silty mud	petite Ponar
III	AB1	Apponagansett Bay	41.584	-70.948	2.4	sandy silt	van Veen
III	AB2	Apponagansett Bay	41.581	-70.947	4.6	sandy silt	van Veen
III	AB3	Apponagansett Bay	41.580	-70.947	5.2	silt	van Veen
III	AB4	Apponagansett Bay	41.578	-70.947	5.2	sandy silt	van Veen
III	AB5	Apponagansett Bay	41.576	-70.945	4.9	sandy silt	van Veen

Dinoflagellate cysts

For dinoflagellate cyst analyses sediment samples of known volume and weight were processed using standard palynological preparation methods (Rochon et al., 1999). Sediment were dried at 40°C, weighed, sieved through a 125-µm and retained on a 10-µm mesh to eliminate coarse and fine material, treated with warm HF (40%) to dissolve silicates, and HCl (10%) to remove carbonates and silicoflourides. Calibrated tablets of *Lycopodium* spores (Stockmarr, 1977), added during processing, allowed for calculation of dinoflagellate cyst concentrations based on the volume of wet sediments.

Aliquots were mounted on microscope slides with glycerin jelly. Dinoflagellate cysts were counted with a transmitted light microscope (63x and 100x objectives). Identification of dinoflagellate cysts was made on the basis of published descriptions in accordance with taxonomy given by Lentin and Williams (1993) and Rochon et al. (1999). However, when species-level identification was not possible, identification was at the genus level. There are different taxonomies for cysts and thecal stages of dinoflagellates because paleontological studies of cysts originally were carried out independently from biological studies of the motile forms. Here we use the paleontological nomenclature according to Head (1996), Head et al. (2001), and Pospelova and Head (2002). A list of the dinoflagellate cysts counted and their known biological name or thecal equivalent is provided in Table 2.

Spiniferites spp. includes all *Spiniferites* cysts except *Spiniferites bentorii*, *Spiniferites elongatus* and *Spiniferites membranaceus*. For statistical treatment, species of the genus *Brigantedinium* (*Brigantedinium cariacoense* and *Brigantedinium simplex*) were grouped together because cyst folding or orientation sometimes obscured the archeopyle characteristics, thus preventing identification to the species level. An average of 317 cysts and a minimum of 102 were counted in each sample. More than 35 dinoflagellate cyst taxa were identified and counted in sediments from 19 sites (Table 3).

RESULTS

Metals, PCBs and organic carbon

Table 2. Taxonomic citation of dinoflagellate cysts used in this study. Thecal equivalents are taken from Head (1996), [1]Pospelova and Head (2002), and [2]Head et al., 2001.

Cyst species (paleontological name)	Dinoflagellate thecate name or affinity (biological name)
AUTOTROPHIC	
Gonyaulacaceae	
———	*Alexandrium tamarense*
Impagidinium spp.	? *Gonyaulax* sp. indet.
Lingulodinium machaerophorum	*Lingulodinium polyedrum*
Nematosphaeropsis spp.	*Gonyaulax spinifera* complex
Operculodinium centrocarpum sensu Wall & Dale 1996	*Protoceratium reticulatum*
Operculodinium israelianum	? *Protoceratium reticulatum*
Spiniferites bentorii	*Gonyaulax digitalis*
Spiniferites elongatus	*Gonyaulax spinifera* complex
Spiniferites membranaceus	*Gonyaulax spinifera* complex
Spiniferites spp.	*Gonyaulax* complex
Tectatodinium pellitum	*Gonyaulax spinifera* complex
Protoperidiniaceae	
———	*Pentapharsodinium dalei*
Pyrophacaceae	
Tuberculodinium vancampoae	*Pyrophacus steinii*
HETEROTROPHIC	
Diplopsalidaceae	
Dubridinium spp.	Diplopsalid group
Gymnodiniales	
———	*Gymnodinium* spp.
Polykrikaceae	
———	*Polykrikos schwartzii*
———	*Polykrikos kofoidii*
Protoperidiniaceae	
Brigantedinium cariacoense	*Protoperidinium avellanum*
Brigantedinium simplex	*Protoperidinium conicoides*
Brigantedinium spp.	? *Protoperidinium* spp.
[1]*Islandinium brevispinosum*	*Protoperidinium* sp. indet.
[2]*Islandinium? cezare*	*Protoperidinium* sp. indet.
[2]*Islandinium minutum*	*Protoperidinium* sp. indet.
Lejeunecysta oliva	*Protoperidinium* sp. indet.
Lejeunecysta sabrina	*Protoperidinium leonis*
Protoperidinium minutum	*Protoperidinium minutum*
Protoperidinium oblongum	*Protoperidinium oblongum*
Protoperidinium spp.	*Protoperidinium* sp. indet.
Peridinium wisconsinense	*Peridinium wisconsinense*
Quinquecuspis concreta	*Protoperidinium leonis*
Selenopemphix nephroides	*Protoperidinium subinerme*
Selenopemphix quanta	*Protoperidinium conicum*
Stelladinium stellatum	*Protoperidinium stellatum*
Trinovantedinium applanatum	*Protoperidinium pentagonum*
Votadinium calvum	*Protoperidinium oblongum*
Votadinium spinosun	*Protoperidinium claudicans*

Table 3. Relative abundance, total counts, and richness of dinoflagellate cyst taxa in surface sediments from New Bedford Harbor, Clarks Cove and Apponagansett Bay. Asterisks denote taxa not counted for cyst richness, including the freshwater *Peridinium wisconsinense*

Group	Sample site	Numbers of counted cysts	Species richness	Ratio autotrophs/heterotrophs	*Alexanrium tamarense*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* spp.	*Dubridinium* spp.	*Gymnodinium spp.*	*Impagidinium* spp.	*Islandinium brevispinosum*	*Islandinium? cezare*	*Islandinium minutum*	*Lejeunecysta oliva*	*Lejeunecysta sabrina*	*Lingulodinium machaerophorum*	*Nematosphaeropsis* spp.	*Operculodinium centrocarpum* sensu Wall & Dale 1966	*Operculodinium centrocarpum* var. *truncatum*	*Operculodinium israelianum*	*Pentapharsodinium dalei*	*Polykrikos kofoidii* & *schwartzii*	*Protoperidinium oblongum*	*Protoperidinium* spp.	*Protoperidinium minutum*	*Peridinium wisconsinense* *	*Quinquecuspis concreta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Spiniferites bentorii*	*Spiniferites elongatus*	*Spiniferites membranaceus*	*Spiniferites* spp.	*Stelladinium stellatum*	*Tectatodinium pellitum*	*Trinovantedinium applanatum*	*Tuberculodinium vancampoae*	*Votadinium calvum*	*Votadinium spinosum*	Cyst type E	Unknown cysts*
I	NBH 146	102	12	1.3	0.0	0.0	1.0	10.8	13.7	0.0	0.0	2.0	1.0	0.0	0.0	0.0	0.0	2.9	8.8	0.0	0.0	1.0	0.0	0.0	12.7	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.0	40.2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.0
I	NBH154	137	15	1.8	0.0	0.0	0.0	6.6	13.1	0.0	0.0	3.6	0.7	0.0	0.0	0.0	1.5	1.5	10.9	0.0	2.2	0.0	0.0	0.0	6.6	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.7	41.6	0.0	0.7	0.0	0.0	0.0	0.7	1.5	7.3
I	NBH204	194	18	1.7	0.0	0.0	0.5	6.2	10.8	0.0	0.0	2.1	0.5	3.1	0.0	0.0	1.5	1.5	10.8	0.5	1.0	1.5	0.5	0.0	11.9	0.0	0.0	0.5	0.5	0.0	1.5	0.0	0.5	43.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
I	NBH236	356	22	1.5	0.6	0.0	1.7	9.0	7.0	0.0	0.3	1.4	0.0	3.7	0.0	0.0	0.3	2.5	14.9	0.0	0.0	2.5	9.3	0.0	3.4	0.3	0.0	1.1	0.0	0.6	1.7	1.1	0.8	34.3	0.3	0.6	0.0	0.0	0.0	0.0	2.0	0.8
I	NBH247	250	19	1.5	1.6	0.0	2.0	3.6	13.2	0.0	0.0	2.0	0.0	3.2	0.0	0.0	1.2	2.0	14.8	0.0	0.0	2.8	4.4	0.0	4.4	0.8	0.0	1.6	0.4	0.0	0.8	2.0	0.8	33.6	0.0	0.0	0.0	0.0	0.0	0.0	3.2	1.6
II	NBH324	621	26	1.6	0.0	0.3	1.1	4.5	4.2	0.2	0.3	3.1	0.6	4.5	0.0	0.2	0.2	1.3	21.4	0.8	0.2	3.4	6.9	0.0	8.4	1.4	0.2	0.6	0.0	0.2	0.8	1.0	0.2	32.4	0.3	0.0	0.0	0.0	0.0	0.2	0.8	0.5
II	CPE	428	24	2.8	0.0	0.0	1.2	3.5	2.3	0.0	0.2	2.1	0.0	3.3	0.0	0.0	0.7	2.1	18.0	1.2	0.2	8.2	5.4	0.0	2.6	0.0	0.0	0.9	0.2	0.5	1.4	1.2	0.2	39.9	0.7	1.9	0.2	0.0	0.0	0.0	1.2	0.7
II	CPC	266	23	1.8	0.0	0.0	1.5	4.5	4.9	0.0	0.0	1.5	0.4	3.8	0.4	0.4	1.1	1.5	19.9	0.0	0.0	3.0	6.8	0.0	2.3	1.5	0.0	1.5	0.4	1.1	1.9	1.1	0.4	34.6	0.8	0.0	0.0	0.0	0.0	0.0	3.8	1.1
II	CPB	268	23	0.9	0.0	0.0	1.5	9.0	8.6	0.0	0.0	2.6	1.5	8.2	0.0	0.4	0.7	0.7	13.8	0.0	0.4	0.7	9.3	0.0	6.7	0.4	0.0	0.0	0.4	0.7	1.9	0.7	0.0	28.0	1.1	0.4	0.0	0.0	0.7	0.0	1.1	0.4
II	CPG	371	27	0.9	0.5	0.5	3.5	4.6	5.1	0.0	0.0	2.7	1.1	6.5	0.0	0.3	1.3	0.8	16.4	0.0	0.0	0.8	6.7	0.3	15.9	0.8	0.0	0.5	0.3	1.1	1.6	0.3	0.3	24.3	0.0	0.5	0.3	0.0	0.8	0.5	0.8	0.8
II	NBH317	446	25	1.4	0.0	0.0	1.1	6.7	6.3	0.0	0.2	3.6	0.0	4.3	0.0	0.0	0.7	2.5	16.1	0.9	0.0	4.0	8.7	0.0	3.6	0.9	0.0	0.7	0.0	0.9	1.8	1.8	0.2	29.4	0.7	0.2	0.0	0.4	0.7	0.7	2.7	0.2
II	NBH325	344	25	2.4	0.0	0.9	1.5	5.2	2.3	0.3	0.0	3.5	0.6	4.9	0.0	0.0	1.2	0.9	19.2	0.3	0.3	12.5	4.1	0.0	1.7	0.6	0.0	0.6	0.3	0.3	0.6	2.3	0.3	32.8	0.0	0.6	0.0	0.0	0.0	0.3	1.7	0.3
II	NBH346	336	21	2.5	0.0	0.0	1.5	5.7	4.5	0.0	0.0	0.6	0.3	6.8	0.0	0.0	1.2	0.0	29.2	0.0	0.0	7.7	3.0	0.0	1.2	0.3	0.0	0.9	0.3	0.6	1.8	1.2	0.6	29.2	0.6	0.0	0.3	0.0	0.0	0.0	1.8	0.9
II	NBH331	331	22	2.9	0.9	0.0	0.6	4.2	4.2	0.0	0.0	1.8	0.3	1.8	0.0	0.0	1.2	0.6	34.4	1.5	0.0	3.9	5.1	0.0	3.6	0.6	0.0	0.0	0.3	0.9	2.1	0.3	0.0	28.7	0.0	0.3	0.6	0.0	0.0	0.0	0.9	0.9
III	AB1	284	21	2.3	0.0	0.0	0.4	5.6	5.3	0.0	0.0	4.2	1.1	1.4	0.0	0.0	0.7	2.1	24.3	0.0	0.7	3.2	9.2	0.0	1.4	0.4	0.0	0.4	0.0	0.4	0.7	2.1	0.7	34.2	0.0	0.0	0.0	0.0	0.0	0.4	0.4	1.1
III	AB2	285	20	4.9	0.0	0.0	0.0	3.2	4.9	0.0	0.0	1.4	0.7	0.4	0.0	0.0	0.4	1.1	28.8	0.0	1.1	3.9	2.5	0.0	1.8	0.0	0.0	0.4	0.0	1.1	2.5	5.3	0.7	39.3	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.4
III	AB3	245	20	0.9	0.0	0.0	0.0	7.3	9.0	0.0	0.0	12.2	0.4	4.1	0.0	0.0	0.8	1.2	18.0	0.0	0.4	3.7	6.5	0.0	10.2	0.4	0.0	0.0	0.0	0.0	0.8	0.4	0.0	22.0	0.4	0.0	0.4	0.0	0.0	0.4	0.4	0.8
III	AB4	274	22	1.9	0.0	0.0	1.5	3.6	2.9	0.0	0.0	9.5	0.0	0.4	0.0	0.0	0.4	2.2	31.4	0.0	0.4	2.9	3.3	0.0	10.2	0.4	0.0	0.4	0.0	0.0	0.7	1.5	0.7	23.0	0.7	0.4	0.4	0.4	0.0	0.0	0.7	2.2
III	AB5	488	24	2.3	0.0	0.2	1.0	3.5	4.7	0.0	0.0	7.6	0.2	0.6	0.0	0.2	1.0	2.5	5.5	0.4	0.8	11.9	5.3	0.0	5.3	0.4	0.0	0.0	0.0	0.2	1.0	2.3	1.2	42.6	0.4	0.4	0.0	0.0	0.0	0.2	0.2	0.2

Samples from the Inner part of New Bedford Harbor (group I) have the highest concentrations of all metals (Table 4, Figure 2), with average concentrations of Zn at 372 μg g^{-1}, Cu at 516 μg g^{-1}, and Pb at 156 μg g^{-1}. The concentrations of metals in the Outer Harbor and Clarks Cove (group II) are lower, on average, by a factor of 3, with Zn 144 μg g^{-1}, Cu 55 μg g^{-1}, and Pb 49 μg g^{-1}. Apponagansett Bay (group III) is characterized by low levels of metals pollution: Zn 92 μg g^{-1}, Cu 40 μg g^{-1}, and Pb 23 μg g^{-1}. The concentration of PCBs follows the same trend (Table 4), the highest concentrations are in group I (~8,600 μg g^{-1}), moderate concentrations (~700 μg g^{-1}) characterize group II, and the lowest (200 μg g^{-1}) occur in group III. The organic carbon content (Table 4, Figure 3) is the highest in the Inner New Bedford Harbor sediments (from 3.0 to 5.3%). Sediment samples from Apponagansett Bay, Outer Harbor and Clarks Cove have comparable organic carbon content ranging from 0.4 to 2.7%.

We calculated Pearson's correlations to determine the degree of covariance between concentrations of contaminants and content of organic carbon (Table 5). Most correlation coefficients are higher than 0.50 ($P \leq 0.01$). Thus, sedimentary concentrations of PCBs, Zn, Cu, Cr, Pb, Ni and organic carbon content are highly covariant and the effect of individual pollutants on the system cannot be separated. All statistical calculations were made using the SPSS 10.1 for Windows software.

Distribution of dinoflagellate cysts

Dinoflagellate cysts were recovered from all the sediment samples. Total dinoflagellate cyst concentrations vary by an order of magnitude, from ~300 to 4200 cysts cm^{-3}, averaging ~2000 cysts cm^{-3} (Table 6, Figure 4). In general, the total cyst concentrations in Inner New Bedford Harbor (group I) are one-third that in the Outer Harbor, Clarks Cove (group II) and Apponagansett Bay (group III). The highest concentrations are found in group II, which is also characterized by the largest range of variation; total cyst concentrations range from ~500 to 4200 cysts cm^{-3} e.g., 8 fold compared to 6 fold in group I and 3 fold in group III.

The ratio between cysts produced by autotrophic and heterotrophic dinoflagellates ranges from 0.9 to 4.9, with an average of 2.0 (Table 3). Cysts of

Table 4. Concentrations of metals, PCBs and % organic carbon in sediments.

Group	Sample site	% OC	PCB total (μg g^{-1})	Zn (μg g^{-1})	Cu (μg g^{-1})	Cr (μg g^{-1})	Pb (μg g^{-1})	Cd (μg g^{-1})	Ni (μg g^{-1})	Ag (μg g^{-1})
I	NBH 146	5.3	16763	564.9	706.8	204.1	222.1	0.73	39.9	1.85
I	NBH154	4.7	11266	339.1	480.0	249.7	194.9	1.06	38.3	4.63
I	NBH204	3.4	7526	362.7	647.0	296.2	160.2	1.39	41.5	3.02
I	NBH236	4.0	5248	349.1	373.0	210.7	132.2	0.85	27.6	3.47
I	NBH247	3.0	2260	245.7	374.4	122.4	71.5	0.54	11.1	2.65
II	NBH324	2.1	1379	153.4	161.2	121.9	64.8	29.43	2.9	14.49
II	CPE	2.3	519	317.7	74.8	197.4	70.6	0.20	40.6	4.64
II	CPC	0.8	469	85.7	22.8	39.0	27.3	0.20	7.9	0.73
II	CPB	1.8	741	205.0	55.5	92.1	60.0	0.42	24.8	2.02
II	CPG	0.4	69	80.2	6.9	23.4	19.4	0.06	5.8	0.22
II	NBH317	2.5	1943	183.5	83.3	111.8	75.5	0.78	20.9	4.42
II	NBH325	1.6	603	108.7	50.6	85.3	51.0	0.24	19.4	1.36
II	NBH346	0.4	31	37.3	4.2	23.4	19.2	0.10	6.6	0.14
II	NBH331	1.6	364	123.7	37.7	78.4	50.4	0.41	23.9	1.15
III	AB1	0.8	67	47.4	19.7	34.3	5.8	0.09	3.0	0.28
III	AB2	2.5	363	112.2	48.7	60.5	28.1	0.30	7.4	0.79
III	AB3	2.7	269	112.5	52.4	63.5	32.6	0.18	11.2	1.03
III	AB4	1.8	199	90.8	39.1	54.2	18.5	0.17	5.0	0.86
III	AB5	2.2	290	96.9	38.0	57.4	30.5	0.21	7.6	0.89

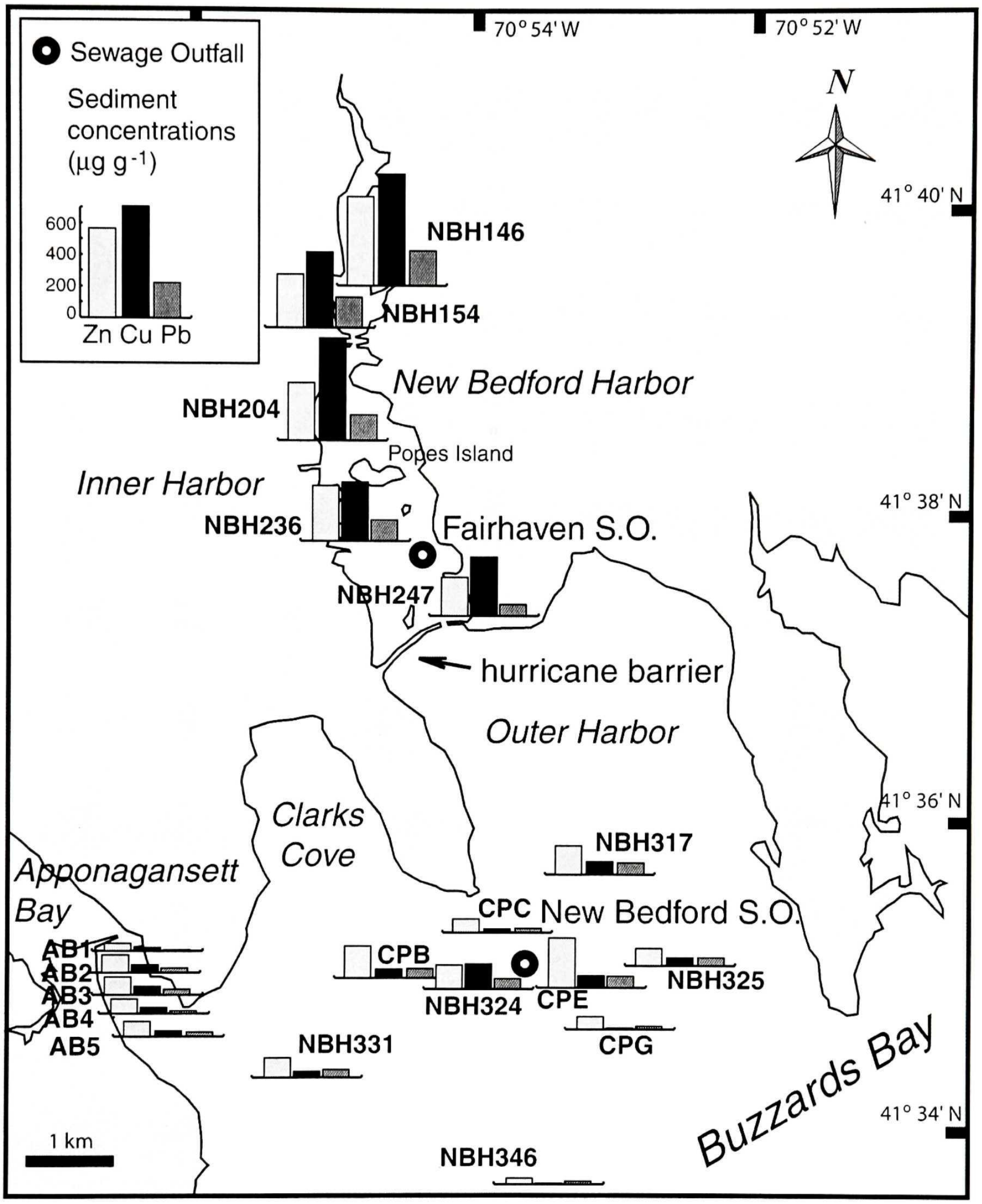

Figure 2. Distributions of the sedimentary concentrations of Zn, Cu and Pb in New Bedford Harbor, Clarks Cove and Apponagansett Bay.

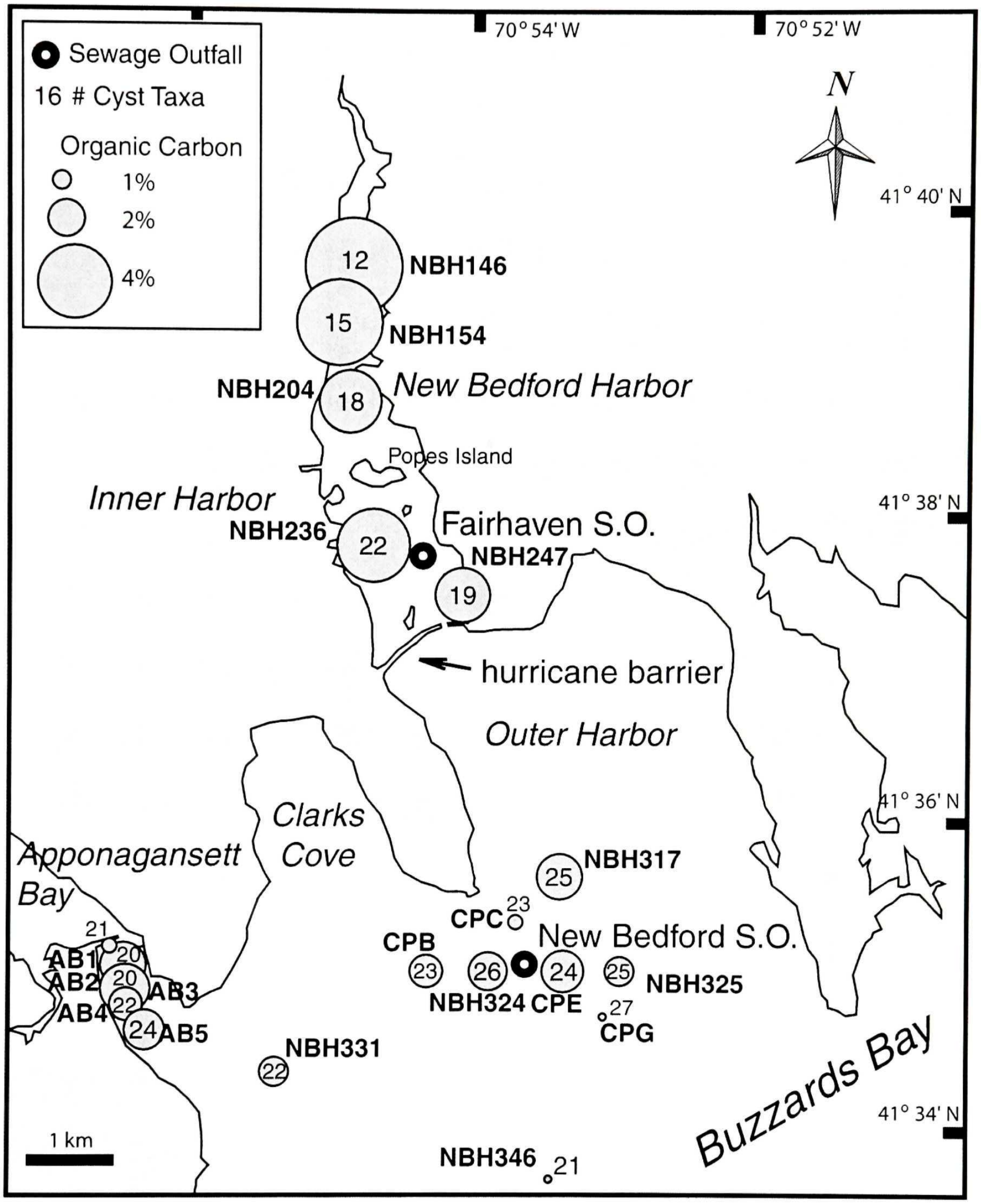

Figure 3. Distribution of the dinoflagellate cyst species richness and sedimentary organic carbon (%) content in New Bedford Harbor, Clarks Cove and Apponagansett Bay.

Table 5. Correlation matrix of organic carbon, PCBs and metal sedimentary concentrations.

	% OC	PCBs	Zn	Cu	Cr	Pb	Cd	As	Ni	Ag
% OC		**0.849**	**0.878**	**0.849**	**0.811**	**0.894**	0.018	0.306	**0.684**	0.285
PCBs	**0.849**		**0.879**	**0.911**	**0.742**	**0.952**	-0.014	-0.011	**0.690**	0.159
Zn	**0.878**	**0.879**		**0.891**	**0.877**	**0.936**	-0.011	0.259	**0.847**	0.272
Cu	**0.849**	**0.911**	**0.891**		**0.853**	**0.930**	0.048	-0.006	**0.684**	0.238
Cr	**0.811**	**0.742**	**0.877**	**0.853**		**0.893**	0.085	0.245	**0.868**	0.416
Pb	**0.894**	**0.952**	**0.936**	**0.930**	**0.893**		0.039	0.143	**0.824**	0.297
Cd	0.018	-0.014	-0.011	0.048	0.085	0.039		-0.466	-0.225	**0.893**
As	0.306	-0.011	0.259	-0.006	0.245	0.143	-0.466		0.497	-0.196
Ni	**0.684**	**0.690**	**0.847**	**0.684**	**0.868**	**0.824**	-0.225	0.497		0.125
Ag	0.285	0.159	0.272	0.238	0.416	0.297	**0.893**	-0.196	0.125	

Coefficients with $R > 0.5$ and probability ≤ 0.01 are indicated in bold

Table 6. Concentrations (cysts cm^{-3}) of dinoflagellate cysts in surface sediments from New Bedford Harbor, Clarks Cove and Apponagansett Bay.

Group	Sample site	Total cyst concentrations (cysts g^{-1})	Total cyst concentrations (cysts cm^{-3})	*Alexandrium tamarense*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* spp.	*Dubridinium* spp.	*Gymnodinium spp.*	*Impagidinium* spp.	*Islandinium brevispinosum*	*Islandinium? cezare*	*Islandinium minutum*	*Lejeunecysta oliva*	*Lejeunecysta sabrina*	*Lingulodinium machaerophorum*	*Nematosphaeropsis* spp.	*Operculodinium centrocarpum* sensu Wall & Dale 1966	*Operculodinium centrocarpum* var. *truncatum*	*Operculodinium israelianum*	*Pentapharsodinium dalei*	*Polykrikos kofoidii* & *schwartzii*	*Protoperidinium oblongum*	*Protoperidinium* spp.	*Protoperidinium minutum*	*Peridinium wisconsinense*	*Quinquecuspis concreta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Spiniferites bentorii*	*Spiniferites elongatus*	*Spiniferites membranaceus*	*Spiniferites* spp.	*Stelladinium stellatum*	*Tectatodinium pellitum*	*Trinovantedinium applanatum*	*Tuberculodinium vancampoae*	*Votadinium calvum*	*Votadinium spinosum*	Cyst E	Unknown cysts
I	NBH146	556	314	0	0	3	34	43	0	0	6	3	0	0	0	0	9	28	0	0	3	0	0	40	0	0	0	0	0	3	0	6	126	0	0	0	0	0	0	3	6
I	NBH154	900	404	0	0	0	27	53	0	0	15	3	0	0	0	6	6	44	0	9	0	0	0	27	0	0	0	0	0	3	0	3	168	0	3	0	0	0	3	6	30
I	NBH204	1291	588	0	0	3	36	64	0	0	12	3	18	0	0	9	9	64	3	6	9	3	0	70	0	0	3	3	0	9	0	3	255	0	0	0	0	0	0	0	6
I	NBH236	6918	1905	11	0	32	171	134	0	5	27	0	70	0	0	5	48	284	0	0	48	177	0	64	5	0	21	0	11	32	21	16	653	5	11	0	0	0	0	37	16
I	NBH247	1846	1058	17	0	21	38	140	0	0	21	0	34	0	0	13	21	157	0	0	30	47	0	47	8	0	17	4	0	8	21	8	356	0	0	0	0	0	0	34	17
II	NBH324	7784	3704	0	12	42	167	155	6	12	113	24	167	0	6	6	48	793	30	6	125	256	0	310	54	6	24	0	6	30	36	6	1199	12	0	0	0	0	6	30	18
II	CPE	8377	3729	0	0	44	131	87	0	9	78	0	122	0	0	26	78	671	44	9	305	200	0	96	0	0	35	9	17	52	44	9	1490	26	70	9	0	0	0	44	26
II	CPC	1672	1160	0	0	17	52	57	0	0	17	4	44	4	4	13	17	231	0	0	35	79	0	26	17	0	17	4	13	22	13	4	401	9	0	0	0	0	0	44	13
II	CPB	3762	1685	0	0	25	151	145	0	0	44	25	138	0	6	13	13	233	0	6	13	157	0	113	6	0	0	6	13	31	13	0	471	19	6	0	0	13	0	19	6
II	CPG	470	504	3	3	18	23	26	0	0	14	5	33	0	1	7	4	83	0	0	4	34	1	80	4	0	3	1	5	8	1	1	122	0	3	1	0	4	3	4	4
II	NBH317	8569	3386	0	0	38	228	213	0	8	121	0	144	0	0	23	84	547	30	0	137	296	0	121	30	0	23	0	30	61	61	8	995	23	8	0	15	23	23	91	8
II	NBH325	8926	4234	0	37	62	222	98	12	0	148	25	209	0	0	49	37	812	12	12	529	172	0	74	25	0	25	12	12	25	98	12	1391	0	25	0	0	0	12	74	12
II	NBH346	1056	1085	0	0	16	61	48	0	0	6	3	74	0	0	13	0	316	0	0	84	32	0	13	3	0	10	3	6	19	13	6	316	6	0	3	0	0	0	19	10
II	NBH331	9392	4153	38	0	25	176	176	0	0	75	13	75	0	0	50	25	1430	63	0	163	213	0	151	25	0	0	13	38	88	13	0	1192	0	13	25	0	0	0	38	38
III	AB1	1091	827	0	0	3	47	44	0	0	35	9	12	0	0	6	17	201	0	6	26	76	0	12	3	0	3	0	3	6	17	6	283	0	0	0	0	0	3	3	9
III	AB2	3360	1916	0	0	0	60	94	0	0	27	13	7	0	0	7	20	551	0	20	74	47	0	34	0	0	7	0	20	47	101	13	753	0	7	0	0	0	0	7	7
III	AB3	7933	3109	0	0	0	228	279	0	0	381	13	127	0	0	25	38	558	0	13	114	203	0	317	13	0	0	0	0	25	13	0	685	13	0	13	0	0	13	13	25
III	AB4	3345	1405	0	0	21	51	41	0	0	133	0	5	0	0	5	31	441	0	5	41	46	0	144	5	0	5	0	0	10	21	10	323	10	5	5	5	0	0	10	31
III	AB5	4723	2507	0	5	26	87	118	0	0	190	5	15	0	5	26	62	139	10	21	298	134	0	134	10	0	0	0	5	26	57	31	1069	10	10	0	0	0	5	5	5

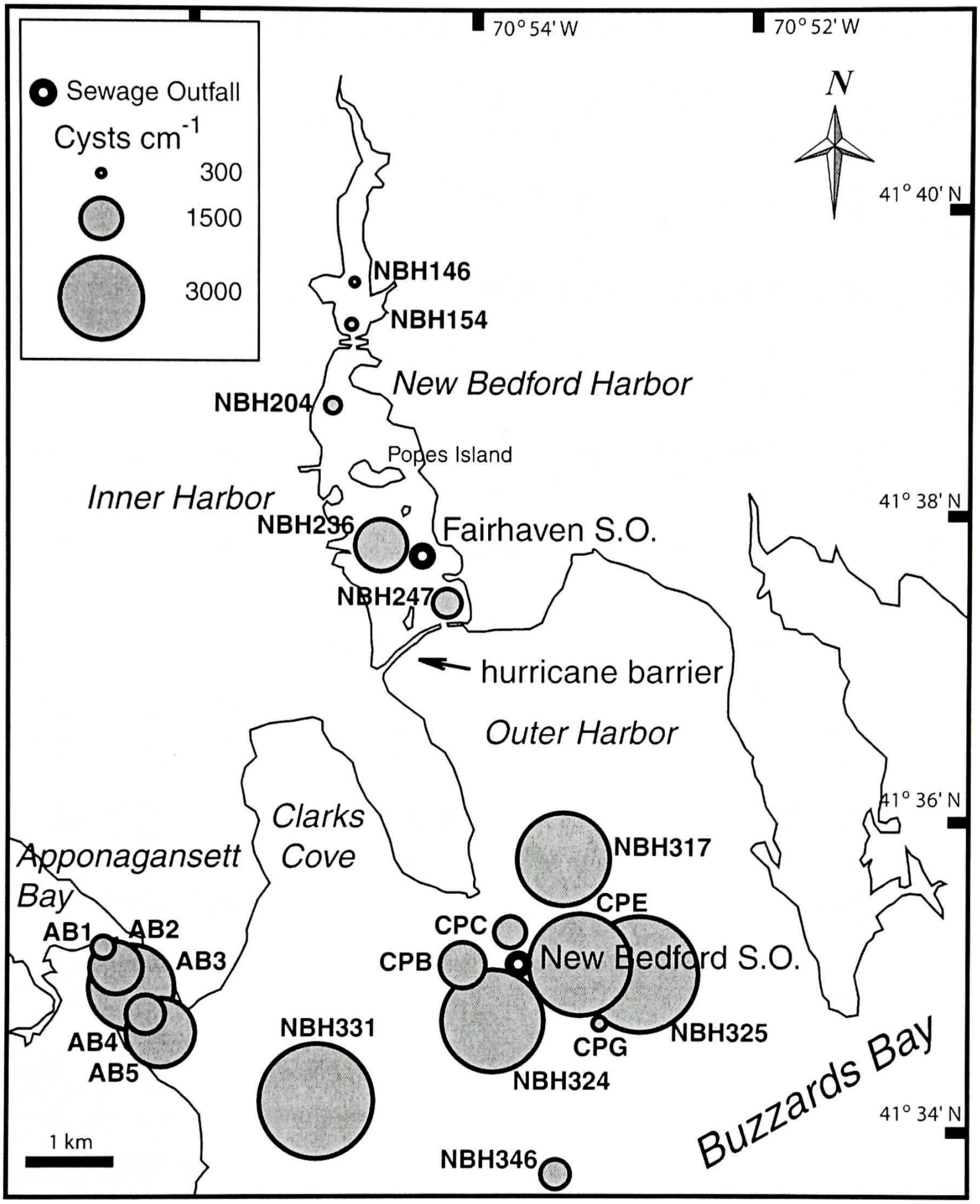

Figure 4. Total dinoflagellate cyst concentration in surface sediments of New Bedford Harbor, Clarks Cove and Apponagansett Bay.

autotrophic dinoflagellates usually comprise more than 50% of the assemblages (Figure 5), with the exception of three sites CPB, CPG, and AB3 (47%). Cysts of all heterotrophic dinoflagellates comprise an average of 36% of each cyst assemblage, ranging from 17 to 53% (Figure 5). The proportion of Diplopsalidaceae and Polykrikaceae is ~12%, at all sites (Figure 5).

A total of 37 dinoflagellate cyst taxa were identified (Table 3). The number of taxa (species richness), in samples ranges from 12 to 27, with an average of 22 (Table 3, Figure 3). Cyst assemblages in group I, the Inner part of New Bedford Harbor, are characterized by lower species richness (an average of 17) compared to assemblages in group II (24 taxa) and III (21 taxa). There are significant ($P<0.01$) negative correlations between dinoflagellate cyst species richness and sedimentary concentrations of Cu, Zn, Pb, PCBs and organic carbon content (Figure 6).

The composition of the dinoflagellate cyst assemblages is described with respect to proportions (Tables 3) and concentration by volume (Table 6). The dominant taxa belong to Gonyaulacaceae, *Spiniferites* spp. and *Operculodinium centrocarpum* sensu Wall & Dale 1966 (Table 3, Figure 7). Cyst taxa that comprise >5% of the assemblages include *Protoperidinium* spp., *Dubridinium* spp., *Pentapharsodinium dalei*, *Islandinium brevispinosum*, *Brigantedinium* spp., *Polykrikos kofoidii & schwartzii*, *Islandinium minutum* and *Spiniferites elongatus*. At four sites, cysts of toxic bloom-forming *Alexandrium tamarense* are found in low proportions (<2%).

Principal component analysis (PCA) was performed on taxa percentages using SPSS 10.1. The first principal component (PC1) represents 90% of the variance, whereas the second and the third component explain less than 5% and 2%, respectively. Thus, only PC1 was considered for further analyses.

The first principal component (PC1) is distributed in two contrasting patterns. It increases from the upper part of New Bedford Harbor seaward towards the hurricane barrier, but decreases from Clarks Cove Point and Inner Apponagansett Bay in the seaward direction (Figure 8). The highest values of PC1 are near the sewage outfalls of Fairhaven and New Bedford Wastewater Treatment Plants, as well as at site AB1, the sample from the most upper reach of Apponagansett Bay included in our study. There is

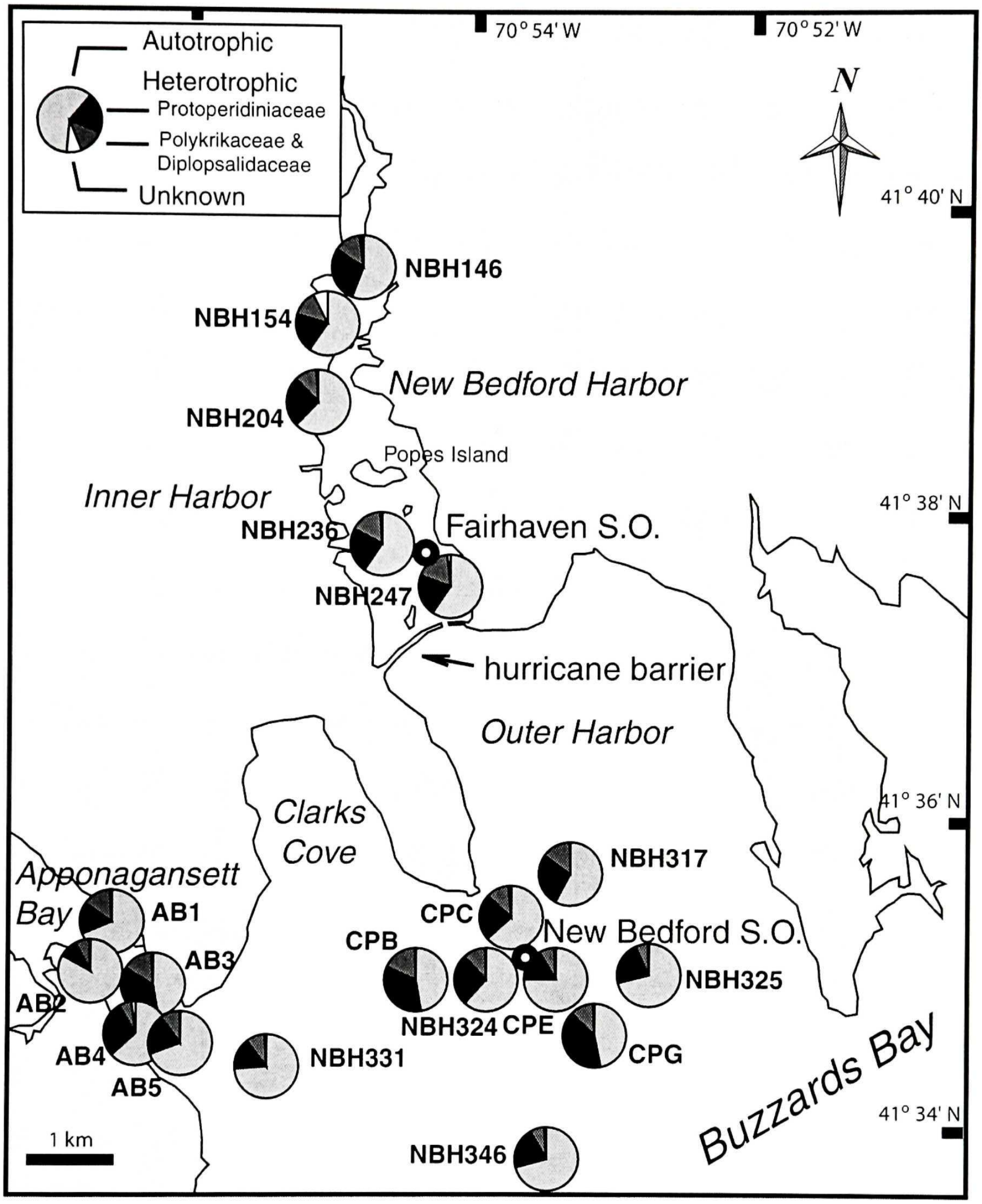

Figure 5. The relative abundance (%) of cysts of heterotrophic (Protoperidiniaceae, Polykrikaceae and Diplopsalidaceae) and autotrophic dinoflagellates in assemblages from New Bedford Harbor, Clarks Cove and Apponagansett Bay.

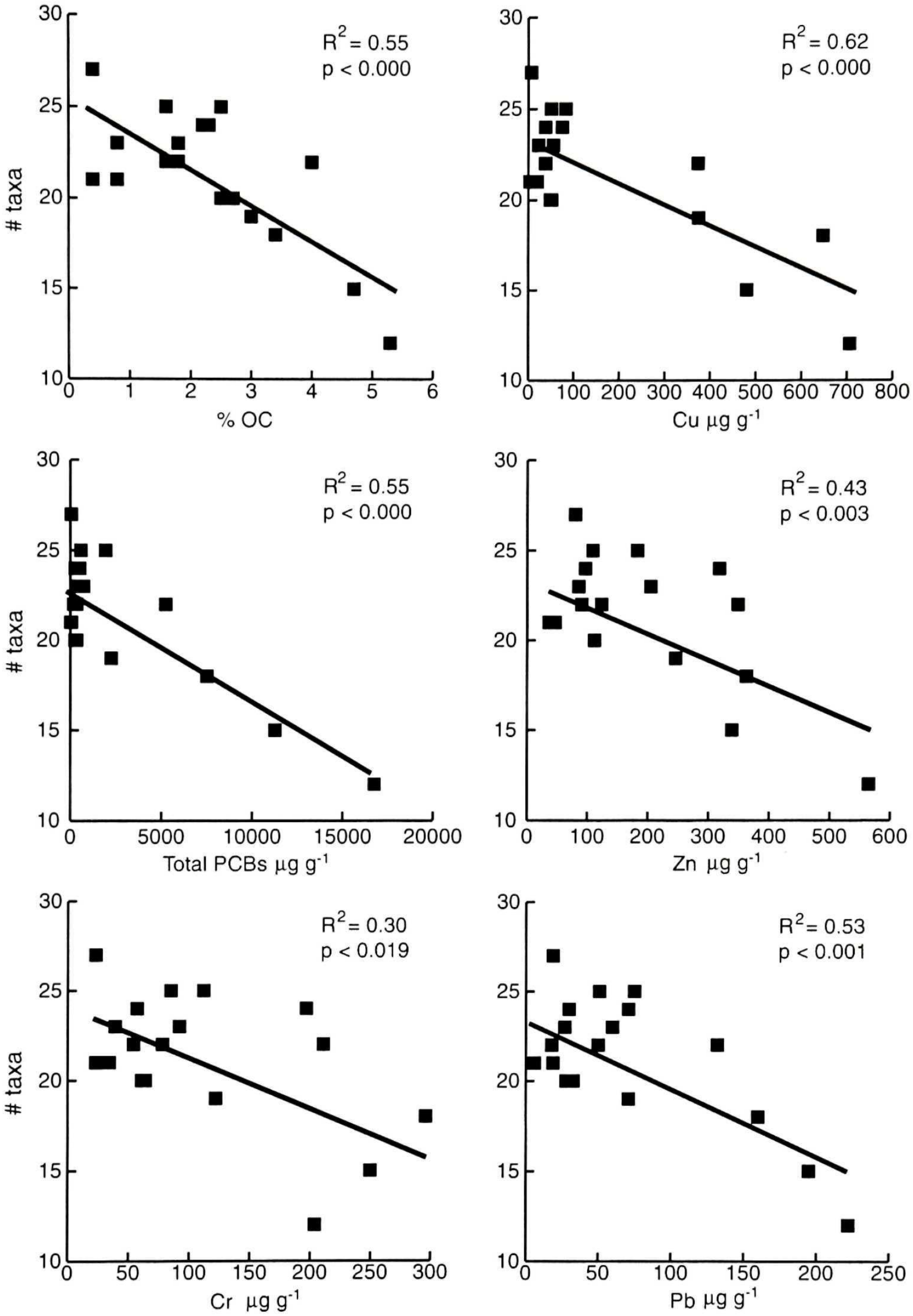

Figure 6. Relationship between dinoflagellate cyst species richness and sedimentary concentrations of Cu, Zn, Cr, Pb, PCBs and % organic carbon.

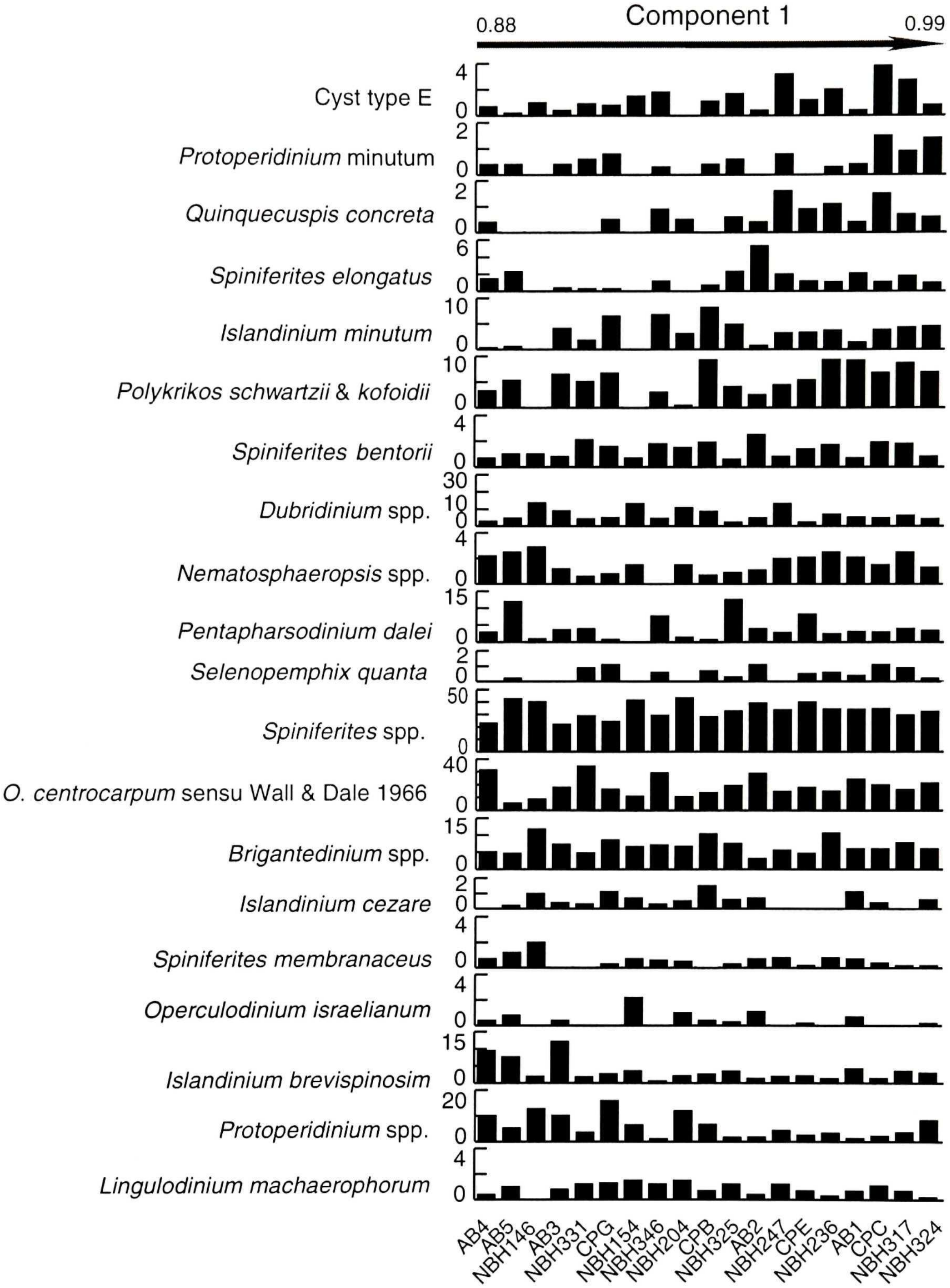

Figure 7. Proportions of selected dinoflagellate cysts in the assemblages from surface sediment samples ordered by the first principal component (PC1).

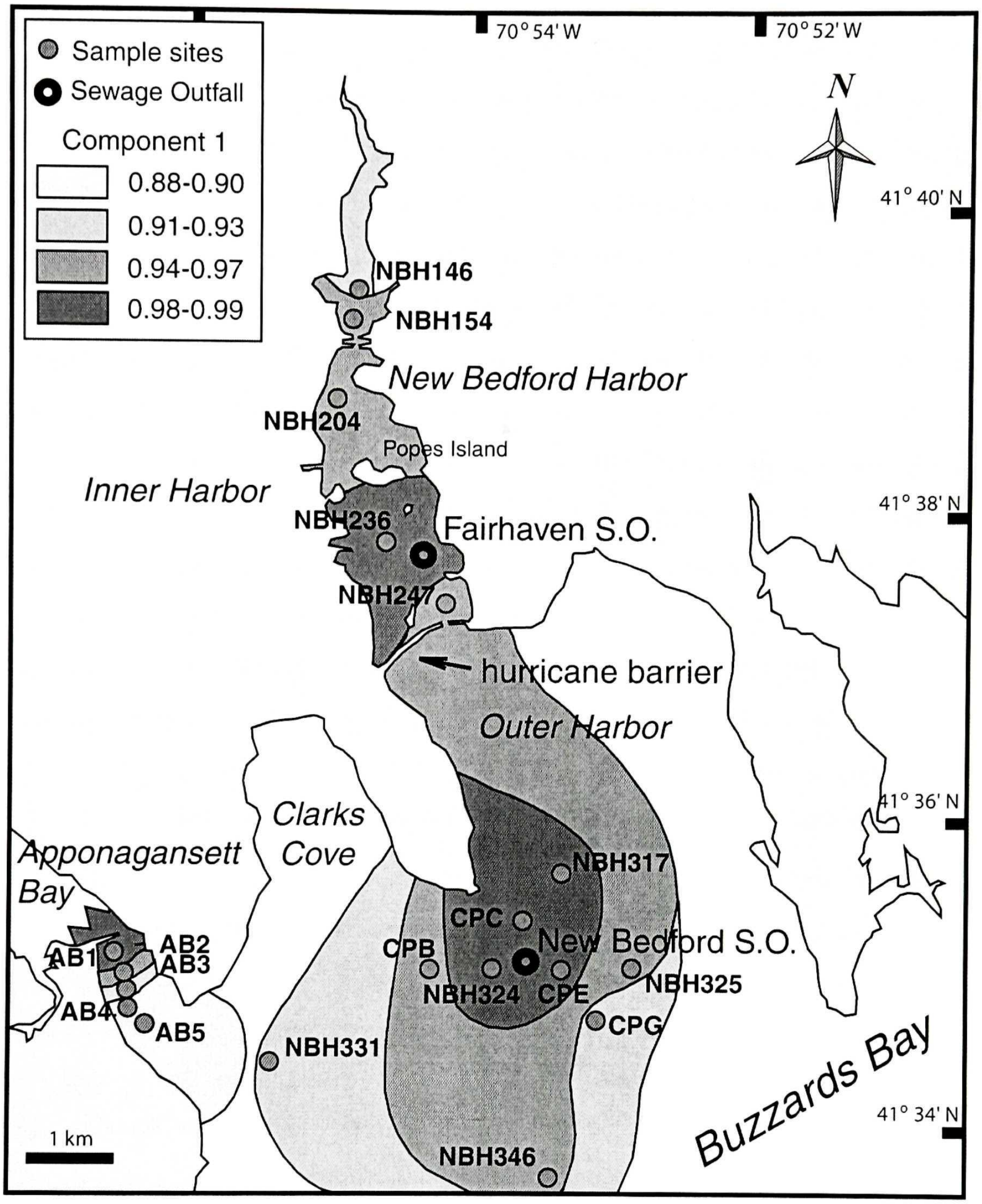

Figure 8. Spatial distributions of the first principal component (PC1) in surface sediments from New Bedford Harbor, Clarks Cove and Apponagansett Bay.

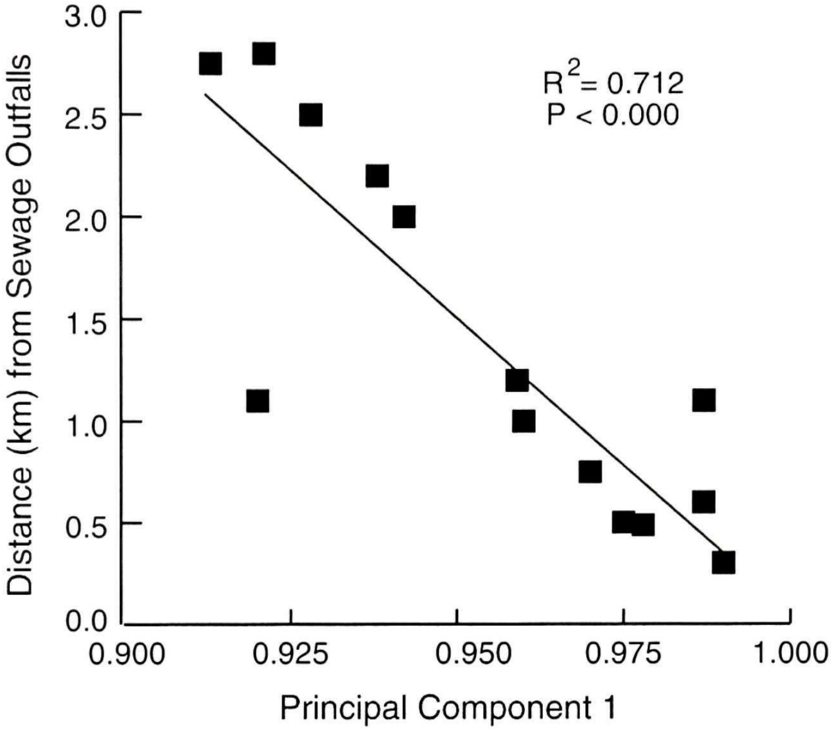

Figure 9. Relationship between principal component 1 (PC1) and distances from municipal sewage outfalls.

a significant ($R^2=0.71$ and $P<0.001$) linear correlation between PC1 scores and the distance to the nearest locations of the sewage outfalls (Figure 9) for sites from group I and II for which the distance from the point sources of sewage discharge can be determined. Sites from group III were not considered, as there is no identified point source of sewage discharge in Apponagansett Bay. Thus, this is a strong indication that PC1 is related to the discharge of sewage enriched with nutrients.

Figure 7 shows relative abundances of the dinoflagellate cysts taxa that constitute >1% of the assemblages. Amongst these taxa, the proportions of *Islandinium brevispinosum* and *Protoperidinium* spp. decrease as PC1 increases i.e., towards the sewage outfalls (Figure 7), whereas the proportions of cysts of *Quinquecuspis concreta*, *Protoperidinium minutum*, *Spiniferites elongatus* and Cyst type E tend to increase with the increase of PC1. The abundance of *Nematosphaeropsis* spp. is more at low (<0.91) and high values of PC1 (>0.97) than at the intermediate values.

Our study of dinoflagellate cysts from surface sediments also reveals dinoflagellate species previously not recorded in the phytoplankton population of Buzzards Bay waters. We found *Gonyaulax digitalis*, *Gonyaulax spinifera*, *Lingulodinium polyedrum*, *Protoceratium reticulatum*, *Pentapharsodinium dalei*, *Polykrikos schwartzii*, *Polykrikos kofoidii*, *Diplopsalidaceae* and multiple species of *Protoperidiniaceae* group never reported in the surveys conducted by Pierce and Turner (1994) and Turner et al. (2000) in Buzzards Bay. This underscores the usefulness of studying the dinoflagellate cyst records in sediments as a source of complimentary information on phytoplankton composition, especially on species that are either rare and/or have a short motile stage (Dale, 1983).

DISCUSSION AND CONCLUSIONS

Sedimentary cyst concentration has been regarded as a proxy of dinoflagellate production (e.g., Dale, 2001). A potential problem with this approach is that the change in the sediment accumulation rate affects dinoflagellate cyst concentrations. In this study, we observe large fluctuations of the total cyst concentrations in the surface sediment samples that can be attributed to varying dinoflagellate production and/or sedimentation rate. However, it is difficult to determine the sedimentation rates station by station. Estimates show that they typically vary between 0.2 and 0.6 cm yr^{-1} in the Inner New Bedford Harbor and between 0.1 and 0.5 cm yr^{-1} in the Outer Harbor, and Apponagansett Bay (Summerhayes et al., 1985; Latimer et al., in press). Low cyst concentrations (~400 cysts cm^{-3}) in the Inner part of New Bedford Harbor, north of the Popes Islands (sites NBH 146, 154 and 204), are one-fifth that at the other sites, which is probably too large a difference to be explained by the variation in the sedimentation rate. Thus the low dinoflagellate cyst concentration in the Upper part of Inner New Bedford Harbor is likely to be the result of reduced dinoflagellate production caused by high levels of toxic pollutants and organic carbon content. In addition to the toxicity of metals and other pollutants, high levels of organic carbon in the water column can further decrease dinoflagellate production by reducing the photic zone. The main source of organic carbon in New Bedford Harbor is terrestrial and likely comes from sewage effluent (Pospelova et al., 2002).

A decline in species richness of phytoplankton has been noted as a possible response to eutrophication (Sommer, 1995; Tsirtsis and Karydis, 1998). A decrease in richness of dinoflagellate cyst taxa has been suggested as a general indicator of polluted and highly eutrophic estuarine systems (Pospelova et al., 2002). Sediment samples from the Inner Harbor (group I) that have lower cyst concentrations also have lower species richness, indicating that the environmental conditions north of Popes Island are less suitable for dinoflagellate population compared to the conditions south of the Island. Further support is found in the negative linear relationship between the dinoflagellate cyst species richness and sedimentary concentrations of Cu, PCBs, Zn, and Pb, as well as %OC. Although the effects of each constituent may differ, their co-variances prevent us from determining more detailed relationships. Thus, the decrease in species richness of dinoflagellate cysts serves as a combined signal of organic and toxic pollution in the harbor.

At our study sites the gradients of salinity and temperature are short as compared to those examined in marine and oceanic studies (Wall et al., 1977; Mudie and Harland, 1996; Dale, 1996; de Vernal et al., 1997; Rochon et al., 1999). They are also smaller than gradients of temperature and salinity found in the coastal lagoons from the same region (Pospelova et al., in press). Water temperature and salinity, commonly identified as two major factors controlling distribution of dinoflagellate cysts, do not vary with the first principle component in this study. New Bedford Harbor and Apponagansett Bay show similar patterns with minor increases in salinity and slight decreases in temperature in the seaward direction, but have opposite trends in PC1 scores (Figure 8).

The availability of nutrients has been identified as an important factor controlling the distribution of phytoplankton and dinoflagellates in particular (Taylor, 1987). Unfortunately, there are no data on the concentrations of nitrogen or other nutrients on the scale of our sample stations. However, we can assume that nutrient concentrations decrease with distance from the sewage outfalls. The strong correlation between PC1 scores and distance from sewage outfalls (Figure 9) suggests that PC1 mainly reflects nutrient gradients, and that cyst assemblages change with distance from point sources of nutrient pollution. We infer that dinoflagellate cyst assemblages in Apponagansett Bay also reflect a nutrient signal, because nutrient gradients decrease in the seaward direction (Figure 8). Since ammonia is the main form of nitrogen from sewage effluent (Borkman and Turner, 1993), it is likely a critical parameter affecting the distribution of the dinoflagellate cyst assemblages in the studied embayments.

Cysts of heterotrophic dinoflagellates constitute a large proportion of the cyst assemblages (~36%) in surface sediments indicating a substantial role of dinoflagellates in modern secondary production. In the study of temporal cyst records from New Bedford Harbor and Apponagansett Bay, the abundance of cysts of heterotrophic dinoflagellates, particularly Polykrikaceae and Diplopsalidaceae, increased with nutrient enrichment exceeding 6% of the assemblage composition (Pospelova et al. 2002). Dinoflagellate cyst assemblages in surface sediments also contain high (up to 18%) proportions of Polykrikaceae and Diplopsalidaceae cysts.

Temporal cyst records show that certain cyst taxa increased in abundance with nutrient enrichment as the system shifted from mesotrophic to eutrophic or highly eutrophic conditions, specifically to *Dubridinium* spp., *Islandinium minutum & cezare*, *Spiniferites bentorii* and cysts of *Polykrikos schwartzii & kofoidii* (Pospelova et al., 2002). In most of the surface sediments of New Bedford Harbor these taxa are present eutrophication and toxic pollution (~7% of *Dubridinium* spp., ~3% of *Islandinium minutum & cezare*, ~1.5% of *Spiniferites bentorii*, and ~5% of *Polykrikos schwartzii & kofoidii*). Species-indicators of oligotrophic to mesotrophic conditions in shallow embayments (Pospelova et al., 2002), such as *Lingulodinium machaerophorum*, *Operculodinium israelianum* and *Selenopemphix quanta*, are absent or contribute ≤1% in most of the surface cyst assemblages.

This study shows that dinoflagellate cysts are useful biological indicators of polluted environmental conditions in estuaries. Sites with the highest toxic pollution are characterized by the lowest dinoflagellate cyst species richness and concentrations, confirming patterns observed in the temporal records. We also find that at small spatial scales, where the salinity and temperature variability is low, the distribution of dinoflagellate cysts is controlled by nutrient gradients.

CHAPTER 4. ENVIRONMENTAL FACTORS INFLUENCING SPATIAL DISTRIBUTION OF DINOFLAGELLATE CYST ASSEMBLAGES IN SHALLOW LAGOONS OF SOUTHERN NEW ENGLAND (USA)

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ABSTRACT

Surface sediment samples from 24 sites within 11 back-barrier lagoons of Rhode Island and Massachusetts (USA) contain abundant (200-6,000 cysts cm^{-3}) and diverse (up to 40 taxa) dinoflagellate cyst assemblages. The lowest cyst concentrations and diversity are observed in lagoons with low salinity (<10 psu). The pattern of spatial distribution of dinoflagellate cysts in these shallow estuarine environments is described. We assessed the relationship between the available multi-year water quality data and the composition of dinoflagellate cyst assemblages using canonical correspondence analysis. Temperature and salinity are found to be the primary abiotic factors influencing cyst distribution in the coastal lagoons.

INTRODUCTION

Coastal lagoons and bays are characteristic features of the southern New England coastline. Lagoons are estuarine systems characterized by shallow depth, a well-mixed water column, slow flushing, and minimal input of freshwater (Boynton et al., 1982). In the past few decades these ecosystems have undergone significant changes as a result of watershed development (Darnell and Soniat, 1981; Nixon, 1982; Lee and Olsen, 1985; Avanzo and Kremer, 1994). In some lagoons, coastal eutrophication has become a serious threat, and so programs has been established to monitor water quality. These monitoring programs have made available long-term databases of water chemistry measurements at high temporal and spatial resolution.

The availability of multi-year water chemistry data for southern New England estuaries creates a unique opportunity to evaluate the importance of abiotic factors that could affect the distribution of dinoflagellate cysts in a variety of lagoons, all located within the same climatic zone. Our research program is the first detailed study of dinoflagellate cyst assemblages in surface sediment samples from back-barrier lagoons of Rhode Island and Massachusetts (USA). The aim of this paper is to document the occurrence of dinoflagellate cyst taxa, their spatial distribution and relationship to hydrographic conditions.

It is widely recognized that the distribution of modern dinoflagellate cysts in oceanic and marine environments is mostly controlled by water temperature, salinity and availability of nutrients (Dale, 1996; de Vernal et al., 1997; Rochon et al., 1999; Devillers and de Vernal, 2000; de Vernal et al., 2001). Our study questions whether the same factors can be related to the distribution of dinoflagellate cysts at the much smaller spatial scales needed to characterize variability in hydrographic conditions in lagoons. The variability in hydrographic conditions in lagoons is responsible for the recognized patchy character in the distribution of phytoplankton (Smayda, 1980), which should lead to a similarly heterogeneous pattern of dinoflagellate cyst distribution (Blanco, 1995). Lagoons are characterized by relatively rapid sedimentation rates, thus the period of deposition of sediment samples corresponds to the period covered by monitoring programs. If sedimentary assemblages of dinoflagellate cysts reflect the living population in overlying waters, then we expect to find cyst assemblages to vary with differences in water chemistry.

Results of this study have application to paleoenvironmental studies in estuaries. They also contribute to our understanding of how human alteration of environmental conditions in lagoons affects populations of cyst-producing dinoflagellates.

STUDY AREA

Our study includes 11 back-barrier lagoons in southern New England, USA. Nine lagoons are located in southern Rhode Island, on Block Island Sound. The remaining two are on the coast of Massachusetts' Vineyard Sound (Fig. 1). Although called Waquoit "Bay", this system on the Massachusetts coast is a shallow semi-enclosed estuary and can be classified as a large lagoon.

Physical Characteristics

Coastal lagoons, locally called salt ponds, are situated behind narrow (200-300 m wide) sandy dunes, up to 3-4 m high. The barriers are topped by ocean waters only during severe storm events (e.g., hurricanes). The lagoons are elongated (Fig. 1) and are parallel to the barriers, with the exception of Point Judith, Potter Pond, and Waquoit Bay that have their long axis oriented perpendicular to the coast.

Physical characteristics of the lagoons are compared in Table 1. Waters are shallow with an average depth of ~1-2 m, unstratified, and characterized by low turbidity

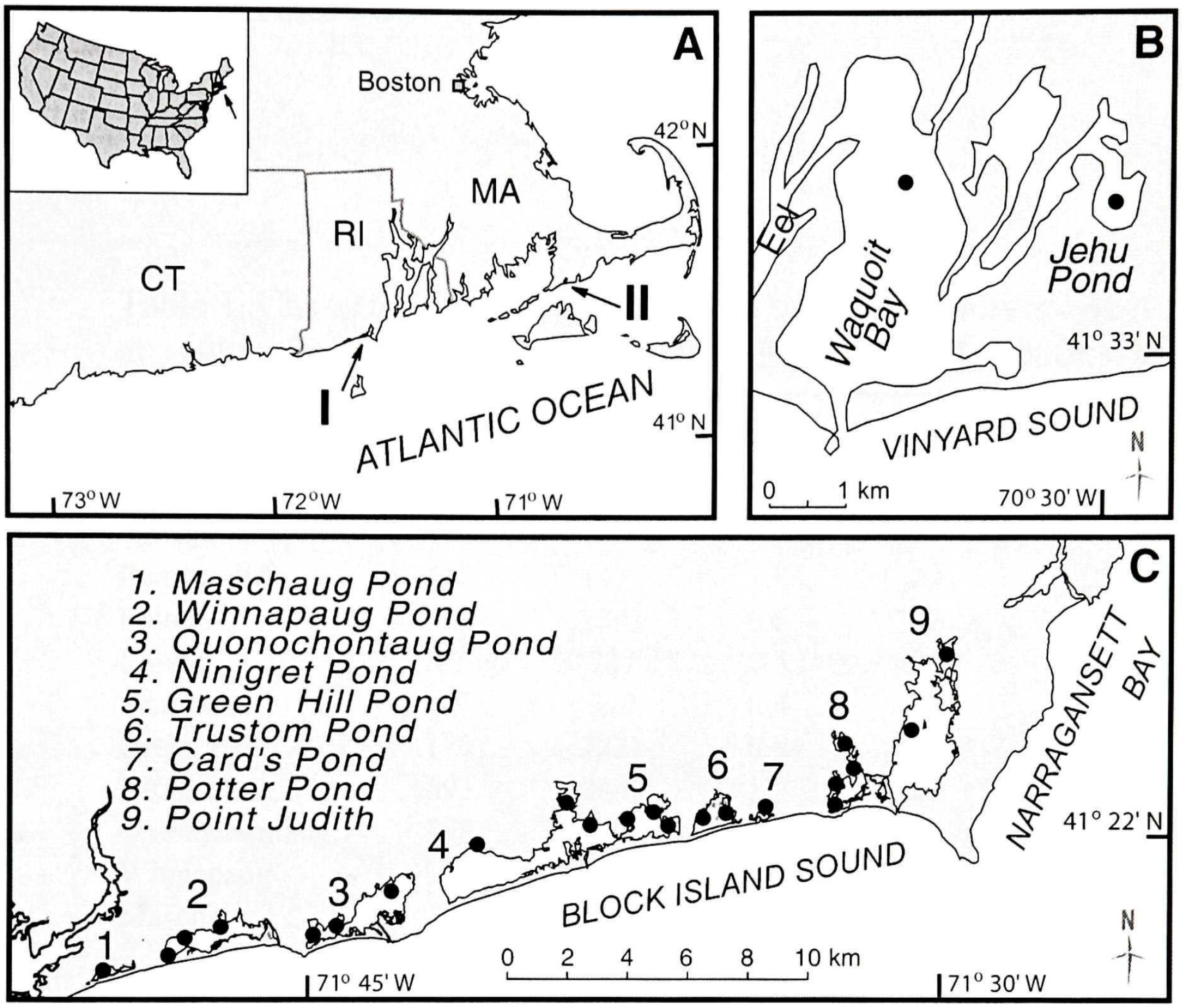


Figure 1. Map of the southern New England (A) showing the locations of lagoons on the Rhode Island (I) and Massachusetts (II) coasts. Location of the sample stations (represented by black dots) in B) Waquoit Bay and Jehu Pond and C) the nine Rhode Island lagoons.

Table 1. Characteristics of the lagoons in this study (Boothroyd et al., 1985; Giblin, 1990; Lee et al., 1997; Brawley et al., 2000).

	Area (hectares) Waterbody	Area (hectares) Watershed	Avg. Depth (m)	Avg. Aug. Temp (°C)	Avg. Salinity
Rhode Island					
Point Judith	613	1432	1.8	22	29
Potter	133	1341	0.6	22	27
Card's	17	737	0.4	23	4
Trustom	65	322	0.4	25	5
Green Hill	175	1231	0.8	23	19
Ninigret	693	2440	1.2	23	24
Quonochontaug	298	934	1.8	21	29
Winnapaug	181	929	1.5	23	28
Maschaug	19	140	2.1	24	7
Massachusetts					
Waquoit Bay	375	4955	0.8	24	29
Jehu	78	422	2.0	23	29

(Lee, 1980; WBNERR, 1996). The primary variant among these lagoons is the exchange with oceanic waters. Twice a day ~2-4% of the lagoon water exchanges with ocean waters through barrier inlets (Sheath and Harlin, 1988). The tidal range averages 1.1 m on the ocean side and is 7-12 cm in most of the lagoons, but about 50 cm in Waquoit Bay.

In the past, ephemeral, natural inlets were the primary mechanism for the introduction of ocean waters. Today many inlets or "breachways" have been permanently stabilized by jetties constructed during the first half of 20th century. Point Judith Pond has the largest inlet (75 m wide, ≤9 m deep) maintained for access by commercial fishing boats. Potter Pond has no direct opening to the sound but receives offshore waters by way of a narrow channel (7 m wide, <1.3 m deep) dug between it and Point Judith Pond. Green Hill Pond receives marine waters through a smaller channel from neighboring Ninigret Pond. Waquoit Bay has two inlets. Its eastern inlet connects directly to the Bay, and the western inlet is on adjacent Eel Pond. Jehu Pond is indirectly linked to marine waters through permanent channels to Waquoit Bay. Trustom, Maschaug, and Card's Ponds have no permanent inlets. These three ponds are isolated from marine waters except for occasional breaching.

Environmental Characteristics

Southern Rhode Island and eastern Massachusetts are characterized by a humid, continental climate with a strong maritime influence. That produces a moderate annual temperature range with mild winters and prolonged, cool summers. July and August are the warmest months of the year, while January and February are the coldest with the mean high temperature through the winter above freezing. The average winter water temperature in the lagoons is ~3°C and the average summer temperature is ~23°C (Lee et al., 1997; WBNERR, 1996). There are large variations in mean summer temperature between the lagoons and sometimes between different stations within the same lagoon. The lowest mean summer temperature is measured in Point Judith Pond (~19°C), with little difference between two stations (0.5°C). Waquoit Bay and Card's Pond have the warmest waters with the mean summer temperature ~25°C. The largest range of mean summer temperature within a single lagoon (>3°C) is recorded in Potter Pond.

Salinity within the lagoons depends upon precipitation events and ther connection to the sea is permanent or temporary. The average annual precipitation in the area is about 105 cm with the maxima occurring in November-December and the minima in June-July (Hoare, 1996). Trustom, Maschaug, and Card's ponds, with no permanent inlets to the Sound, have the lowest salinity (4-7 psu) whereas Point Judith, Quonochontaug Ponds and Waquoit Bay have the highest salinity (~29 psu) (Table 1). The largest range in the mean summer salinity within a single system (~5 psu) is observed in Ninigret Pond.

As a result of the low freshwater runoff into the lagoons, nutrient inputs to these systems are generally lower than in other estuaries (Nixon, 1982). Concentrations of nutrients in the waters are seasonally variable. For example, the concentration of nitrates varies from 0.2 in July-August to 43.6 $\mu M \cdot l^{-1}$ in February-March. In contrast, the concentration of inorganic phosphorus ranges from 0.1 in March-April to 2.2 $\mu M \cdot l^{-1}$ in late summer (Lee et al., 1997). The concentration of phosphorus within the lagoons is always lower than observed offshore, whereas the concentration of nitrogen is higher.

MATERIAL AND METHODS

Station location and sediment collection

Surface sediments were collected from 24 water quality monitoring stations (Fig. 1). Samples were taken at multiple stations in most of the lagoons. Distance between stations within lagoons varies from 150-2000 m and averages about 500 m. Stations 6, 7, and 8 of Potter Pond are located in coves where water circulation is restricted. Potter Pond station 5 is near the inlet on a sandy subtidal flat. Point Judith station 1 is situated at the northern end of the pond in a cove that receives the discharge of the Saugatucket River. Thus, freshwater inflow to upper Point Judith Pond is considerably higher than to the other lagoons. Ninigret Pond has three stations: 12, 13 and 14. Stations 12 and 14 are located in low-energy basins. Green Hill Pond stations 9, 10 and 11 are in the coves where circulation is restricted. Stations 16 and 16A of Quonochontaug Pond are located in the western part of the pond, whereas station 18 is in the eastern part. Winnapaug Pond has three stations: stations 19 and 19A are in the western part the lagoon, which is the most distant from the inlet, and station 21 is in the northern low-energy basin. Waquoit Bay has one station (65) in its northern section. Station 66 is in the central part of Jehu Pond in a cove with restricted water circulation.

Surface sediments were collected with a grab corer deployed from a small boat or by hand, using a mini-piston corer. The top 2 cm were retained from each of 3 replicate cores taken within a radius of 3 m. In these rapidly accreting systems, the upper 2 cm of sediments represent less than 10 years of deposition (Boothroyd et al., 1985). Sediments are characterized as fine sand, silt and mud. All 24 samples were stored frozen prior to sectioning and further analysis.

Sample preparation

Sediment samples of known volume were first dried at room temperature, then treated with cold 10% hydrochloric acid (HCl) to remove calcium carbonate particles. Material was then rinsed twice with distilled water and sieved through 125 μm and retained on 10-μm nylon mesh to eliminate coarse and fine material. To dissolve siliceous particles, samples were placed in a water bath with 40% hydrofluoric acid (HF) for 20 min, then treated for 10 min with cold HCl (10%) to remove fluorosilicates. The residue was rinsed twice with distilled water, sonicated for 1-2 min and finally collected on a 10-μm mesh. Calibrated tablets of *Lycopodium* spores (13911 spores per tablet), added during processing (Stockmarr, 1977), allowed for calculation of dinoflagellate cyst concentrations based on the volume of sediments. Aliquots of residue were mounted in glycerine jelly, and dinoflagellate cysts were studied under a light microscope (63x and 100x objectives).

Dinoflagellate cyst analysis

Identification of dinoflagellate cysts was made on the basis of published descriptions in accordance with taxonomy given in Lentin and Williams (1993). When species-level identification was not possible, identification was done at the genus level. The dinoflagellate cyst nomenclature conforms to Head (1996), Rochon et al. (1999), Head et al. (2001) and Pospelova and Head (2002). A list of counted dinoflagellate cysts and their known thecal equivalent is provided in Table 2. From 33 to 1448 cysts were counted in each sample (Table 3), averaging 300 cysts. Card's Pond was excluded from statistical analyses because of the low cyst count in this sample.

More than 40 dinoflagellate cyst taxa were identified in the sediment samples. For statistical treatment some taxa were grouped together on the basis morphological similarities. In particular, species of the genus *Brigantedinium* (*B. cariacoense* and *B. simplex*) were grouped together because cyst folding or orientation sometimes obscured the archeopyle characteristics, thus preventing identification to the species level. Since the distinction between *Protoperidinium nudum* and *Selenopemphix quanta* is debatable (Head, 1996; Rochon et al., 1999) we also grouped these species together. Because of great morphological variability species of the genus *Spiniferites*, all taxa excluding *S. elongatus* were grouped as *Spiniferites* spp.

Prior to statistical treatment, dinoflagellate cyst data were transformed as described by de Vernal et al. (2001). A natural log (ln) transformation was applied to percentage data to increase the weight of less represented taxa. These species often have more narrow ecological affinities and are likely to be most diagnostic of environmental conditions (de Vernal et al., 2001). In order to deal with whole numbers and to avoid decimals, which yield negative values when they are logarithmically transformed, we expressed relative abundance per thousand, instead of per cent. Another minor modification was to replace zero values with one (1) in order to deal with values greater than zero. Thus, the relative abundances of dinoflagellate cyst taxa range from 1 to 1000 before logarithmic transformation.

Hydrological data

Water quality conditions in the lagoons were monitored over a period of years (3-9 yr) by volunteer "Pondwatchers" (Lee et al., 1997), staff of the Waquoit Bay National Estuarine Research Reserve (WBNRR) and a group of researchers lead by Dr. I. Valiela (Boston University, MA). These groups measured temperature, salinity, nitrates, phosphates, and chlorophyll *a* on a monthly or weekly basis. Measurements were taken at a depth of approximately 30 cm below the water surface. Water clarity was measured as

Table 2. Taxonomic citation of dinoflagellate cysts used in this study. Thecal equivalents are taken from Head (1996), Rochon et al. (1999), Head et al. (2001), and Pospelova and Head (2002).

Cyst species (paleontological name)	Dinoflagellate thecate name or affinity (biological name)
Ataxiodinium choane	*Gonyaulax spinifera complex*
———	*Alexandrium tamarense*
Brigantedinium cariacoense	*Protoperidinium avellanum*
Brigantedinium simplex	*Protoperidinium conicoides*
Brigantedinium spp.	? *Protoperidinium* spp.
Dubridinium spp.	Diplopsalid group
———	*Gymnodinium* spp.
Impagidinium spp.	? *Gonyaulax* sp. indet.
Islandinium brevispinosum	*Protoperidinium* sp. indet.
Islandinium minutum	*Protoperidinium* sp. indet.
Islandinium ? *cezare*	*Protoperidinium* sp. indet.
Lejeunecysta oliva	*Protoperidinium* sp. indet.
Lejeunecysta sabrina	*Protoperidinium leonis*
Lingulodinium machaerophorum	*Lingulodinium polyedrum*
Nematosphaeropsis spp.	*Gonyaulax spinifera* complex
Operculodinium centrocarpum sensu Wall & Dale 1966	*Protoceratium reticulatum*
Operculodinium israelianum	? *Protoceratium reticulatum*
———	*Pentapharsodinium dalei*
———	*Peridinium limbatum*
———	*Pheopolykrikos hartmannii*
———	*Polykrikos kofoidii*
———	*Polykrikos schwartzii*
———	*Protoperidinium americanum*
———	*Protoperidinium minutum*
———	*Protoperidinium nudum*
Protoperidinium spp. indet	*Protoperidinium* group
Quinquecuspis concreta	*Protoperidinium leonis*
Selenopemphix nephroides	*Protoperidinium subinerme*
Selenopemphix quanta	*Protoperidinium conicum* ; *P. nudum*
Spiniferites elongatus	*Gonyaulax spinifera* complex
Spiniferites spp.	*Gonyaulax spinifera* complex
Stelladinium stellatum	*Protoperidinium stellatum*
Tectatodinium pellitum	*Gonyaulax spinifera* complex
Trinovantedinium applanatum	*Protoperidinium pentagonum*
Tuberculodinium vancampoae	*Pyrophacus steinii*
Votadinium calvum	*Protoperidinium oblongum*
Votadinium spinosum	*Protoperidinium claudicans*

Table 3. Relative abundance (%) of dinoflagellate cyst taxa in our samples. Asterisks denote taxa not counted for cyst richness, including the freshwater *Protoperidinium wisconsinense*.

Lagoon	Station #	Cyst counts	Species Richness	Total cyst concentrations (cysts cm-3)	Ratio autotrophs/heterotrophs	*Alexandrium tamarense*	*Ataxiodinium choane*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* spp.	*Dubridinium* spp.	*Impagidinium* spp.	*Islandinium brevispinosum*	*Islandinium ? cezare*	*Islandinium minutum*	*Gymnodinium* spp.	*Lejeunecysta oliva*	*Lejeunecysta sabrina*	*Lingulodinium machaerophorum*	*Nematosphaeropsis* spp.	*Operculodinium centrocarpum* sensu Wall & Dale 1966	*Operculodinium centrocarpum* var *truncatum*	*Operculodinium israelianum*	*Pentapharsodinium dalei*	*Pheopolykrikos hartmannii*	*Polykrikos schwartzii* & *P. kofoidii*	*Protoperidinium americanum*	*Protoperidinium oblongum*	*Protoperidinium* spp. indet	*Protoperidinium nudum*	*Protoperidinium minutum*	*Peridinium limbatum**	*Quinquecuspis concreta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Spiniferites elongatus*	*Spiniferites* spp.	*Stelladinium stellatum*	*Tectatodinium pellitum*	*Trinovantedinium applanatum*	*Tuberculodinium vancampoae*	*Votadinium calvum*	*Votadinium spinosum*	Cyst type E	Cyst type D	Unknown cysts*
Green Hill	9	125	13	214	0.8	0.0	0.0	0.0	0.8	9.6	1.6	0.0	0.0	0.0	0.8	0.0	0.0	1.6	0.8	0.8	1.6	0.0	0.0	0.0	0.0	0.8	0.8	0.0	33.6	0.0	0.0	0.0	0.0	0.0	1.6	0.0	40.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6
Green Hill	10	203	13	1020	5.9	4.4	0.0	0.0	0.0	1.5	1.0	0.0	0.0	0.0	0.5	0.0	0.5	0.0	2.0	0.5	1.5	0.0	1.0	0.0	0.0	0.5	0.0	0.0	8.9	0.0	0.0	0.0	0.0	0.0	1.5	0.0	74.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Green Hill	11	202	10	1394	38.2	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	2.5	0.0	0.5	1.0	0.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.5	88.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
Ninigret	12	307	16	5953	2.7	1.0	0.0	0.0	0.0	1.0	5.2	0.0	0.0	1.3	0.0	0.0	0.0	0.0	3.6	1.6	1.3	0.0	0.7	2.0	0.0	2.6	0.0	0.0	9.8	0.0	0.0	0.0	2.6	0.0	0.7	0.0	60.9	0.0	1.3	0.0	0.0	0.0	0.0	2.3	0.0	2.3
Ninigret	13	269	14	2896	7.1	0.0	0.0	0.0	0.0	1.5	2.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	14.1	0.4	0.4	44.2	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.4	1.9	26.0	1.1	0.4	0.0	0.0	0.0	0.0	3.0	0.0	0.7
Ninigret	14	261	15	2054	2.1	0.0	0.0	0.0	0.8	4.6	3.1	0.0	0.0	0.0	0.4	0.8	0.4	0.0	0.8	0.4	0.4	0.0	2.7	1.1	0.0	7.3	0.0	0.0	11.5	0.0	0.0	0.0	1.9	0.0	0.0	0.0	58.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4
Point Judith	1	231	15	1797	1.9	0.0	0.0	0.0	0.0	12.6	2.2	0.0	0.0	3.0	2.2	0.4	0.0	0.0	0.0	0.9	5.6	0.0	0.0	9.1	0.0	0.4	0.0	0.0	11.3	0.0	0.0	1.7	0.4	0.0	0.0	0.9	45.9	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	2.6
Point Judith	4	802	26	1766	2.3	0.0	0.0	0.0	0.5	7.0	9.6	0.2	0.0	0.0	1.9	0.1	0.0	0.1	0.0	0.7	19.6	0.1	0.2	15.8	0.0	1.2	0.0	0.0	3.4	0.0	0.2	0.0	0.4	0.4	1.5	3.7	27.4	0.4	0.4	0.0	0.1	0.9	0.2	1.9	0.0	1.9
Potter	5	286	20	1481	5.2	0.3	0.3	0.0	0.0	0.7	1.4	0.0	0.0	1.0	0.3	0.3	0.0	0.0	2.1	0.7	35.0	0.7	1.0	17.1	0.0	0.0	0.0	0.0	9.1	0.0	0.3	0.0	0.0	0.0	0.7	0.3	24.8	0.0	1.0	0.0	0.0	0.0	0.0	0.3	0.3	1.8
Potter	6	258	15	3299	7.7	0.0	0.0	0.0	0.0	2.3	0.4	0.0	0.4	0.0	0.4	0.0	0.0	1.6	11.2	0.8	0.0	0.0	0.8	2.3	0.0	0.8	0.0	0.4	3.5	0.0	0.0	0.0	0.4	0.0	0.0	0.0	70.9	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	2.7
Potter	7	1448	24	5249	2.1	0.0	0.0	0.0	0.1	2.1	17.2	0.1	0.0	0.0	0.3	0.0	0.3	0.8	1.5	44.5	3.7	0.0	0.1	5.0	0.0	1.4	0.0	0.7	4.5	0.1	0.0	0.1	0.3	0.1	1.9	0.0	12.6	0.2	1.9	0.0	0.0	0.3	0.1	0.0	0.0	0.3
Potter	8	240	16	1083	8.5	0.0	0.0	0.0	0.0	1.7	0.4	0.0	0.0	0.0	0.0	0.0	0.8	2.5	17.5	0.4	3.8	0.0	38.3	0.4	0.0	0.0	0.4	0.4	1.7	0.0	0.8	0.4	1.3	0.0	0.0	0.0	27.9	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.8
Quonochontaug	16	219	16	694	0.7	1.4	0.0	2.7	0.0	23.7	6.8	0.0	0.0	2.3	1.4	0.0	0.0	0.9	0.0	0.9	2.7	0.0	0.0	10.5	0.9	5.5	0.0	0.0	11.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.6	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.8
Quonochontaug	16A	228	17	353	2.8	0.9	0.0	0.9	0.0	8.8	0.4	0.0	0.0	2.2	2.2	0.0	0.0	2.2	0.0	1.8	5.3	0.0	0.9	13.2	0.4	0.4	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.0	2.2
Quonochontaug	18	217	16	861	5.1	0.5	0.0	0.0	0.0	6.9	0.9	0.9	0.0	0.0	0.5	0.0	0.0	0.9	0.0	0.5	10.6	0.0	0.5	22.6	0.0	0.9	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	1.4	0.0	47.5	0.0	1.4	0.5	0.0	0.0	0.0	0.0	0.0	0.9
Trustom	60	289	5	280	47.2	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.4	0.0	97.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trustom	61	188	4	260	93.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	98.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Winnapaug	19A	187	15	314	3.0	1.1	0.0	0.0	0.0	5.9	1.1	0.0	1.1	0.0	7.5	1.1	0.0	0.0	0.0	0.5	3.2	0.0	3.7	0.0	0.0	2.1	0.0	0.0	3.2	0.0	0.0	0.5	0.0	0.0	0.0	0.0	63.1	0.0	1.1	0.0	0.0	0.5	0.0	0.5	0.0	3.7
Winnapaug	19	252	20	2165	7.1	0.0	0.0	0.0	0.4	3.6	1.6	0.0	0.0	0.0	0.8	0.0	0.0	1.6	0.4	0.8	19.0	0.4	1.2	32.1	0.0	0.4	0.0	0.0	1.6	0.0	0.4	0.4	0.0	0.0	0.8	0.8	32.1	0.4	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.4
Winnapaug	21	313	18	4320	4.0	0.0	0.0	0.0	0.3	6.4	2.6	0.0	0.0	1.0	1.3	0.0	0.0	1.0	0.3	0.0	14.7	0.3	0.3	31.3	0.3	0.6	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.6	3.5	29.1	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.6
Waquoit	65	212	18	728	0.5	0.5	0.0	0.0	3.2	13.4	6.0	0.0	4.7	0.9	6.0	0.0	0.0	1.4	0.5	0.0	9.3	0.0	0.0	1.4	0.0	1.4	0.0	0.0	17.1	0.0	0.0	0.0	1.4	0.0	0.9	0.0	21.8	0.0	1.4	0.0	0.0	0.0	0.0	2.3	0.0	6.4
Jehu	66	219	16	1009	2.5	0.0	0.0	0.0	0.0	5.0	2.8	0.0	3.7	0.5	1.4	1.4	0.0	0.0	0.5	1.4	6.4	0.0	16.5	0.5	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.9	0.9	0.0	0.0	0.0	43.1	0.0	0.5	0.0	0.0	0.0	0.0	4.1	0.0	2.3
Machaug	30	212	8	212	10.1	0.0	0.0	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	2.8	0.0	23.6	0.5	0.0	0.5	0.0	0.0	2.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0	54.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7
Card's	33	33	4	430	4.2	0.0	0.0	0.0	0.0	12.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	0.0	0.0	3.0	0.0	0.0	0.0	0.0	72.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0

secchi depth. However, the shallowness of most of the sites limits the usefulness of this parameter and rather determines water depth at the site. Compilation of mean water depth (D), temperature (T), salinity (S), nitrates (N), phosphates (P) and chlorophyll *a* (Chl) for winter (w; December-January-February), summer (s; June-July-August), and September (st) for each sampling station are summarized in Table 4.

To reduce bias in interpretation of the multivariate results, environmental variables of high inter-collinearity were eliminated with the exception of one representative variable. Thus, mean monthly measurements for individual months (June, July and August) were dropped from the environmental data because of collinearity, and mean summer values were used. Data on winter water parameters, including temperature, are incomplete, but we are aware that the lagoons sampled can become ice-covered in cold winters. We selected the entire summer season and September values for statistical analysis, although values for August and February are commonly used to explain dinoflagellate cyst distribution in high latitudes (Rochon et al., 1999). Studies of temporal distribution of phytoplankton in temperate North American estuaries indicate that dinoflagellates are most abundant during the entire summer period and at the beginning of the fall (Smayda, 1980).

Statistical methods

Relationship between environmental data and dinoflagellate cyst species abundances were assessed with Canonical Correspondence Analysis (CCA), a widely used method for direct gradient analysis. It is a constrained correspondence analysis with selected environmental variables (ter Braak, 1995, 1996). The analysis is an eigenanalysis method applied to a matrix of dinoflagellate cyst data (samples-by-taxa) and, simultaneously, to a matrix of environmental data (samples-by-water quality measurements) to identify patterns of distribution and influence among species and environmental variables. Canonical Correspondence Analysis was performed using the CANOCO program (CANOCO Version 4.02, Agricultural Mathematics Group, Wageningen, the Netherlands).

Table 4. Compilation of the mean water quality parameters and the water depth for each individual sample site. Environmental parameters selected for CCA are in bold.

			Winter					Summer					September				
Lagoon	Station	**D**	T	S	N	P	Chl	**T**	**S**	**N**	**P**	**Chl**	**T**	**S**	**N**	**P**	**Chl**
Green Hill	9	1.3	2.2	11.9	26.6	0.6	0.7	21.9	20.3	0.7	0.4	3.3	18.5	20.3	0.8	0.4	2.2
Green Hill	10	1.5	3.1	21.0	14.6	0.2	1.9	22.6	18.9	3.8	0.6	5.1	20.2	21.6	2.0	0.5	3.8
Green Hill	11	0.9	N/A	N/A	N/A	N/A	N/A	22.4	20.0	5.1	0.6	4.9	19.8	19.4	4.1	0.4	6.9
Ninigret	12	2.7	4.1	24.5	0.8	0.2	8.3	22.0	23.4	0.4	0.6	7.4	19.7	24.4	0.8	0.7	10.3
Ninigret	13	1.5	5.0	31.0	6.0	1.1	2.4	20.4	26.2	2.4	0.8	5.5	18.6	25.4	3.2	0.6	3.5
Ninigret	14	1.2	N/A	N/A	N/A	N/A	N/A	23.3	21.1	1.8	0.5	6.9	20.1	21.2	2.4	0.4	11.1
Point Judith	1	1.7	5.3	30.3	1.7	0.3	1.0	19.6	28.1	0.3	0.5	1.8	18.0	28.2	1.1	0.4	2.4
Point Judith	4	5.3	N/A	N/A	N/A	N/A	N/A	19.1	28.5	0.3	0.4	2.2	19.8	30.8	0.4	0.3	2.6
Potter	5	0.7	3.0	28.7	4.0	0.7	0.7	19.7	26.8	0.7	0.8	4.7	17.2	25.5	0.7	0.7	4.4
Potter	6	1.4	N/A	N/A	N/A	N/A	N/A	21.6	26.3	1.7	0.8	13.0	18.8	26.8	3.3	0.5	16.4
Potter	7	1.8	N/A	N/A	N/A	N/A	N/A	22.8	25.7	0.9	0.9	6.6	20.5	26.6	0.8	0.7	8.1
Potter	8	1.1	N/A	N/A	N/A	N/A	N/A	22.7	26.5	1.1	0.4	5.6	18.8	27.1	1.2	0.3	5.4
Quonochontaug	16	1.9	N/A	N/A	N/A	N/A	N/A	20.5	28.0	0.5	0.9	3.8	18.7	27.5	0.3	0.6	3.8
Quonochontaug	16A	2.0	3.1	29.2	2.3	0.5	4.6	20.5	28.7	0.7	0.8	2.9	17.3	29.1	0.8	0.7	3.1
Quonochontaug	18	3.0	N/A	N/A	N/A	N/A	N/A	19.6	29.0	0.4	0.6	2.9	17.5	30.1	0.4	0.6	2.7
Trustom	60	2.3	N/A	N/A	N/A	N/A	N/A	23.0	4.0	0.3	0.2	2.2	19.0	3.0	0.0	0.4	25.4
Trustom	61	2.0	N/A	N/A	N/A	N/A	N/A	23.0	4.0	0.3	0.2	2.2	19.0	3.0	0.0	0.4	25.4
Winnapaug	19	0.9	5.0	30.0	1.7	2.2	5.5	22.9	27.6	1.2	0.7	6.2	20.9	28.2	1.6	0.4	7.8
Winnapaug	19A	0.8	1.0	26.0	8.2	0.6	1.0	22.1	26.7	1.6	1.0	20.4	18.6	27.0	3.7	0.9	9.3
Winnapaug	21	1.6	N/A	N/A	N/A	N/A	N/A	20.3	28.1	0.6	0.5	6.3	18.9	28.7	1.0	0.7	3.7
Waquoit	65	2.3	4.4	29.4	N/A	N/A	N/A	24.6	27.9	0.7	0.8	5.5	21.3	27.8	0.2	0.6	3.2
Jehu	66	2.8	3.4	27.9	N/A	N/A	N/A	23.7	28.8	0.7	N/A	7.5	20.4	28.8	0.1	N/A	N/A
Machaug	30	1.6	N/A	10.0	0.6	0.1	N/A	23.2	7.2	0.2	0.2	13.6	19.3	6.0	0.3	0.3	4.9
Card's	33	1.2	2.5	0.0	43.6	1.1	2.5	24.4	3.6	6.2	1.1	11.0	19.8	4.0	4.4	0.6	20.9
mean values	all	1.8	3.5	23.1	10.0	0.7	2.9	21.9	22.3	1.4	0.6	6.3	19.2	22.5	1.4	0.5	8.1

D - depth (m); T - temperature °C; S - salinity ; N - nitrates (μM); P - phosphates (μM); Chl - chlorophyll a (μg l^{-1}).

The relationship between dinoflagellate cyst distribution and environmental parameters was identified by species scores and their ordination patterns. Forward selection was used to identify the variables that could effectively explain the greatest amount of variance in the species data sets. The significance of each environmental variable was determined by testing the significance of the first canonical axis using Monte Carlo testing (based on 999 unrestricted permutations). On the CCA biplot, environmental variables are represented by arrows, which extend in both directions from the center although only the positive direction is shown. The arrows point in the direction of maximum variation and length of the arrows demonstrates the relative importance of each environmental variable. The center of the ordination diagram indicates the mean value for each environmental variable. The greater the angle between two environmental arrows, the less likely that they are related to one another. The projection of species scores against these arrows allows for inferences to be made about the dominant environmental factors affecting species composition (ter Braak and Prentice, 1988).

RESULTS

Dinoflagellate cysts were recovered from all the sediment samples. Total cyst concentrations range from 10^2 to 10^3 cysts cm^{-3} (Table 3). The lowest concentrations (< 300 cysts cm^{-3}) are from stations in Trustom and Maschaug Ponds, as well as Green Hill station 9. However, even these low numbers probably reflect high productivity, as sedimentation rates in these lagoons are relatively high (~0.2 cm yr^{-1}; Boothroyd et. al., 1985). The highest concentrations of dinoflagellate cysts (> 5,000 cysts cm^{-3}) occur at Potter 7 and Ninigret 12.

The ratio between cysts produced by autotrophic and heterotrophic dinoflagellates, commonly considered an indication of the dominant trophic mode and the level of primary productivity (Mudie and Rochon, 2001), ranges from 0.5 to 93.0 with a mean of 11 (Table 3). Cysts of heterotrophic dinoflagellates usually comprise less then 33% of the assemblages (Fig. 2), with the exception of Waquoit Bay (61%), Quonochontaug 16 (57%) and Green Hill 9 (52%). Both stations in Trustom Pond (60

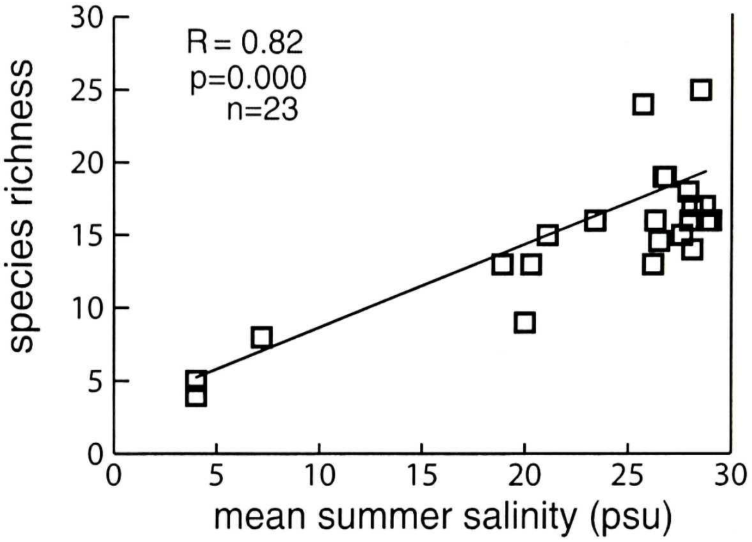


Figure 2. Relationship between species richness of dinoflagellate cyst and mean summer salinity at lagoon sample stations.

and 61) are characterized by the highest proportion of *Spiniferites* spp. (>97%), cysts produced by autotrophic dinoflagellates (Fig. 3).

The dinoflagellate cyst assemblages from the lagoons are generally diverse. A total of 40 taxa were found (Table 3). Species richness of samples ranges from 4 to 26, with an average of 15 (Table 3). There is a significant ($P<0.001$) correlation (R=0.82) between species richness and mean summer salinity (Fig. 3). Dinoflagellate cyst assemblages with the lowest cyst diversity (4 to 8 taxa) are found in low salinity (4.0 - 7.2 psu) lagoons, e.g., Trustom and Maschaug.

Distribution of dinoflagellate cyst taxa

The distribution patterns of the relative abundances of selected dinoflagellate cyst taxa (those that comprise ≥5% of at least one cyst assemblage) are shown in Figures 4-9. The following classes have been applied: present (>0-1%); rare (1-5); common (5-30%); abundant (30-50); dominant (>50%).

Cysts of ***Alexandrium tamarense*** (Fig. 4; Plate I, 1)

Remarks: The elongate to cylindrical cysts (~30 μm) contain an orange accumulation body. A mucilaginous substance with incorporated detrital particles often covers the smooth cell wall.

Occurrence: Cysts of *Alexandrium tamarense* were observed at eight stations. The abundance of *Alexandrium tamarense* varies from 4.4% in Green Hill 10 to ~0.5% in Waquoit Bay, Quonochontaug 18 and Potter 5, with values of ~1% in Ninigret 12, Quonochontaug 16 and 16A and Winnapaug 19A.

Lingulodinium machaerophorum (Fig. 5; Plate I, 4).

Remarks: Folding of the cysts prevented determination of the exact number of precingular plates involved in archeopyle formation. Cysts bear characteristic processes, striated at their bases with grana on the distal ends. Most showed fully developed processes reaching ~1/4 of the cyst diameter.

Occurrence: This species reaches a maximum abundance of 17.5% in Potter 8 and 11.2% in Potter 6. Its occurrence is rare in Potter 5, Green Hill 10 and Ninigret 12 and it is absent from Point Judith, Quonochontaug, Trustom, Maschaug and Card's.

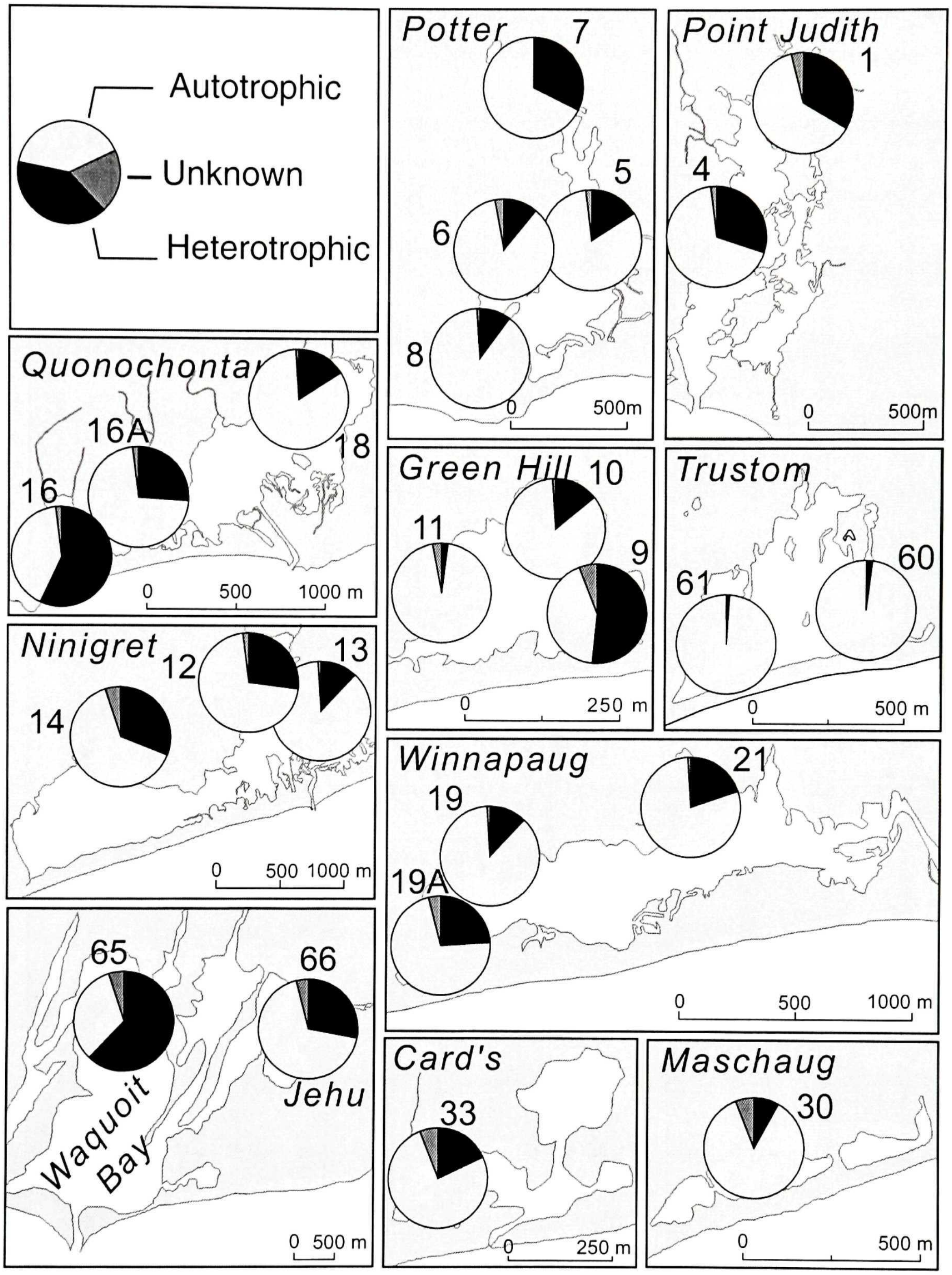


Figure 3. The relative abundance (%) of cysts of heterotrophic and autotrophic dinoflagellates in assemblages from southern New England lagoons.

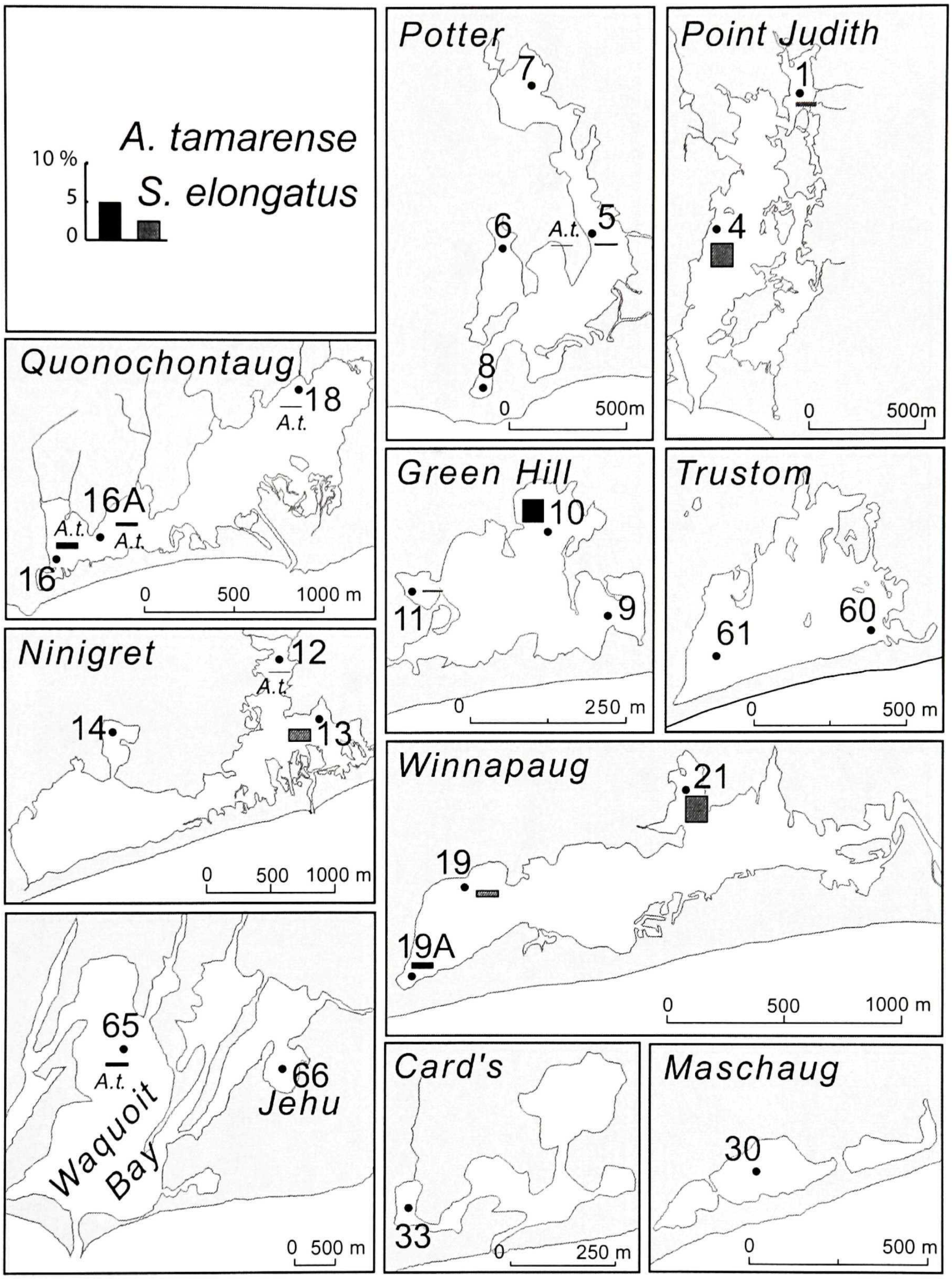


Figure 4. Abundance (%) of cysts of *Alexandrium tamarense* and *Spiniferites elongatus* at each sample station.

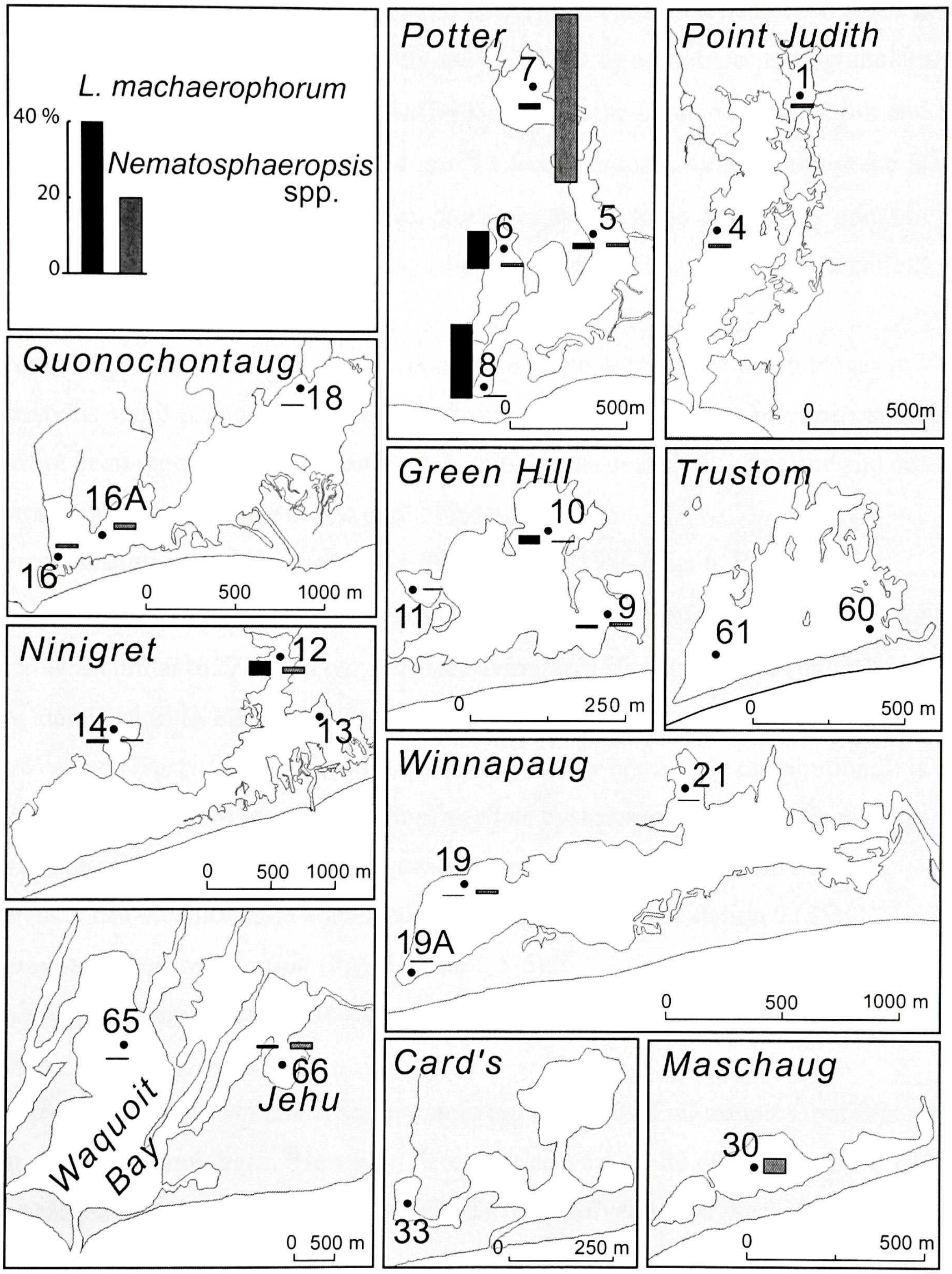


Figure 5. Abundance (%) of *Lingulodinium machaerophorum* and *Nematosphaeropsis* spp. at each sample station.

***Nematosphaeropsis* spp.** (Fig. 5; Plate I, 2-3).

Remarks: Most of the observed cysts have an ovoid to elongated body with slight apical protuberance. The cyst wall is relatively thick and can be smooth to microgranulate. Most of the observed cysts have central bodies within the range of 31 to 52 μm and a maximum process length from 9 to 14 μm (13 specimens measured). Despite the fact that the paratabulation is not expressed, processes appear to be exclusively gonal in distribution. Rod-shaped processes are solid at the base and have distal trifurcations. Trabecules are solid and threadlike.

Occurrence: *Nematosphaeropsis* spp. constitute 0.4 to 4.2% of the assemblages at ¾ of the stations and it is abundant (44.5%) at Potter station 7. *Nematosphaeropsis* species have not been reported before now in such abundances in shallow estuarine and coastal waters (Wall et al., 1977; Rochon et al., 1999).

***Operculodinium centrocarpum* sensu Wall & Dale 1966** (Fig. 6; Plate I, 7).

Remarks: Most processes of *O. centrocarpum* are well developed, beings ~9 μm long. Specimens similar to *O. centrocarpum* but having very short processes (up to 2 μm) were identified as *O. centrocarpum* var. *truncatum.*

Occurrence: *Operculodinium centrocarpum* apparently has a wide distribution. It is a common component of most of the dinoflagellate cyst assemblages with an average abundance of 7.0%. *Operculodinium centrocarpum* is absent only from Potter 6, whereas it has the maximum abundance in the same lagoon, at station 5 (35%).

Operculodinium israelianum (Fig. 6; Plate I, 5-6).

Remarks: Cysts are quite fragile and whole specimens with clearly visible archeopyles are rare.

Occurrence: *Operculodinium israelianum* is found in 2/3 of all samples, but it is rare in most of the assemblages. However, it comprises up to 23.6% and 16.5% of cyst assemblages in Maschaug and Jehu Ponds, respectively, and occurs at its highest abundance (38.3%) at Potter 8.

Cysts of *Pentapharsodinium dalei* (Fig. 6; Plate I, 8).

Remarks: These small spherical colorless cysts can be easily overlooked in slides containing large quantities of terrigenous organic material and require counting at high magnification or interference contrast microscopy.

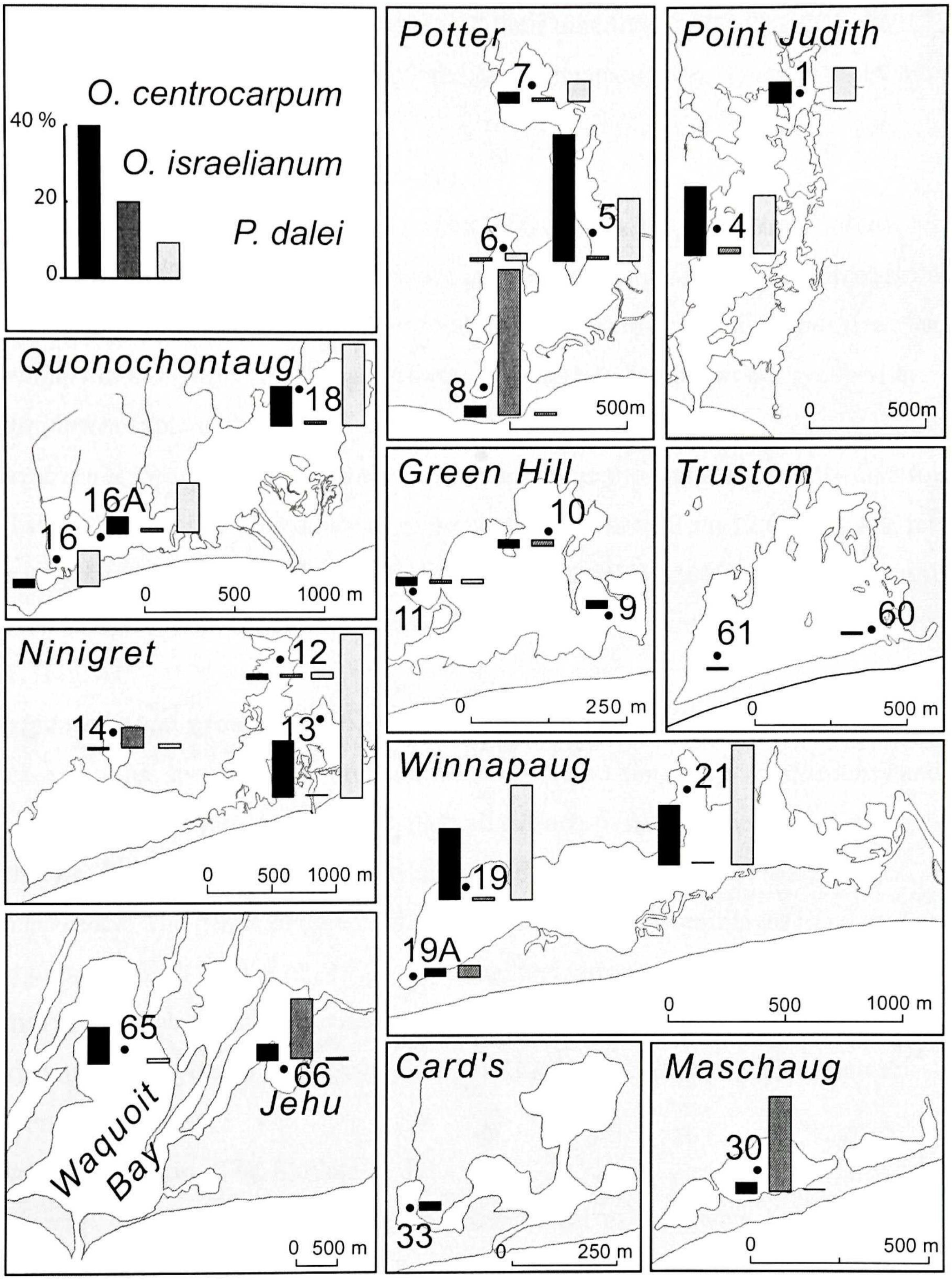


Figure 6. Abundance (%) of *Operculodinium centrocarpum* sensu Wall & Dale (1966), *Operculodinium israelianum* and cysts of *Pentapharsodinium dalei* at each sample station.

Occurrence: Cysts of *Pentapharsodinium dalei* comprise from 0.4 to 32.1% of the assemblages, averaging of 8.8%, and reach their maximum of 44.2% at Ninigret 13. This species is absent at Green Hill 9 and 10, Winnapaug 19A, Trustom and Card's Ponds.

***Spiniferites* group** (Fig. 7; Plate I, 9-12).

Remarks: *Spiniferites* species show a great deal of variation in the size, process length and development as well as the presence and absence of paratabulation. Because of the great morphological variations, *Spiniferites* species were grouped as *Spiniferites* spp. *Spiniferites elongatus* (Plate II, 1) was easy to identify and it was not grouped in *Spiniferites* spp.

Occurrence: *Spiniferites* spp. is the most abundant group and it is the only taxa found in all sites. The relative abundance of *Spiniferites* spp. varies from 12.6 to 98.4%, reaching its maximum in Trustom 60 and 61 assemblages. *Spiniferites elongatus* occurs only in seven samples, with a maximum abundance of ~3.5% in Point Judith 4 and Winnapaug 21 (Fig. 4).

***Brigantedinium* group** (Fig. 8).

Remarks: This species group includes *Brigantedinium simplex*, *B. cariacoense* and all spherical brown cysts having a smooth wall surface. Where species identification was possible, *B. simplex* was more abundant than *B. cariacoense* in the assemblages.

Occurrence: The genus *Brigantedinium* often dominates assemblages in coastal and estuarine waters (Wall et al., 1977; de Vernal and Giroux, 1991; Rochon et al., 1999), but it is never abundant in our samples. However, it occurs in all samples except Trustom 61, varying in abundance from 5.1 to 29.2%. It reaches a maximum at Quonochontaug 16.

***Dubridinium* spp.** (Fig. 8; Plate II, 3).

Remarks: This group includes brown subspherical to somewhat lenticular cysts with well-developed cingular lists. A theropylic archeopyle is rarely observed. Phragma typically consists of two layers; a thick smooth endophragm and a thin granular periphragm. The apical pore complex is clearly seen.

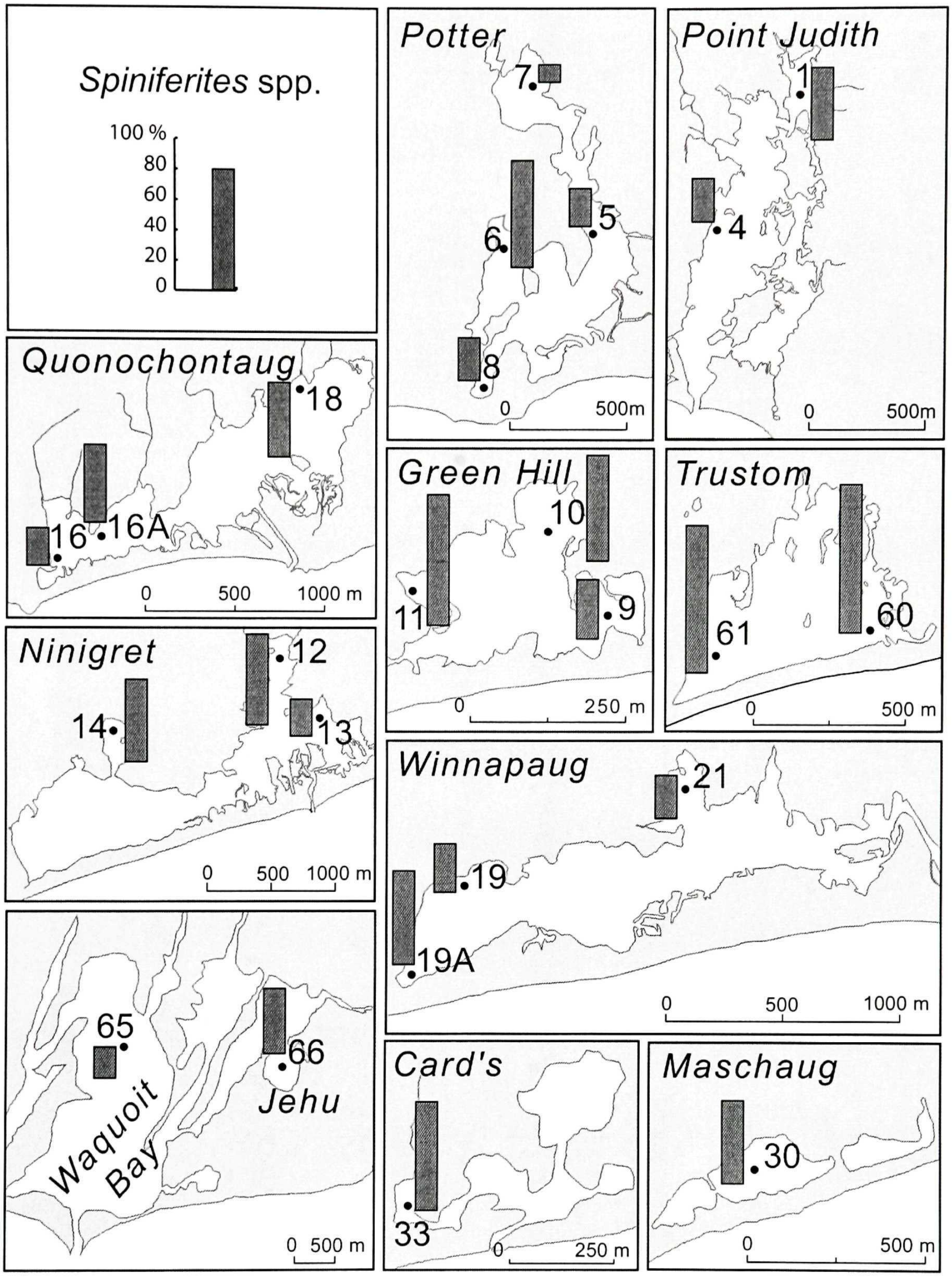


Figure 7. Abundance (%) of *Spiniferites* spp. at each sample station.

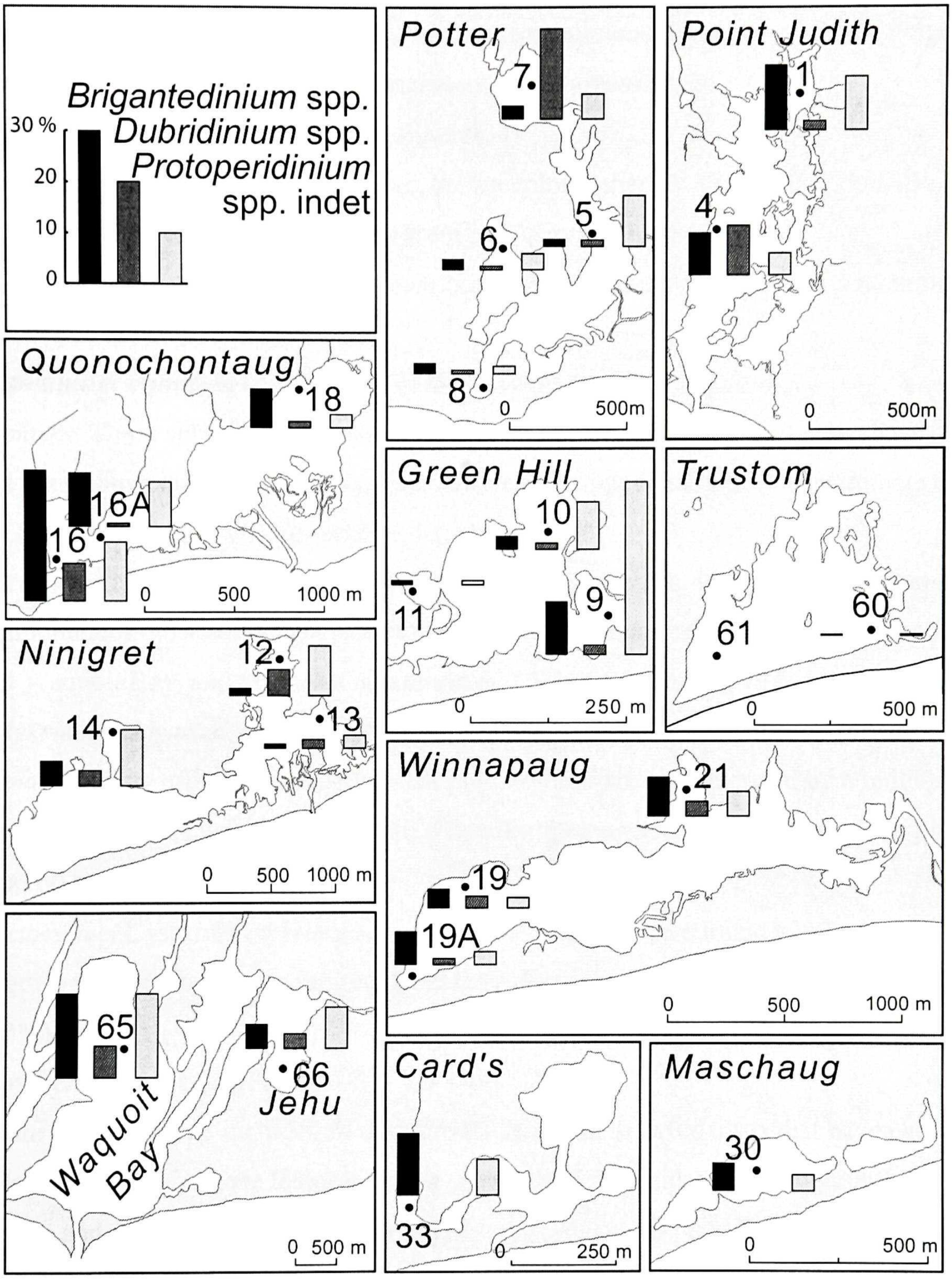


Figure 8. Abundance (%) of *Brigantedinium* spp., *Dubridinium* spp. and *Protoperidinium* spp. indet. at each sample station.

Occurrence: *Dubridinium* spp. is only common in Ninigret 12, Point Judith 4, Quonochontaug 16 and Waquoit Bay with a maximum abundance of 17.2% in Potter 7. Elsewhere it is at best only a rare component in the assemblages.

Islandinium brevispinosum (Fig. 9; Plate II, 4).

Remarks: The characteristic small size, brown color, spherical shape, smooth wall surface and numerous solid spines prevent confusion with other species.

Occurrence: *Islandinium brevispinosum* occurs only in four samples, with a maximum abundance of 4.7% in Waquoit Bay.

Islandinium minutum (Fig. 9; Plate II, 5).

Remarks: These spherical, brownish cysts are characterized by a granulate wall surface, and numerous randomly dispersed processes terminating distally in fine acuminate tips. No cysts with clearly visible archeopyles were found.

Occurrence: This species is rare or absent in ¾ of all samples. It is, however, a common component of the assemblages from Quonochontaug 16 and 16A, Point Judith Pond, and Waquoit Bay, and reaches a maximum of 7.5% at Winnapaug 19A.

Polykrikos schwartzii (Fig. 9; Plate II, 6) ***& P. kofoidii.***

Remarks: Cysts of *Polykrikos schwartzii* & *P. kofoidii* are characterized by a reticulate surface structure. Cysts vary widely in shape, from elongated to ovoid, and in length from 60 to 120 μm.

Occurrence: Cysts of *Polykrikos schwartzii* & *P. kofoidii* were found in 17 of 24 samples with an abundance ranging from 0.4% to a maximum of 7.3% in Ninigret 14 (7.3%).

***Protoperidinium* type** (Fig. 8).

Remarks: This group includes all dark brown spherical to ovoid cysts that have neither processes nor archeopyle features visible. Cysts have a granular to micro granular wall surface and range in size from 30-60 μm.

Occurrence: Cysts occur at all stations except Trustom 61. The average abundance of *Protoperidinium* type is ~7%, with a maximum of 33.6% in Green Hill 9.

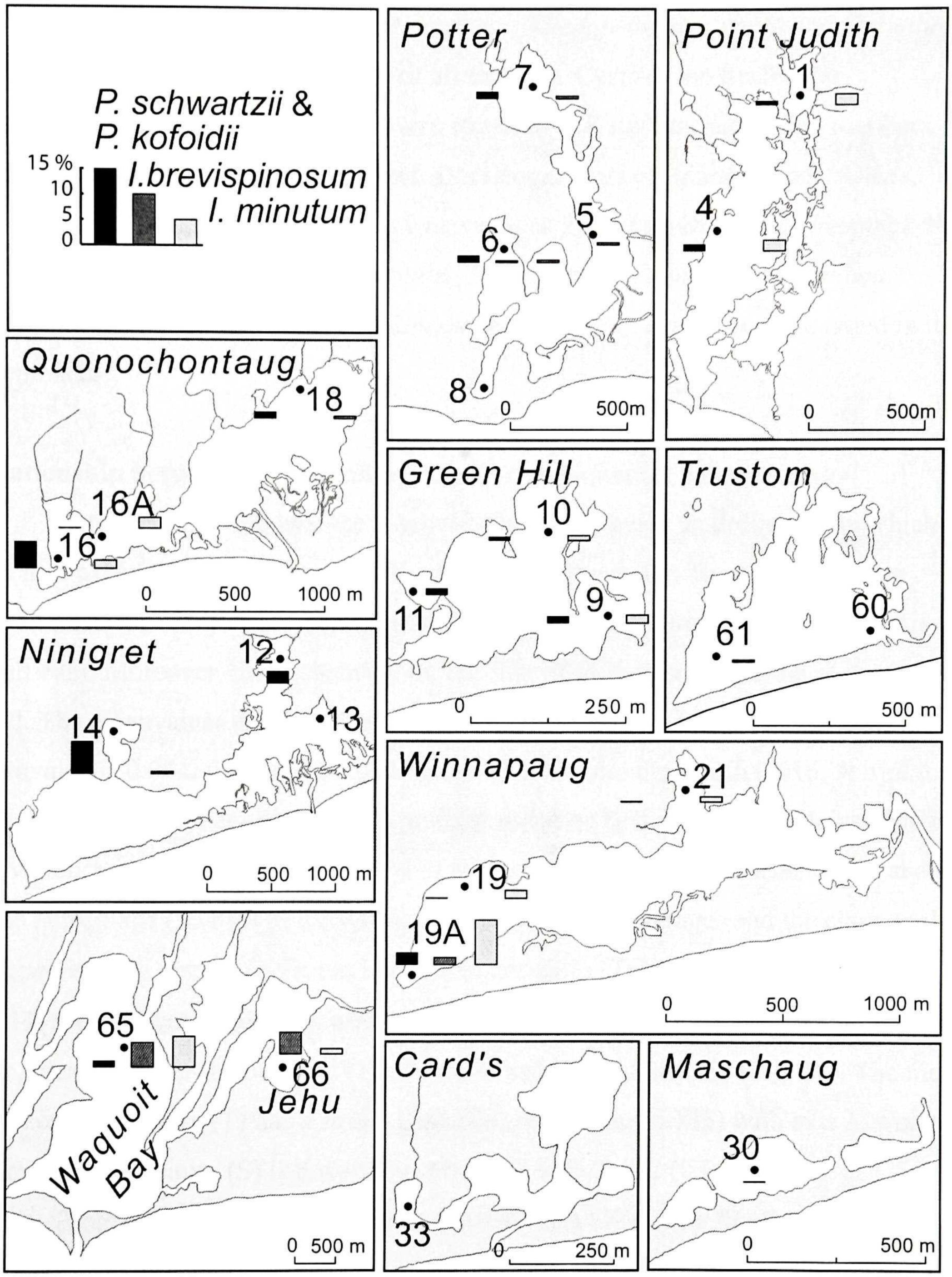


Figure 9. Abundance (%) of cysts of *Polykrikos schwartzii* & *P. kofoidii*, *Islandinium brevispinosum* and *Islandinium minutum* at each sample station.

Rare cysts *Tectatodinium pellitum*, *Gymnodinium* spp., *Islandinium*? *cezare*, *Lejeunacysta sabrina*, *Quinquecuspis concreta*, *Selenopemphix quanta* and *Stelladinium stellatum* were found in less than 1/2 of all samples. Cysts of the freshwater dinoflagellate *Peridinium limbatum* were recorded at 8 stations and in low numbers, with a maximum of 3% in Card's Pond. Occasional cysts of *Ataxiodinium choane*, *Impagidinium* spp., *Tuberculodinium vancampoae*, *Lejeunecysta oliva*, *Pheopolykrikos hartmannii*, *Protoperidinium americanum*, *P. oblongum*, *P. minutum*, *P. nudum*, *Trinovantedinium applanatum*, *Votadinium calvum* and *V. spinosum* were noted in the assemblages.

Relationship between the assemblages and environmental parameters

Canonical Correspondence Analysis (CCA) produced an ordination in which the first four axes (Table 5) are statistically significant (P = 0.03). These probabilities indicate that the relationship between the species and the environmental variables is significant. Moreover, the probability for the first CCA axis is significant at the 0.5% level. The eigenvalues measure the importance of each of the CCA axis. The first eigenvalue is 0.044, the second 0.024, the third 0.017 and the fourth 0.016. A triplot of samples, species and environmental variables based on first two axes explains 28% of the variance in the species data, 50.8% of the variance in the fitted species data, and the same percentage (50.8%) of the variance in the weighted averages and the class totals of the species with respect to the environmental variables (Table 5). However, only two of the 11 environmental variables were significantly correlated ($P \leq 0.01$) with the CCA axes, mean summer temperature (T) and mean summer salinity (S) (Fig. 10). The mean summer temperature (T) has a strong negative correlation (-0.735) with axis 1, whereas, mean summer salinity (S) is positively correlated with axis 2 (0.668).

Table 6 shows each species cumulative fit in a CCA. The fit of *Pentapharsodinium dalei* in a CCA ordination diagram of the first axes, correlated with mean summer temperature, is the highest (72%), followed by *Spiniferites elongatus* (39%) and *Operculodinium israelianum* (29%). The first two species are known to indicate cool marine waters (Dale, 1996; Rochon et al., 1999), whereas *Operculodinium*

Table 5. Eigenvalues for CCA axes 1 to 4, *P* values for the significance tests of the first and all four CCA axes, species-environment (spp.-env.) correlations and cumulative percent species-environment variation.

	CCA axes				
CCA	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalues	0.044	0.024	0.017	0.016	
P-value	0.005				0.030
Species-environment correlations:	0.972	0.936	0.799	0.861	
Cumulative % species data	18.1	28	34.9	41.5	
Cumulative % spp.-env. variation	32.9	50.8	63.5	75.4	

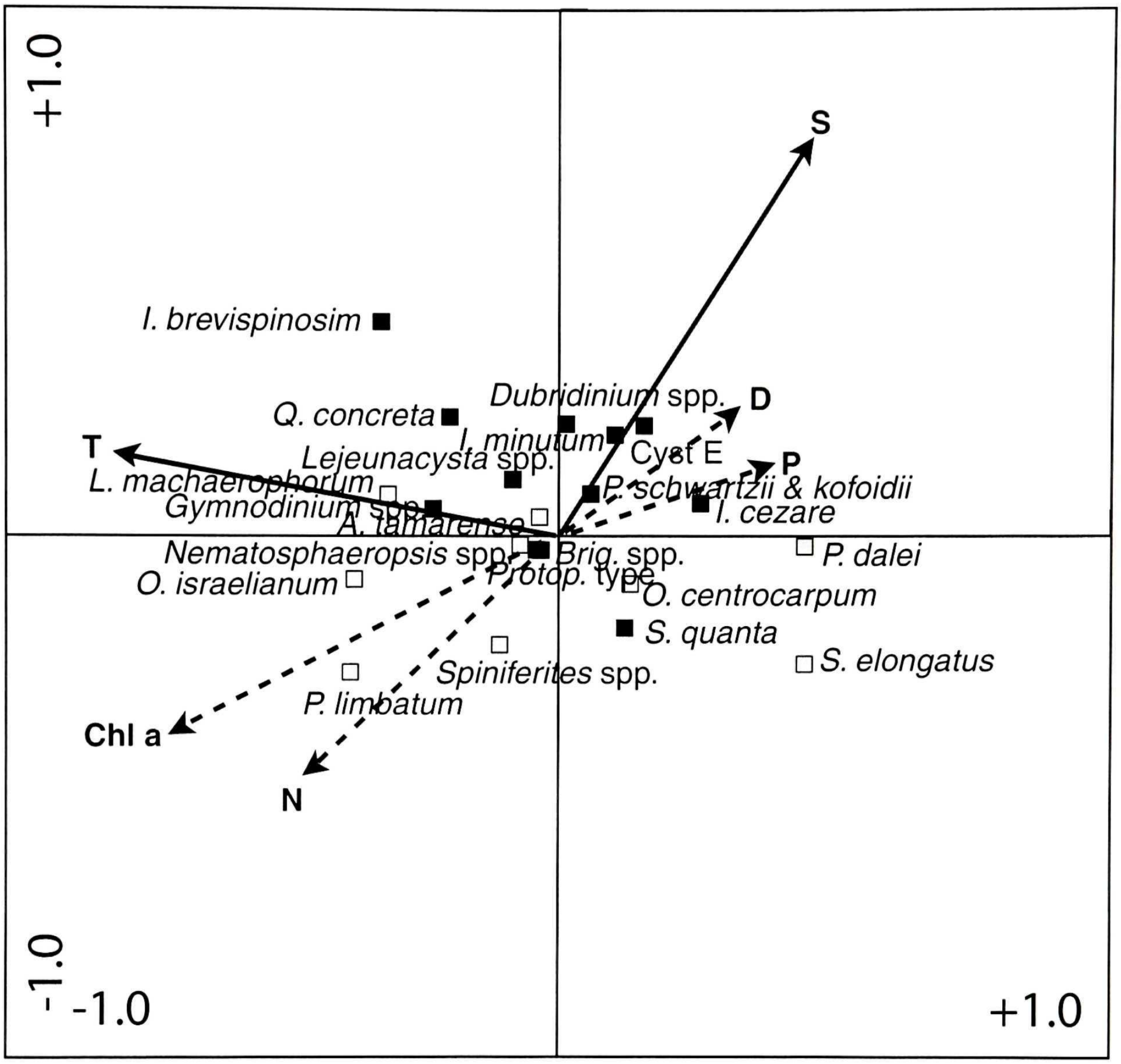


Figure 10. Ordination diagram generated from canonical correspondence analysis (CCA), showing results for axes 1 (horizontal) and 2 (vertical). The length of arrows (which represent environmental variables) indicates the importance of that variable in explaining the dinoflagellate cyst distribution. Solid arrows represent forward-selected variables and dashed arrows represent non-significant environmental variables. The direction of the arrows shows approximate correlation to the ordination axes. The abbreviations of the environmental variables are: T - mean summer temperature; S - mean summer salinity; N - mean summer nitrates; P - mean summer phosphates; Chl a - mean summer chlorophyll a; D - depth.

Table 6. Cumulative fit per dinoflagellate cyst species (selected taxa) as fraction of variance of species.

	CCA axes				
Cyst taxa	Axis 1	Axis 2	Axis 3	Axis 4	%EXPL
Alexandrium tamarense	0.00	0.01	0.31	0.32	48
Brigantedinium spp.	0.01	0.02	0.04	0.05	41
Dubridinium spp.	0.18	0.52	0.52	0.54	65
Islandinium brevispinosum	0.20	0.51	0.60	0.64	73
Islandinium ? cezare	0.19	0.20	0.21	0.22	48
Islandinium minutum	0.00	0.23	0.23	0.24	33
Gymnodinium spp.	0.16	0.17	0.31	0.32	54
Lejeunecysta spp.	0.02	0.06	0.26	0.39	53
Lingulodinium machaerophorum	0.18	0.19	0.23	0.29	46
Nematosphaeropsis spp.	0.02	0.02	0.02	0.04	14
Operculodinium centrocarpum	0.20	0.30	0.31	0.32	47
Operculodinium israelianum	0.29	0.30	0.42	0.53	61
Pentapharsodinium dalei	0.72	0.72	0.73	0.86	90
Polykrikos kofoidii & P. schwartzii	0.02	0.04	0.05	0.12	27
Protoperidinium spp. indet	0.03	0.04	0.09	0.10	36
Peridinium limbatum	0.25	0.37	0.37	0.39	53
Quinquecuspis concreta	0.12	0.27	0.30	0.38	53
Selenopemphix quanta	0.04	0.13	0.16	0.37	47
Spiniferites elongatus	0.39	0.50	0.65	0.65	76
Spiniferites spp.	0.12	0.60	0.60	0.79	90
Tectatodinium pellitum	0.07	0.33	0.36	0.36	60
Cyst type E	0.03	0.13	0.31	0.37	45

%EXPL - the percentage fit by all environmental variables together.

israelianum is most abundant in warm lagoonal waters (Wall et al., 1977; Morzadec-Kerfourn, 1989). The species with the highest fit for the second axis, representing summer salinity, are *Spiniferites* spp., *Dubridinium* spp., *Islandinium brevispinosum* and *Peridinium limbatum*. The percentage fit by all environmental variables together, given in the last column Table 6, shows that given environmental factors can explain >50% of the distribution of *Spiniferites* spp., *Pentapharsodinium dalei*, *Islandinium brevispinosum*, *Dubridinium* spp. and *Operculodinium israelianum*. Environmental range (mean summer temperature, salinity, nitrates and phosphates) for individual cyst taxa is summarized in Table 7.

Nematosphaeropsis spp. has the lowest cumulative fit (14%) by all environmental variables together (Table 6). The unusually high proportion (44.5%) of *Nematosphaeropsis* spp. in the assemblages is found in Potter 7. We assume that this abnormal abundance of *Nematosphaeropsis* spp. in Potter 7 indicates a bloom event caused by an abrupt environmental change not detected in our environmental measurements. Indeed, when this site is removed from the CCA analyses the fit of *Nematosphaeropsis* spp. in a CCA ordination increases up to 37%.

DISCUSSION AND CONCLUSIONS

There are few published works focussed on dinoflagellate cysts in estuarine environments. We can find no studies of variability in cyst distribution on similar scales on the temperate coasts of the western Atlantic with which to compare our results. Previous studies of spatial distribution of dinoflagellate cysts in the St. Lawrence Estuary (de Vernal and Giroux, 1991), Baffin Bay (Mudie and Short, 1985), Australian (McMinn, 1989; 1990; 1991), Japanese (Matsuoka, 1992) and Spanish (Blanco, 1995) estuaries as well as the global surveys by Wall et al. (1977) and Harland (1983) show cyst concentrations of the same order of magnitude and species richness comparable to our study.

We have found that relatively low cyst concentrations (<430 cysts cm^{-3}) characterize lagoons with salinity below 10 psu. Such low concentrations can be explained by low dinoflagellate production in these environments, as few species

Table 7. Tolerance limits (mean summer temperature, salinity, nitrates, phosphates) for individual cyst taxa in New England lagoons and worldwide. *Worldwide data based on Marret and Zonneveld (in press); ** from Pospelova and Head (2002). Bold indicates the extension of the tolerance limits.

	Temperature (°C)				**Salinity**				**Nitrates (µM)**				**Phosphates (µM)**			
	Lagoons		Worldwide*		Lagoons		Worldwide*		Lagoons		Worldwide*		Lagoons		Worldwide*	
Cyst taxa	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max
Alexandrium tamarense	19.6	24.6	-0.5	27.0	**18.9**	29.0	20.5	35.5	0.4	3.8	0.1	7.50	0.6	**0.9**	0.2	0.8
Brigantedinium spp.	19.1	24.6	-2.0	29.5	**3.6**	29.0	17.0	37.0	0.2	6.2	0.1	23.50	0.2	1.1	0.1	1.8
Dubridinium spp.	19.1	24.6	N/A	N/A	18.9	29.0	N/A	N/A	0.3	3.8	N/A	N/A	0.4	1.0	N/A	N/A
*Islandinium brevispinosum***	21.6	24.6	23.0	25.0	27.0	28.8	27.0	31.0	0.7	1.7	N/A	2.00	0.7	0.8	N/A	1.7
Islandinium ? cezare	19.6	**22.0**	-2.0	19.0	23.4	28.7	21.5	35.5	0.3	0.7	0.1	7.00	0.5	0.9	0.1	1.1
Islandinium minutum	19.1	24.6	-2.0	27.5	**4.0**	29.0	21.5	35.5	0.3	3.8	0.1	21.00	0.2	1.0	0.1	1.5
Gymnodinium spp.	19.1	23.7	N/A	N/A	21.1	28.8	N/A	N/A	0.3	1.8	N/A	N/A	0.4	0.8	N/A	N/A
Lejeunecysta spp.	19.1	24.6	N/A	N/A	18.9	29.0	N/A	N/A	0.3	3.8	N/A	N/A	0.4	1.0	N/A	N/A
Lingulodinium machaerophorum	19.7	24.6	-1.5	29.0	18.9	28.8	17.0	37.0	0.4	3.8	0.2	8.0	0.4	**1.0**	0.2	0.7
Nematosphaeropsis spp.	19.1	23.7	-2.0	29.5	**7.2**	29.0	16.5	37.0	0.2	5.1	0.1	23.0	0.2	1.0	0.1	1.7
Operculodinium centrocarpum	19.1	24.6	-2.0	29.5	**3.6**	29.0	16.0	37.0	0.2	6.2	0.1	23.0	0.2	1.1	0.1	1.6
Operculodinium israelianum	19.1	23.7	1.5	29.0	**7.2**	29.0	26.0	37.0	0.2	5.1	0.1	20.0	0.2	1.0	0.1	1.7
Pentapharsodinium dalei	19.1	24.6	-2.0	29.5	**7.2**	29.0	21.5	36.7	0.2	5.1	0.1	23.0	0.2	1.0	0.1	1.4
Polykrikos kofoidii & *P. schwartzii*	19.1	24.6	-1.0	27.5	**7.2**	29.0	28.5	37.0	**0.2**	5.1	0.5	7.5	0.2	**1.0**	0.1	0.7
Protoperidinium spp. indet	19.1	24.6	N/A	N/A	3.6	29.0	N/A	N/A	0.2	6.2	N/A	N/A	0.2	1.1	N/A	N/A
Peridinium limbatum	19.6	24.4	N/A	N/A	3.6	28.8	N/A	N/A	0.2	6.2	N/A	N/A	0.2	1.1	N/A	N/A
Quinquecuspis concreta	19.1	24.6	N/A	N/A	21.1	28.8	N/A	N/A	0.3	1.8	N/A	N/A	0.4	0.9	N/A	N/A
Selenopemphix quanta	19.1	24.6	-2.0	29.5	**4.0**	29.0	17.0	37.0	0.3	5.1	0.1	13.5	0.2	1.0	0.1	1.2
Spiniferites elongatus	19.1	22.4	-2.0	26.7	**20.0**	28.5	21.5	36.5	0.3	5.1	0.1	7.5	0.4	1.0	0.1	1.2
Spiniferites spp.	19.1	24.6	N/A	N/A	3.6	29.0	N/A	N/A	0.2	6.2	N/A	N/A	0.2	1.0	N/A	N/A
Tectatodinium pellitum	19.1	24.6	14.5	29.5	**23.4**	29.0	33.0	37.0	0.3	2.4	0.2	7.6	0.4	**0.8**	0.1	0.7

tolerate salinity below 20 psu (Dale, 1996). However, sediment samples from low salinity sites often contained abundant organic detritus that would dilute dinoflagellate cyst concentrations.

Some investigators (Wall et al., 1977; Dale 1996; Ellegaard, 2000; Mudie and Rochon) also have noted that oligohaline environments are characterized by low species diversity (≤8 taxa) and cyst assemblages mainly dominated by the *Spiniferites* group, similar to our results. *Spiniferites* spp., the dominant group in most of our samples, occurs throughout a wide range of salinity reaching its maxima at low salinity sites. In addition, dinoflagellate cyst assemblages at low salinity stations contain ≤8 taxa, approximately half that found in the lagoons with >10 psu waters. The latter are characterized by generally abundant and more diverse (≥10 taxa) cyst assemblages.

The novelty of our results is in the quantitative analysis of the environmental factors controlling the composition and distribution of dinoflagellate cyst assemblages in the lagoons. With the help of CCA, we identify temperature and salinity as the main environmental factors affecting the distribution of dinoflagellate cysts in the New England lagoons. The CCA reveals that variation in temperature has the largest impact on the composition of the dinoflagellate cyst assemblages, but the concentration of nutrients shows no clear correlation with dinoflagellate cyst assemblages.

Nitrogen is generally considered to be a limiting nutrient for phytoplankton production in estuarine waters (Boynton et al., 1982) and an important factor for dinoflagellate development (Taylor, 1987), yet nitrates are not found as a significant factor in the composition of dinoflagellate assemblages in our lagoons. This may be because nitrate measurements do not reflect the total nitrogen availability. Marine phytoplankton preferentially take up ammonium over nitrate (Valiela, 1995). Thus, various nitrogen compounds need to be measured for future evaluations of the relation between dinoflagellate cysts and environmental factors in estuarine systems. In fluvially dominated estuaries covariance between nutrients and salinity is always a problem. In our lagoons these two parameters are covariant, but not significantly. The major input of nitrogen to the lagoons is domestic sewage discharged to groundwaters, the latter is the main source of freshwaters to the lagoons. Indeed, the CCA points the mean summer salinity (S) and the mean summer nitrates (N) in the opposite directions (Fig.

10) indicating that they are negatively but not significantly correlated. An extension of this data set would provide an opportunity to examine separate impacts of these parameters on dinoflagellate cyst distribution without the complication of covariance.

The CCA reflects the environmental "preferences" of dinoflagellate cysts taxa deduced from studies of dinoflagellate cyst distributions in marine and oceanic environments (Wall et al., 1977; Morzadec-Kerfourn, 1989; Edwards and Andrle, 1992; Dale, 1996; Rochon et al., 1999). In particular, *Operculodinium israelianum*, *Islandinium brevispinosum*, and *Dubridinium* spp. have a positive relationship to temperature, whereas *Pentapharsodinium dalei*, *Spiniferites elongatus*, and *Operculodinium centrocarpum* have a negative relationship relationship to temperature. The CCA also shows a negative relation between salinity and *Peridinium limbatum* and *Spiniferites* spp., as expected from their predominance in Trustom, Maschaug and Card's Ponds, all low salinity lagoons. *Peridinium limbatum* is a freshwater species (Evitt and Wall, 1968) and *Spiniferites* spp. is the most abundant taxon in temperate low salinity environments (Wall et al., 1977). In addition, other dinoflagellate cysts encountered in lagoons with low salinity are *Brigantedinium* spp., *Protoperidinium* spp., and *Operculodinium israelianum*. *Dubridinium* spp. and *Islandinium brevispinosum* were found at the sites with the highest salinity. A salinity of ~27 psu is the lowest tolerance limit for *Islandinium brevispinosum* (Pospelova and Head, 2002).

More important than statistical confirmation of species preferences, our results demonstrate that variability in temperature and salinity is reflected even at the small spatial scales that characterize lagoons. Thus, dinoflagellate cyst assemblages can be used for the paleoreconstruction of water temperature and salinity on scales relevant to estuaries, as well as marine systems. However, in contrast to marine environments reconstruction of environmental parameters cannot be used directly for paleoclimatic interpretations in lagoons. This is because both temperature and salinity in lagoons are primarily controlled by the flushing rate, which in turn depends on the nature of the inlets connecting lagoons to the ocean. Waters in lagoons without permanent inlets have longer residence time resulting in lower salinity and higher temperature, exemplified by Trustom, Maschaug and Card's Ponds (Table 4). Lagoons with permanent, large, stabilized inlets such as Point Judith and Quonochontaug Ponds have a dominating marine influence thus high salinities and the low temperatures (Table 4).

Changes in the inlet characteristics should affect the dinoflagellate population as well as the phytoplankton population in general. Temporal variations in the dinoflagellate cyst assemblages from shallow estuarine systems may primarily reflect changes in local hydrodynamics that cause (possibly large) fluctuations in water temperature and salinity, rather than climatic changes. To this end, it will be useful to investigate past dinoflagellate cyst records in some lagoons such as Point Judith or Potter Pond prior to the construction of permanent inlets to see if such a change is indeed reflected in the assemblages.

Our conclusion that dinoflagellate cyst distributions in the lagoons are correlated with water conditions are further supported by the patterns of variability within the same estuary. In addition to the differences in hydrological characteristics between the lagoons there is a substantial spatial variability in water quality parameters within each particular system. Water temperatures in the peripheral parts of the lagoons are generally warmer during the summer and most likely are colder during the winter. For example, the environmental parameters in Potter Pond vary among stations; notably the mean summer temperature varies by as much as 3.1°C, with the coolest waters near the inlet. This variability of water quality is commonly observed in estuarine waters, and deemed responsible for the heterogeneous distribution of estuarine phytoplankton (Smayda, 1980), and dinoflagellates in particular. Our study shows that even within the same lagoon the dinoflagellate cyst assemblages can widely vary between different stations. In Potter Pond *Operculodinium centrocarpum* constitutes (35%) dinoflagellate cyst assemblage at station 5, *Spiniferites* spp. (71%) at station 6, *Nematosphaeropsis* spp. (45%) at station 7 and *Operculodinium israelianum* (38%) at station 8. On the other hand, dinoflagellate cyst assemblages are relatively homogenous between stations in Trustom and Point Judith Ponds, where the environmental parameters such as temperature and salinity vary little between the stations. Our observation of heterogeneous pattern of dinoflagellate cyst distribution is consistent with the results of a similar study along the Spanish coast (Blanco, 1995) but differs from the conclusion drawn by McMinn (1990; 1991) who studied Australia estuaries. Although McMinn

(1991) stated that cyst distribution was homogeneous within a single system, careful inspection of his assemblage data (see Appendix 1) indicates that some of the lagoons are characterized by a high degree of heterogeneity. For example, the relative abundance of *Operculodinium centrocarpum* ranges 0-100%, *Operculodinium israelianum* 0-20%, *Selenopemphix quanta* 0-14% and *Lejeunacysta sabrina* 0-25% in the assemblages collected from Lake Macquarie, a lagoon in New South Wales. On the other hand, in Tuggerah Lakes dinoflagellate cyst assemblages are more similar between the sites. Unfortunately, it is not possible to tie the heterogeneous pattern of dinoflagellate cyst distribution in Lake Macquarie and the homogeneous pattern in Tuggerah Lakes to the water quality parameters, as these measurements are not provided in the paper.

In marine and oceanic studies the proportion of cysts of heterotrophic dinoflagellates has been suggested as an indicator of nutrient availability due to increasing shore proximity or presence of upwelling zones (Wall et al., 1977; Bujak, 1984; Mudie, 1992; Harland et al., 1998, Dale, 1996; Mudie and Rochon, 2001). Mudie and Rochon (2001) consider this is an indication of the dominant trophic mode and the level of primary productivity. The proportion of heterotrophic dinoflagellates is correlated with the availability of preferred prey such as diatoms and microflagellates, in turn influenced by environmental factors. Generally, the proportion of the cysts of heterotrophic dinoflagellates in the assemblages within each lagoon tends to increase with the distance from the inlet (Fig. 3), except in lagoons without permanent inlets. The distance from sample stations to the inlets is an important parameter reflecting the degree of the lagoonal water exchange with the ocean, whereas lagoons without permanent inlets have no such a gradient. We suspect that the variance in the proportion of cyst of heterotrophic dinoflagellates may be related to the differences in the water residence time. However, the ecology of heterotrophic dinoflagellates in estuarine systems is complex and needs further studies.

Plate I. Photomicrographs are bright field images. Scale bar, 20 μm.

1. Cyst of *Alexandrium tamarense*, Potter Pond 5, MGU 982, slide 1, K44/3, optical section, mid focus showing protoplasm within cysts.

2-3. *Nematosphaeropsis* spp., Point Judith Pond 1, MGU 1247, slide 1, D41/1, ventral view, upper (2) and mid (3) focus.

4. *Lingulodinium machaerophorum*, Potter Pond 5, MGU 982, slide 1, P44/3, orientation unknown, mid focus showing protoplasm within cysts.

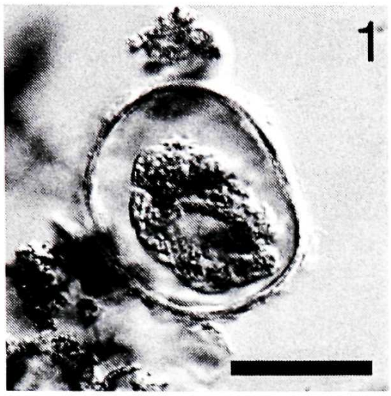
5-6. *Operculodinium israelianum*, Potter Pond 8, MGU 985, slide 1, R31/3, lateral view, upper (5) and low (6) foci.

7. *Operculodinium centrocarpum* sensu Wall & Dale 1966, Potter Pond 7, UQAM 1300-5, slide 1, T38/3, orientation unknown, low focus.

8. Cyst of *Protoperidinium dale*, Potter Pond 7, MGU 1300-5, slide 1, V43/2, orientation unknown, upper focus.

9-12. Cysts of *Spiniferites* group (9. Quonochontaug Pond 16A, MGG 1235, slide 1, lateral view, upper focus; 10.Trustom Pond 60, MGU 1300-6, slide 2, lateral view, upper focus; 11. Ninigret Pond 14, MGU 1246, slide 3, lateral view, upper focus; 12. Trustom Pond 61, MGU 1091, slide 1, optical section.

PLATE I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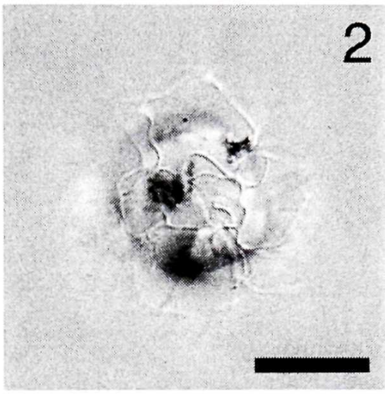
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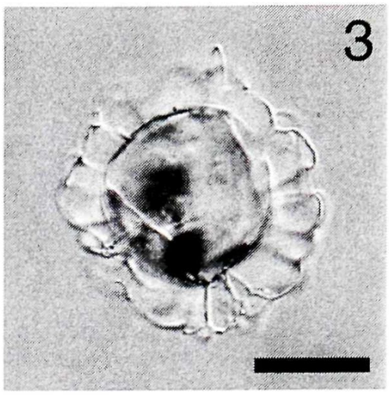
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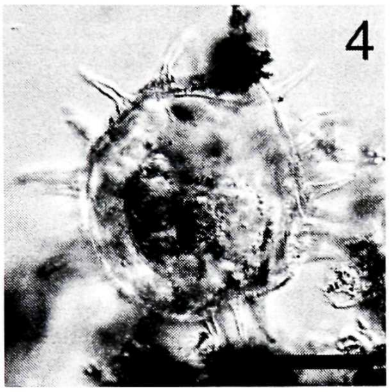
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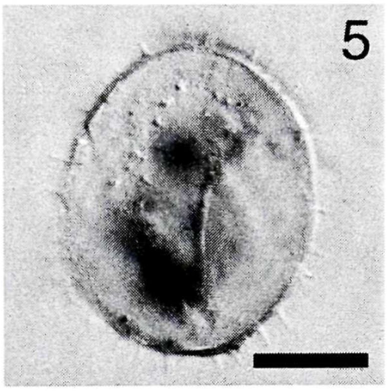
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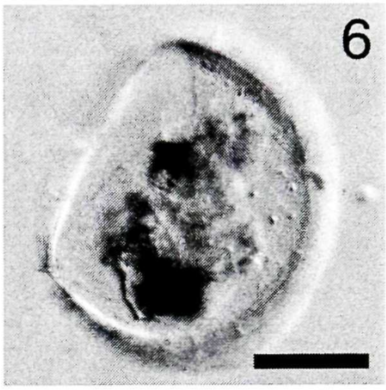
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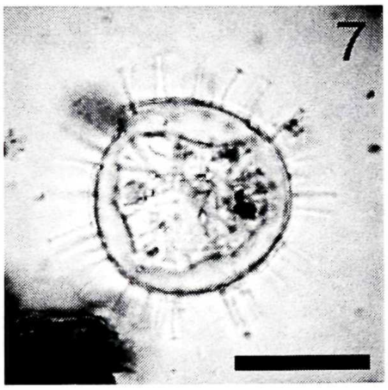
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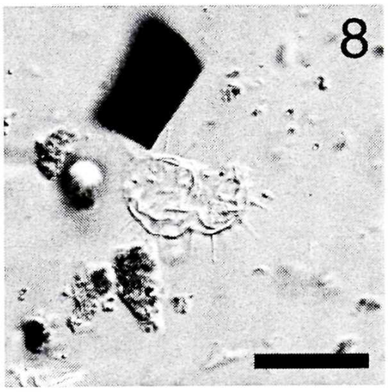
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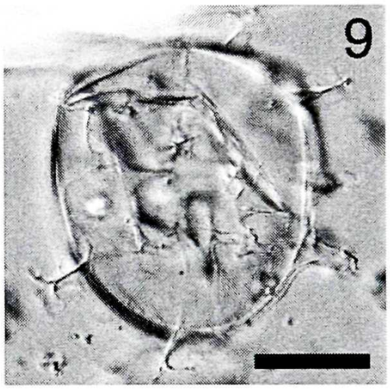
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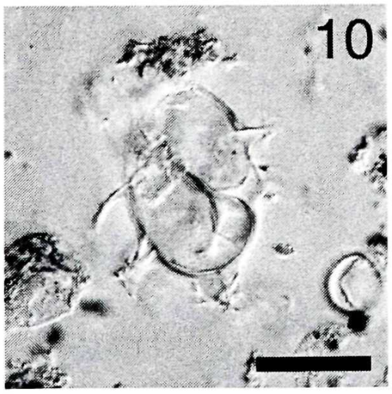
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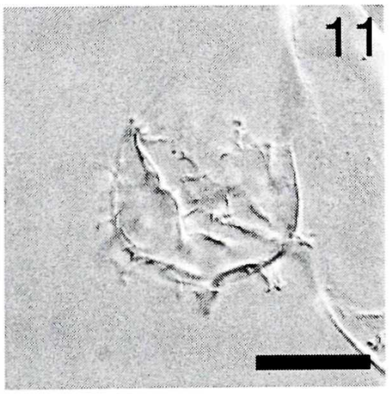
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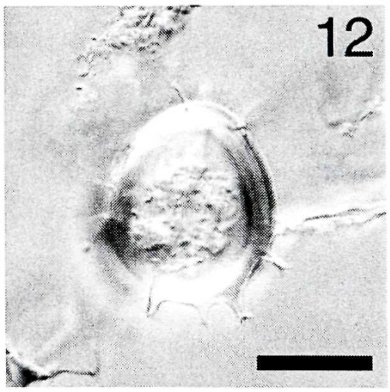
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Plate II. Photomicrographs are bright field images. Scale bar, 20 µm.

1. *Spiniferites elongatus*, Winnapaug Pond 19, MGU 1300-4, slide 2, R30/0, ventral view, upper focus.

2. *Tuberculodinium vancampoae*, Point Judith Pond 4, MGU 1300-2, slide 2, antapical surface, low focus.

3. *Dubridinium* spp., Potter Pond 7, MGU 1300-5, slide 1, O37/1, apical view, upper focus.

4. *Islandinium brevispinosum*, Winnapaug Pond 19A, MGU 1228, slide 1, P27/0, orientation unknown, upper focus.

5. *Islandinium minutum*, Green Hill Pond 10, MGU 1030, slide 2, L43/3, orientation unknown, upper surface.

6. Cyst of *Polykrikos schwartzii*, Potter Pond 7, MGU 1300-5, slide 1, F52/1, equatorial view, low focus.

7. *Selenopemphix quanta*, Trustom Pond 60, MGU 1090, slide 1, R25/3, apical view, mid focus.

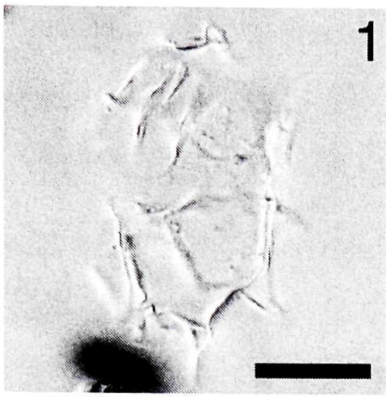
8. *Quinquecuspis concreta*, Potter Pond 7, MGU 1300-5, slide 1, S41/3, ventral surface, upper focus.

9. *Lejeunecysta oliva*, Potter Pond 7, MGU 1300-5, slide 1, T31/3, dorsal surface, upper view.

10. *Peridinium limbatum*, Potter Pond 7, MGU 1300-5, slide 1, B43/0, optical section.

11. *Votadinium calvum* & 12. *Votadinium spinosum*, Point Judith Pond 4, MGU 1300-2, slide 1, dorsal surface, upper focus.

PLATE II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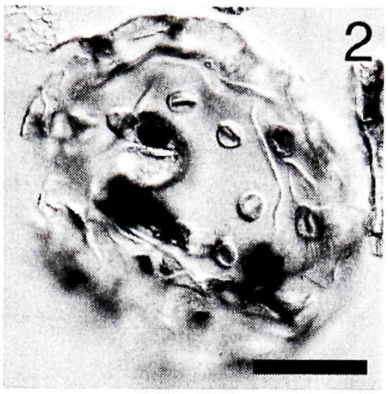
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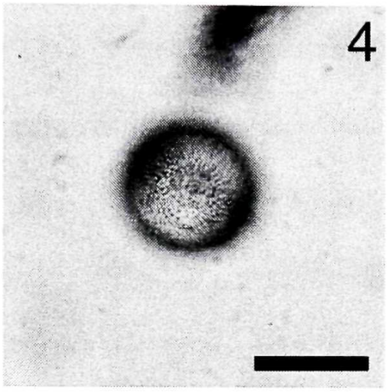
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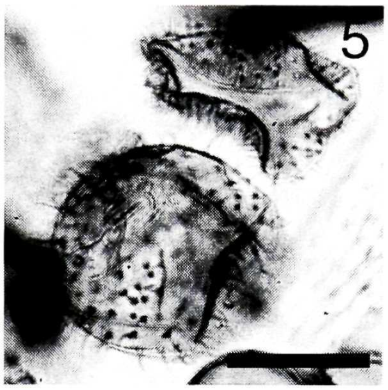
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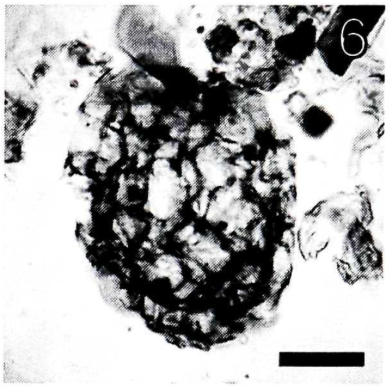
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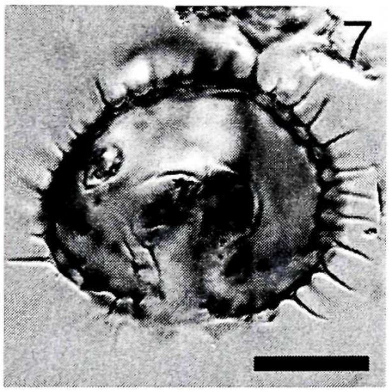
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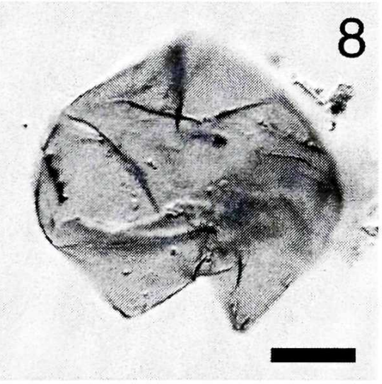
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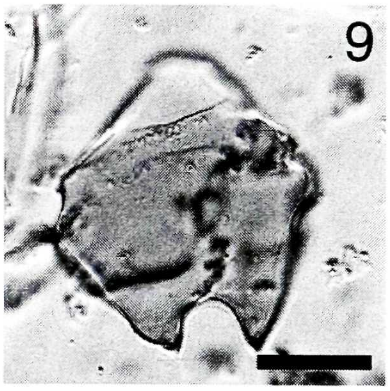
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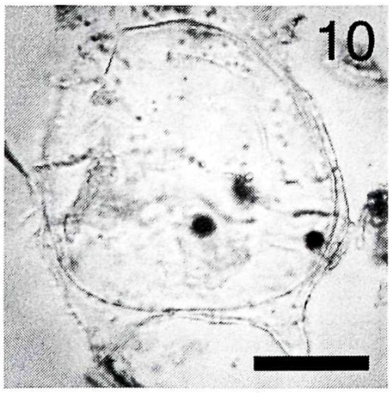
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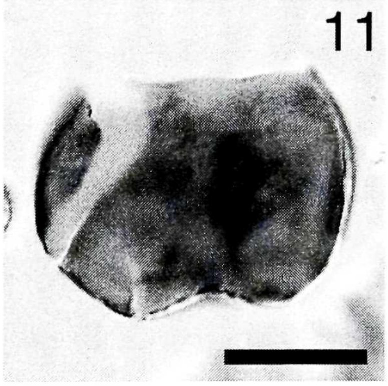
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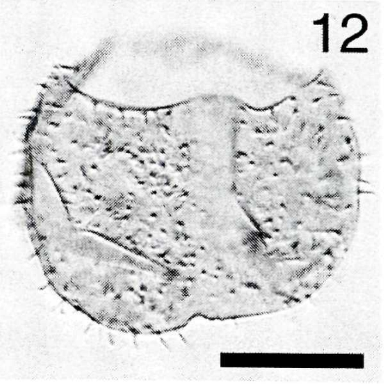
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CHAPTER 5. *ISLANDINIUM BREVISPINOSUM* SP. NOV. (DINOFLAGELLATA), A NEW ORGANIC-WALLED DINOFLAGELLATE CYST FROM MODERN ESTUARINE SEDIMENTS OF NEW ENGLAND (USA)

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ABSTRACT

Modern estuarine environments remain underexplored for dinoflagellate cysts, despite a rapidly increasing knowledge of cyst distributions in open marine environments. A study of modern estuarine sediments in New England has revealed the presence of *Islandinium brevispinosum* sp. nov., a new organic-walled dinoflagellate cyst that is locally common and probably of heterotrophic affinity. Resistance of this cyst to standard palynological processing indicates its geological preservability, although fossils are not yet known. Previously assigned species of the genus *Islandinium* Head et al., 2001 are characteristic of polar and subpolar environments today and cold paleoenvironments in the Quaternary. The present record of *Islandinium brevispinosum* extends the ecological and geographical range of this genus into the warm temperate zone, where *I. brevispinosum* occupies specific environments with reduced salinities and elevated nutrient levels.

INTRODUCTION

Dinoflagellate cysts are being studied increasingly in modern marine systems where they reflect environmental conditions with considerable sensitivity. Northern North Atlantic and Arctic cyst distributions are now well documented (Rochon et al. 1999, de Vernal et al. 2001) and provide the basis for detailed quantitative reconstructions of the Quaternary oceanic record in this region (e.g., de Vernal et al. 1996, de Vernal et al. 2000, de Vernal and Hillaire-Marcel 2000, Hillaire-Marcel et al. 2001). In contrast to the open ocean, coastal waters adjoining the North Atlantic have a more variable hydrography, and the mapping of cyst distributions is therefore more complex. The distribution of cysts in these coastal regions is not well known, estuarine systems being generally underexplored for dinoflagellate cysts. Of the few studies that have focused solely on North American estuaries, most have been conducted along the Canadian Atlantic coast (Mudie and Short 1985, de Vernal and Giroux 1991). Dinoflagellate cysts from the temperate zone of the east coast of the USA have been studied either in low detail (Wall et al. 1977, Dale 1996) or to describe the biogeographical distribution of selected toxic species (Anderson et al. 1994, Anderson 1998). Comprehensive surveys have not been undertaken previously.

This work is part of a larger investigation to map and explain the distribution of dinoflagellate cysts from selected environments along the New England (northeastern U.S.A.) coastline. Well-preserved material has been investigated from surface and core sediments that represent less than 500 years of deposition. Localities studied include several embayments of Buzzards Bay, New Bedford Harbor, Clarks Cove, Apponagansett Bay, Waquoit Bay, Jehu Pond, Narragansett Bay, and coastal lagoons of Rhode Island (Fig. 1). The present paper describes *Islandinium brevispinosum* sp. nov., a locally common component of dinoflagellate cyst assemblages in modern estuarine sediments of New England where it is particularly associated with nutrient rich waters.

Islandinium is a recently proposed protoperidiniacean cyst genus (Head et al. 2001) that accommodates round brown spiny cysts with an apical archeopyle. This genus until now comprised only *I. minutum* (Harland and Reid in Harland et al., 1980) Head et al., 2001 and *I.? cezare* (de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999) Head et al., 2001. Both these species are known principally from modern high-latitude sediments and from cold-climate Quaternary deposits. Our record of *Islandinium brevispinosum* sp. nov. unequivocally extends the ecological range of this genus into warm temperate waters. This paper provides a formal description of this cyst species and discusses its ecological significance.

MATERIALS AND METHODS

Samples. Samples were collected from three embayments in Buzzards Bay (New Bedford Harbor, Apponagansett Bay, and Clarks Cove), in Waquoit Bay and adjacent Jehu Pond (MA), in eight back-barrier coastal lagoons of Rhode Island, and in the central part of Narragansett Bay (RI) (Figs. 1 and 2). Sediments analyzed were generally fine sands, silt and mud from surface and core sediments.

Surface sediments from New Bedford Harbor, Apponagansett Bay, Clarks Cove, Waquoit Bay, Jehu Pond and coastal lagoons of Rhode Island were collected by a grab corer deployed from a boat, or by hand using a mini-piston corer while snorkeling. The top 2 cm were retained and we assume they represent less than 10 yr deposition in these generally rapidly accreting systems (Boothroyd et al. 1985, Pospelova, unpublished data). Sediments taken from experimental tanks at the Marine Environmental Research

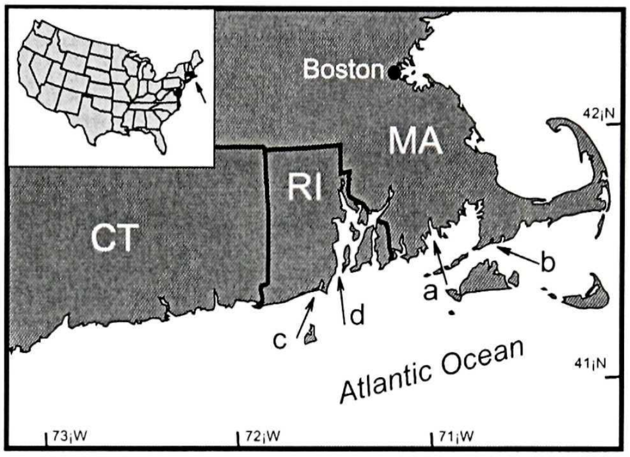


Figure 1. Location of New England sites where *Islandinium brevispinosum* sp. nov. has been found. *Islandinium brevispinosum* is reported from modern sediments of: (a) Apponagansett Bay, Clarks Cove, New Bedford Harbor; (b) Waquoit Bay and Jehu Pond (Massachusetts, USA); (c) coastal lagoons of Rhode Island (USA); and (d) Narragansett Bay.

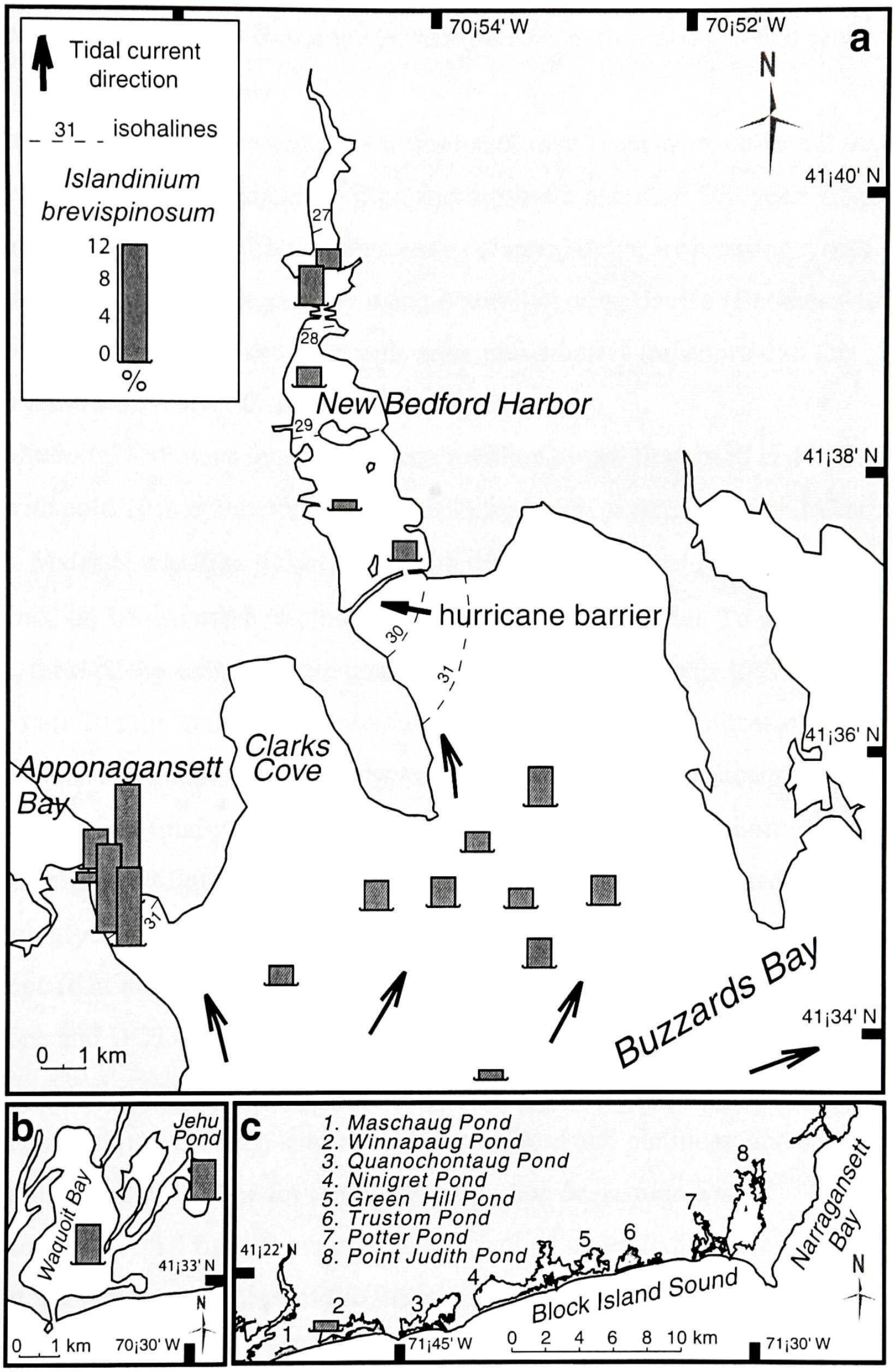


Figure 2. Map of the spatial distribution and relative abundance of *Islandinium brevispinosum* sp. nov. in New England estuaries: (a) Apponagansett Bay, Clarks Cove, and New Bedford Harbor (MA); (b) Waquoit Bay and Jehu Pond (MA); (c) coastal lagoons of Rhode Island.

Laboratory (University of Rhode Island) had originated as surface sediment from the central part of Narragansett Bay prior to their transfer to the experimental tanks. See Keller et al. (1999) for details.

In addition to surface sediments, three sediment cores were collected from New Bedford Harbor and Apponagansett Bay, and represent less than 500 years of deposition (Pospelova et al., in press). These cores were collected either by pressing a core liner into the sediments (hand corer) or by using a gravity coring device (Benthos Model 2171). Upon collection, all the sediments were immediately transported to the laboratory and stored at 4° C in the dark until processing.

Methods. Sediment samples of known volume were first dried at 40° C, then treated with cold 10% hydrochloric acid (HCl) for 2 min to remove calcium carbonate particles. Material was then rinsed twice with distilled water and sieved through 125 μm and retained on 10-μm mesh to eliminate coarse and fine material. To dissolve siliceous particles, most of the samples were treated in a hot water bath with 40% hydrofluoric acid (HF) for 20 min, and 10 min with cold HCl to remove fluorosilicates. Subsequently, the residue was rinsed twice with distilled water, sonicated for between 30 s and 2 min and finally collected on a 10-μm mesh sieve, having been centrifuged between each step. Aliquots of residue (one or two drops) were mounted on microscope slides with glycerine jelly, and dinoflagellate cysts were studied under a light microscope (63x and 100x objectives). Illustrations were made using a Leica DML-RB microscope and DC3 digital camera. For Scanning Electron Microscopy (SEM), residues were suspended in deionized water and placed on coverslips to dry. The mounted coverslips were then sputter coated with gold and platinum, and searched under Hitachi (S-2300) SEM for cysts of *Islandinium brevispinosum*.

Repository. All figured material photographed under light microscopy is deposited in the type collection of the British Geological Survey, Keyworth, U.K., under the accession numbers MPK 12549–12553. All remaining microscope slides and residues are stored in the Paleoenvironmental Laboratory, McGill University, Canada.

RESULTS

Islandinium brevispinosum Pospelova et Head sp. nov.

Division: Dinoflagellata (Bütschli, 1885) Fensome et al., 1993
Subdivision: Dinokaryota Fensome et al., 1993
Class: Dinophyceae Pascher, 1914
Subclass: Peridiniphycidae Fensome et al., 1993
Order: Peridiniales Haeckel, 1894
Suborder: Peridiniineae (Autonym)
Family: Protoperidiniaceae Balech, 1988
Subfamily: Protoperidinioideae Balech, 1988
Genus: *Islandinium* Head et al., 2001
Species: *Islandinium brevispinosum* Pospelova et Head sp. nov.

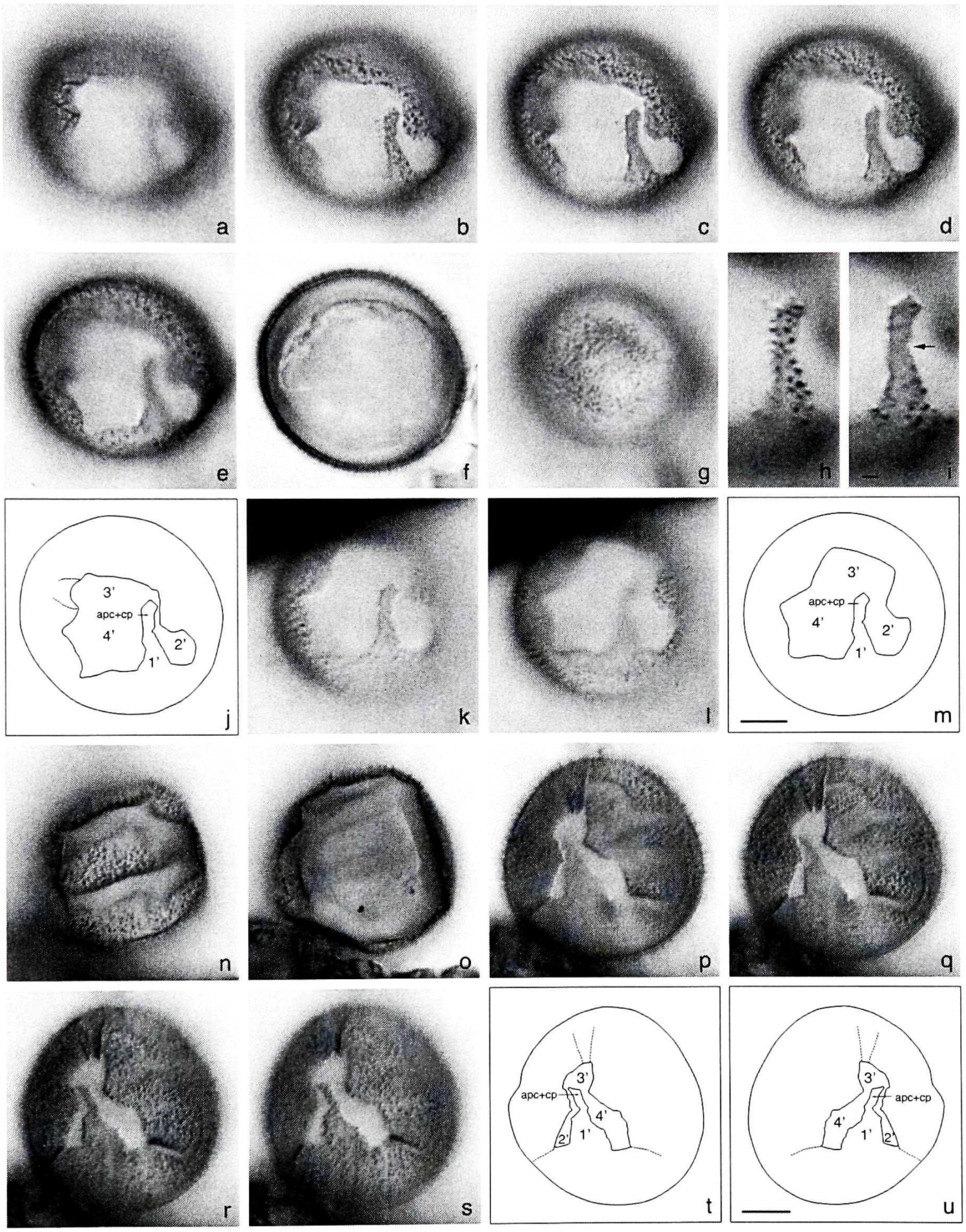
Diagnosis. Cystae parvae, proximae vel proximochoratae cum copore in medio globali vel subglobali. Murus fuscus vel fulvus colore; superficies levis tecta solidis spinulis. Spinula, fere similes longitudine figuraque, fastigata ad cacumines acres vel hebetes, nontabulare distribuuntur. Archeopyla saphopylica formata est laminis apicalibus secundis, tertiis et quartis separate amissis; tertia apicalis lamina fere aequalis circum dorsoventralem lineam mediam. Suturae archeopylae adiectae praeterea adsint; alioqui nullum indicium clarum tabulationis.

Small proximate to proximochorate cysts with spherical to subspherical central body. Wall is brown to pale brown in color; surface smooth and covered with numerous solid spinules. Spinules more-or-less similar in length and shape, taper to sharp or blunt tips, and have nontabular distribution. Archeopyle saphopylic, formed by separate loss of the second, third and fourth apical plates; third apical plate approximately symmetrical about the dorso-ventral midline. Accessory archeopyle sutures may also be present; otherwise no clear indication of tabulation.

Etymology. Latin *brevis* short, small; and *spinosus* thorny. With reference to the small spines that characterize this species.

Holotype. Sample NBH-324 slide 7, England Finder reference S30/3 (label to left); specimen MPK 12549; Figure 3a–m. Modern sediment from New Bedford Harbor, Atlantic coast of Massachusetts (USA).

Figure 3. *Islandinium brevispinosum* sp. nov. Photomicrographs are interference contrast images. (a–m) holotype from modern sediments of New Bedford Harbor, Massachusetts (USA), NBH-324/7, S30/3, MPK 12549, central body max. diameter 22 μm; apical view of specimen in present (a–j) and original (k–m) condition; (a–g) upper surface with archeopyle and successively lower foci to antapical surface, with (f) showing cell contents; (h, i) magnified view of upper (h) and lower (i) surfaces of plate 1', showing notch (marked by an arrow) indicating the interpreted border between plate 1' and the canal plate; (j, m) tracings of holotype in present (j) and original (m) condition; scale bar represents 5 μm for (a–g, j–m) and 1 μm for (h, i). (n–u) paratype from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4/1, S62 1/2, MPK 12550, central body diameter 21 μm; (n–s) antapical view of antapical surface and successively lower foci to apical surface with archeopyle; and (t, u) tracings of paratype where (u) is a reversed image of (t) to compare with holotype; scale bar represents 5 μm. (j, m, t, u) tracings show principal archeopyle suture (solid line), folds (dashed line), and interpreted tabulation. Designations cp and apc represent the canal plate and apical pore complex, the latter being presumed present but not identified with certainty.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Description. Cysts brown to pale brown in color. Central body spherical to subspherical, with smooth surface under light microscopy and SEM, and wall thickness of about 0.3 μm or less, appearing unstratified under light microscopy. Surface bears numerous, solid, nontabulate, closely but irregularly distributed spinules with basal diameter of approximately 0.3 μm. Adjacent spinules usually separated at base by about 1.0 μm, but some basal fusion occurs in some specimens; density of spinule distribution varies somewhat between and within individual specimens. Length of spinules varies from 0.3 μm where they may appear as small bumps, up to 3.5 μm where they may be curved. Spinule length fairly constant for individual specimens; ranges from 1% to 14 % of body diameter, averaging 5%. Spinules taper to fine or blunt points, as observed under both light (Figs. 3–4) and scanning electron microscopy (Fig. 5). Archeopyle is saphopylic, formed by separate loss of the three apical plates 2', 3' and 4'. Canal plate (and presumably apical pore complex) remains attached to first apical plate (1') (Fig. 3a–u, and possibly Fig. 4i–m) or is lost during archeopyle formation (Fig. 4a–h, n–p). Boundary between canal plate and 1' is marked by a notch in archeopyle outline (Fig. 3i). Plates 3' and 4' are approximately the same size, whereas plate 2' might be slightly smaller. Archeopyle, including position of third apical plate, broadly symmetrical about dorso-ventral midline. Cysts show no epifluorescence.

Measurements. Holotype: central body diameter 22 μm; average length of process 1.0 μm. Range: central body diameter 18(21.5)25 μm (standard deviation 1.8 μm); average process length: 0.3(1.1)3.0 μm (standard deviation 0.6 μm). Twenty-nine specimens were measured.

Discussion. The archeopyle was seldom seen clearly in the 315 specimens scrutinized during the present study, owing largely to the very thin cyst wall which readily collapses and folds. The holotype has a clearly visible archeopyle, and was inflated when freshly mounted and examined in Montreal (Fig. 3k–m). It had become slightly distorted upon its arrival in Cambridge, although all major features remain seldom observed. The paucity of accessory archeopyle sutures, along with a lack of information on the number of intercalary plates, prevents full determination of the episomal tabulation. However, on the basis that *Islandinium brevispinosum* probably

Fig. 4. *Islandinium brevispinosum* sp. nov. Photomicrographs are interference contrast (a–f, n–p) or bright field (i–l) images. (a–h) specimen from modern sediments of New Bedford Harbor, Massachusetts (USA), sample NBH-324/2, R28/2, MPK 12551, central body diameter 24 μm; (a–f) antapical view of antapical surface and successively lower foci to apical surface with archeopyle, and (g, h) tracings of specimen where (h) is a reversed image of (g) to compare with holotype; the three apical plates and canal plate are all lost from this specimen; scale bar represents 5 μm. (i–m) specimen from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4/21, S46/0, MPK 12552, central body diameter 23 μm; (i–l) apical view of apical surface with archeopyle, and successively lower foci to mid focus; and (m) tracing of specimen; scale bar represents 5 μm. (n–p) specimen from modern sediments of New Bedford Harbor, Massachusetts (USA), sample NBH-324/xx, H27/1, MPK 12553, central body diameter 21 μm; apical view of (n) apical surface showing release of plates 2', 3' and canal plate, but 4' still adherent, (o) slightly lower focus, and (p) mid focus showing protoplasm within cyst; scale bar represents 5 μm.

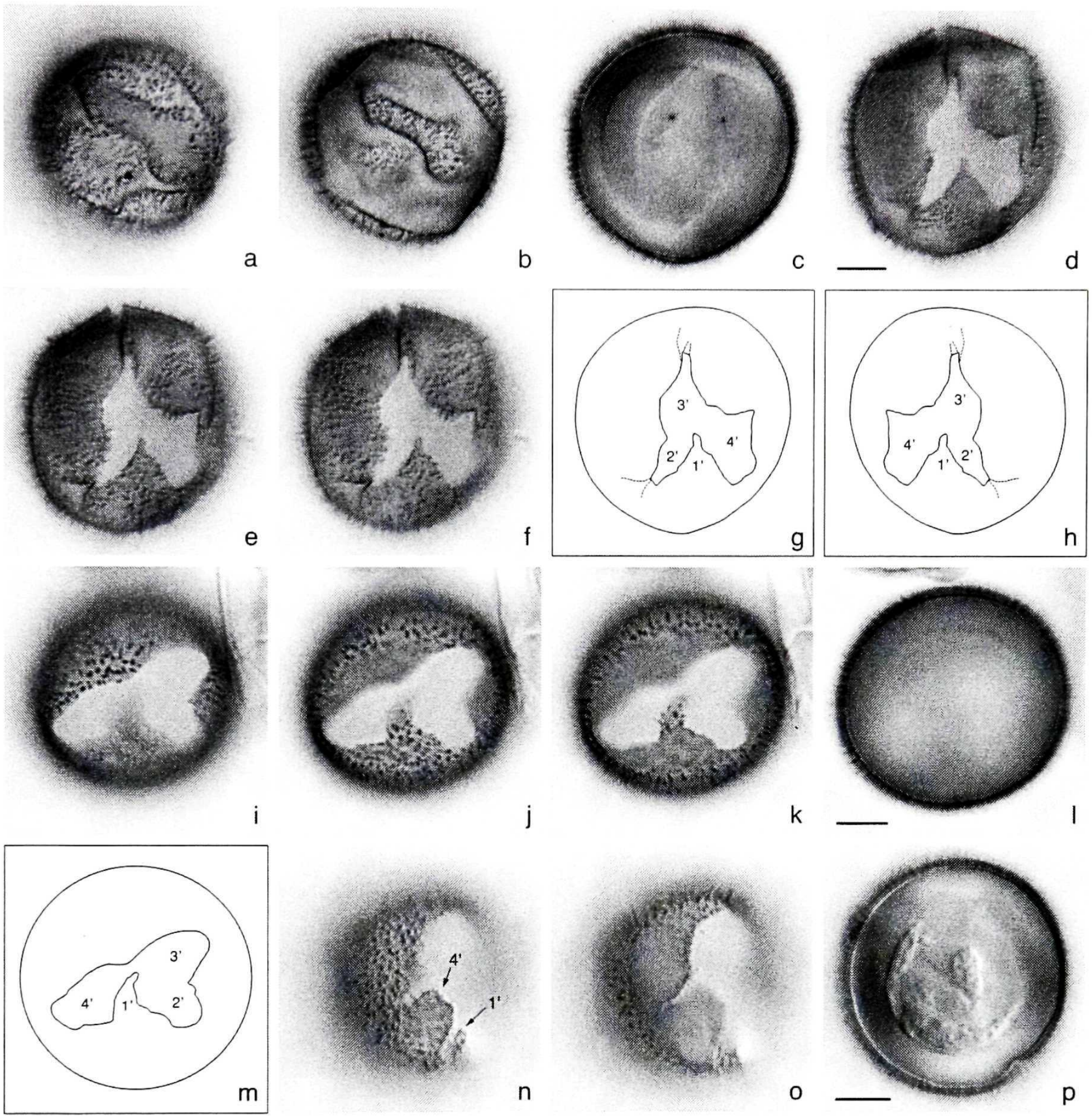
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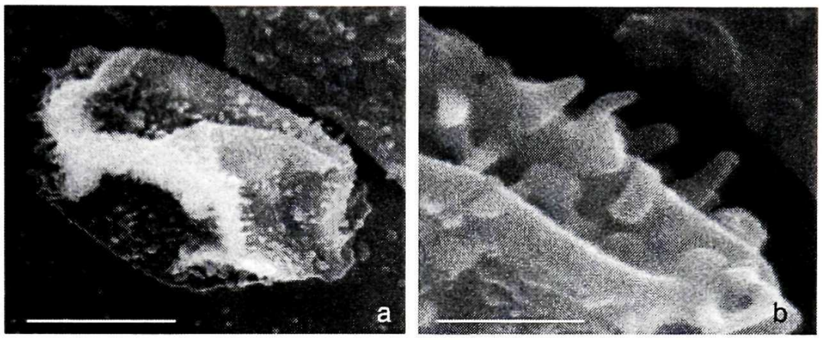
Fig. 5. *Islandinium brevispinosum* sp. nov. SEM images of specimen from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4. (a) portrait showing process distribution; and (b) high magnification view of (a) showing smooth wall surface and spinules tapering to blunt points. Scale bars represent 10 μm (a) or 2 μm (b).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represents the cyst of a species of the genus *Protoperidinium* Bergh, 1881, two possibilities are preferred. The first assumes the presence of three intercalary plates (Fig. 6b), which is a common feature of *Protoperidinium* species having a symmetrical episomal tabulation. The archeopyle in *Islandinium brevispinosum* is relatively symmetrical about the dorsoventral midline, particularly regarding the position of the third apical plate, implying (but not proving) a symmetrical episomal tabulation. The second less likely possibility (Fig. 6c) is of four intercalary plates. Although a highly unusual configuration within the genus *Protoperidinium*, this possibility is owed to a strong similarity between the archeopyles of *Islandinium brevispinosum* and of the cyst of *Protoperidinium americanum* (Gran and Braarud, 1935) Balech, 1974 (Lewis and Dodge 1987; Fig. 6g). Not only does *Protoperidinium americanum* have four intercalary plates (Fig. 6h), it is also the only motile-defined species within the genus *Protoperidinium* whose cyst is known to have an apical archeopyle. Hence, based on the above considerations, we favor three or perhaps even four intercalary plates for *Islandinium brevispinosum*.

Comparison. *Islandinium brevispinosum* closely resembles *Islandinium minutum* (Harland and Reid in Harland et al., 1980) Head et al., 2001 described from modern sediments of the Beaufort Sea, Canadian Arctic. However, *Islandinium minutum* is larger (central body maximum diameter 29–50 μm; average process length 3.5–7.0 μm; Head et al. 2001), and has a granulate wall surface compared to the smooth wall surface of *Islandinium brevispinosum*. Statistical analysis of average process length vs. central body diameter for *Islandinium brevispinosum* and *Islandinium minutum* demonstrates two separate clusters in the distribution (Fig. 7). The archeopyle of *Islandinium brevispinosum* differs from that of *Islandinium minutum* in its greater symmetry: plate 3' is offset strongly to the left on *Islandinium minutum* (Fig. 6d–f), and implies a different configuration of intercalary plates (Fig. 6, e and f). Also, plate 2' appears to be pentagonal in *Islandinium brevispinosum* whereas it is more-or-less quadrangular in *Islandinium minutum*.

Islandinium? *cezare* (de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999) Head et al., 2001, described from late glacial sediments of Québec, differs from

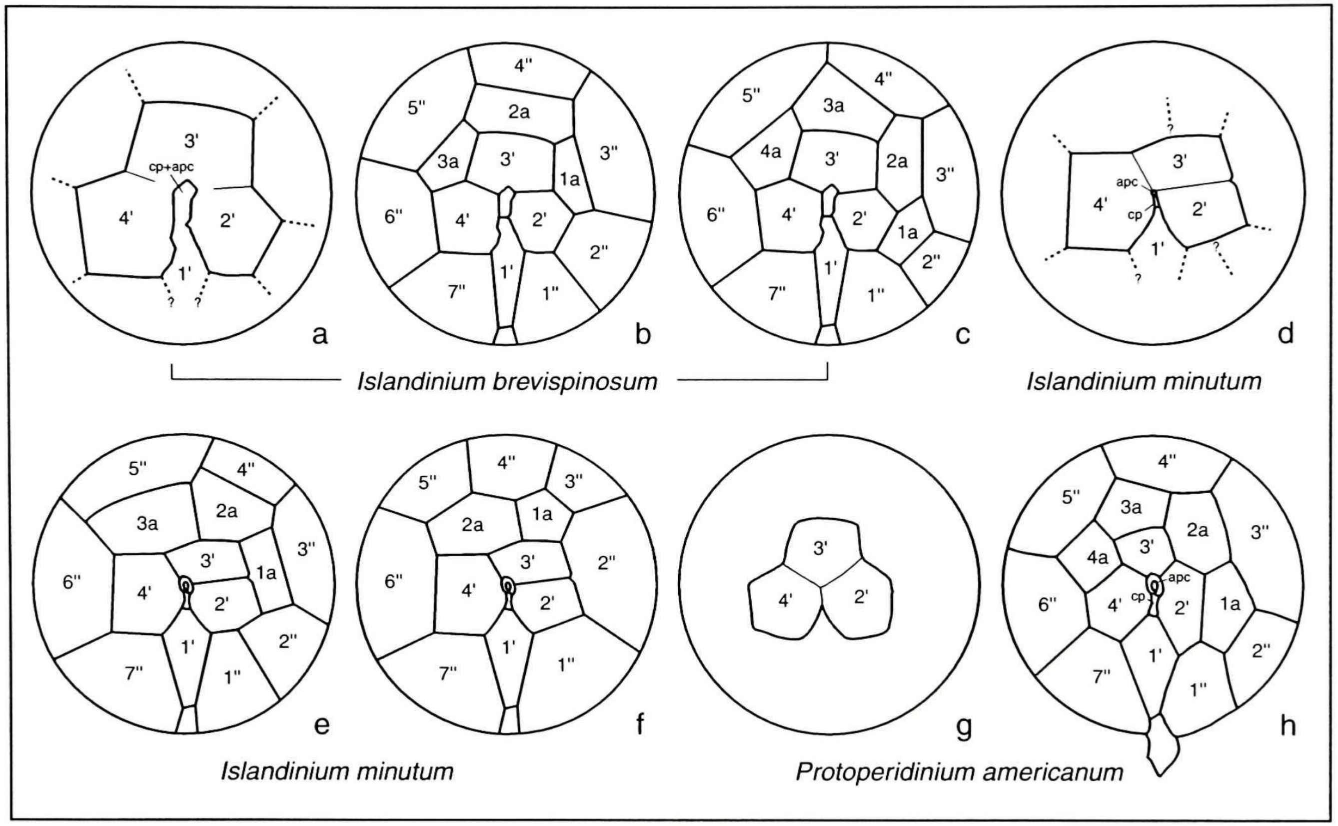

Figure 6. Schematic episomal tabulation patterns of *Islandinium brevispinosum* sp. nov. and morphologically similar cysts with 3A apical archeopyles. (a-c) *Islandinium brevispinosum*; (a) shows the 3A apical archeopyle (dashed lines indicate presumed adjoining plate boundaries), and (b, c) are interpretations of the epitabulation involving either three (1a-3a) or four (1a-4a) anterior intercalary plates, respectively; ortho-style tabulation is assumed but not observed (this study). (d-f) *Islandinium minutum* (Harland and Reid in Harland et al., 1980) Head et al., 2001; (d) shows the 3A apical archeopyle (dashed lines indicate presumed adjoining plate boundaries), and (e, f) are interpretations of the epitabulation involving either three (1a-3a) or two (1a-2a) anterior intercalary plates, respectively; ortho-style tabulation is assumed (from Head et al. 2001). (g, h) *Protoperidinium americanum* (Gran and Braarud, 1935) Balech, 1974; (g) shows a cyst with 3A apical archeopyle, and (h) is the observed epitabulation from a motile cell showing four anterior intercalary plates and ortho-style tabulation (from Lewis and Dodge 1987). The abbreviations cp and apc represent canal plate and apical pore complex, respectively.

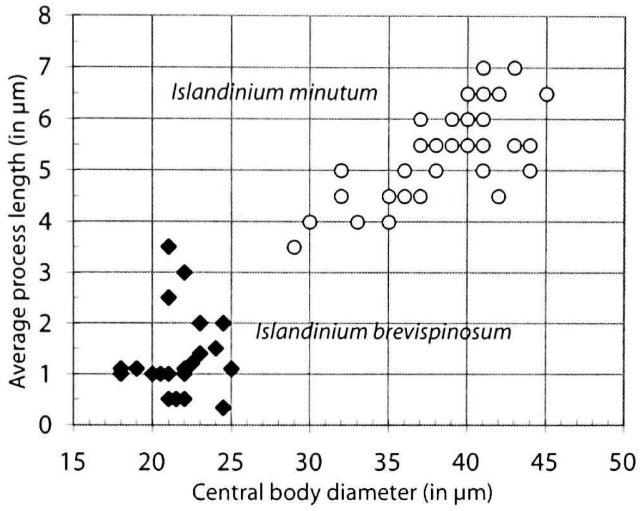

Figure 7. Central body diameter vs. average process length for *Islandinium brevispinosum* sp. nov. (black diamonds) and *Islandinium minutum* (open circles; from the Kara Sea, based on Head et al. 2001). The two separate clusters demonstrate that size is a factor in distinguishing these species.

Islandinium brevispinosum in its larger size, granulate wall surface, and in having long processes with expanded process tips.

The cyst of *Protoperidinium americanum* differs in its larger size (diameter 34–52 µm), prominent wall layering, and absence of processes (Lewis and Dodge 1987; Fig. 6g). Its archeopyle is relatively smaller than that of *Islandinium brevispinosum*, although similar in shape.

Occurrence. Islandinium brevispinosum has been found only in modern (between <500 and <10 yr) estuarine sediments of New Bedford Harbor, Clarks Cove, Apponagansett Bay, Waquoit bay and Jehu Pond (Atlantic coast of Massachusetts, USA), Winnapaug Pond and Narragansett Bay (Rhode Island, USA) (Fig. 2). The highest abundance (12%) is found in nutrient rich waters characterized by 23°C mean summer temperature and 30 psu mean summer salinity. Distribution is presumably more widespread than presently described. Cell contents occur in some cysts including the holotype, indicating that this is an extant species.

Thecal affinity. As with *Islandinium minutum*, an affinity with the subfamily Protoperidinioideae is indicated from the epicystal tabulation and overall morphology of the cyst (Head et al. 2001). The brown cyst wall coloration and lack of epifluorescence suggest a species whose motile stage has a heterotrophic feeding strategy, which is predominant in the Protoperidiniaceae. Because the cysts are extant, the motile stage must be present in the water column. However, the only species of *Protoperidinium* presently reported for Buzzards Bay (New Bedford Harbor, Apponagansett Bay, and Clarks Cove) are *P. bipes* (Paulsen, 1904) Balech, 1974, *P. claudicans* (Paulsen, 1907) Balech, 1974, *P. pellucidum* Bergh, 1881 and *P. steinii* (Jörgensen, 1900) Balech, 1974 (see Pierce and Turner 1994). Of these, *P. claudicans* is known to produce a cyst morphologically different from *I. brevispinosum* (Head 1996), *P. bipes* has a strongly asymmetrical episomal tabulation, and *P. pellucidum* and *P. steinii* are both probably too large to produce a cyst consistently as small as *I. brevispinosum*. No attempt to germinate *Islandinium brevispinosum* has yet been made, but this approach will ultimately establish the thecal affinity of this cyst species.

ECOLOGICAL DISTRIBUTION

A total of 315 complete and fragmented specimens of *Islandinium brevispinosum* was observed in 54 sediment samples. All studied sites are characterized by shallow water in which depth ranges from 1 to 12 m. Embayments of Buzzards Bay were studied in most detail, with the analysis of 19 surface sediment samples (Pospelova, unpublished data) and 31 sediment samples from three cores (Pospelova et al., in press). Figure 2a shows the spatial distribution of *Islandinium brevispinosum* and its proportion in dinoflagellate cyst assemblages from Apponagansett Bay, Clarks Cove, and New Bedford Harbor. *Islandinium brevispinosum* was encountered in all surface samples with its abundance ranging from 1 to 12% with the highest proportion in the outer part of Apponagansett Bay. All studied sites in Buzzards Bay are characterized by mean August water temperatures ranging from 23 to 25° C and salinities from 27 to 31 psu (Howes et al. 1999). Waters in this part of Buzzards Bay are considered to be nutrient rich, with the mean August nitrate concentrations 1.8 μM and phosphate 1.7 μM. (Howes et al. 1999).

In estuaries neighboring Buzzards Bay, Waquoit Bay and adjacent Jehu Pond, *Islandinium brevispinosum* was present and comprised 4% of total dinoflagellate cyst assemblages (Fig. 2b). These waters are characterized by a mean August temperature of 24° C and salinities ranging from 28 to 29 psu (Waquoit Bay National Estuarine Research Reserve). We do not have exact measurements of nutrient concentrations for Waquoit Bay and Jehu Pond waters, although it is known that these systems are also nutrient rich (Lamontagne and Valiela 1995).

The eight back-barrier lagoons of Rhode Island (Fig. 2c) are characterized by a range of mean August water temperatures and salinities from 19 to 23° C and from 5 to 29 psu, respectively (Lee et al. 1997). Cysts of *Islandinium brevispinosum* were found only in Winnapaug Pond (1.5%; Fig. 2c), where mean August water temperature is 24° C, salinity 27 psu, concentrations of nitrates 2.0 μM, and phosphates 1.4 μM (Lee et al. 1997).

The presence of *Islandinium brevispinosum* in the surface sediments of Narragansett Bay is inferred through our study of sediments from experimental tanks at the Marine Environmental Research Laboratory (University of Rhode Island) which originate from the central part of Narragansett Bay (Keller et al. 1999).

SUMMARY AND CONCLUSIONS

The large family Protoperidiniaceae contains only three extant species that are known with certainty to have apical archeopyles: *Islandinium minutum* (the type of the genus), *Islandinium brevispinosum,* and the cyst of *Protoperidinium americanum* (which has no cyst-defined name). Head et al. (2001) suggested a biological affinity between *Islandinium minutum* and the large motile-defined genus *Protoperidinium*, but noted that the apical plates of *Islandinium minutum* are arranged asymmetrically, whereas they are arranged symmetrically in the cyst of *Protoperidinium americanum.* The apical plates in *Islandinium brevispinosum* are relatively symmetrical in configuration, as with the cyst of *Protoperidinium americanum,* and this adds support for an affinity between the genera *Islandinium* and *Protoperidinium.* A lack of accessory archeopyle sutures in *Islandinium brevispinosum* prevents the total number of anterior intercalary plates from being determined, but three or even four are likely. *Islandinium brevispinosum* undoubtedly fossilizes, but neither fossils nor extant specimens have been reported previously. The small size, propensity to crumple, and unusual archeopyle style may have caused this species to be overlooked until now.

The genus *Islandinium* has been associated principally with modern high-latitude environments, where relative abundances may exceed 50%, although low abundances of *Islandinium minutum* have been reported occasionally in mid latitudes (Rochon et al. 1999, Head et al. 2001). The presence of *Islandinium brevispinosum* with up to 12% relative abundance throughout the warm embayments of New England now extends the ecological range of this genus unquestionably into the warm-temperate zone.

Islandinium brevispinosum commonly occurs in shallow nutrient-rich estuarine waters that are generally characterized by mean August temperatures ranging from 23 to 25° C and salinities from 27 to 31 psu. It is possible that the presence/absence of this species in estuarine waters is regulated by this narrow range of temperature and salinity and by elevated nutrient content. Therefore this species may be of interest for environmental and paleoenvironmental reconstructions. Further studies of dinoflagellate cyst assemblages in estuarine systems on a larger scale will provide more detailed understanding of the ecology of *Islandinium brevispinosum.*

CHAPTER 6. GENERAL CONCLUSIONS

Detailed analysis of dinoflagellate cyst records in sediments from New England estuaries reveals abundant cyst assemblages. The sediment concentration of cysts ranges from 10^2 to 10^4 cyst g^{-1}, which corresponds to substantial cyst production when the sediment accumulation rates are considered. About 40 dinoflagellate cyst taxa were identified.

Dinoflagellate cyst assemblages are dominated by coastal species already recognized by Dale (1996) in his description of the cyst "temperate biogeographic zone". In some samples substantial numbers of the warm water species *Operculodinium israelianum*; cold water species *Pentapharsodinium dalei*, *Selenopemphix quanta*, *Islandinium*? *cezare* and *Islandinium minutum*; as well as the oceanic taxon *Nematosphaeropsis* spp. were found in lagoons and embayments. This work expands the biogeographic boundaries of these taxa. However, the presence of those taxa may be due, in part, to the greater temperature range in shallow as compared to marine waters.

This work contributes to the taxonomic as well as the ecological classifications of dinoflagellate cysts. A new species of dinoflagellate cyst, *Islandinium brevispinosum*, has been discovered and described. This species is distributed over a narrow range of water temperature and salinity, and at elevated nutrient levels. *Islandinium brevispinosum* is fossilized and can be an informative indicator of environmental conditions in the past. The recognition of *Islandinium brevispinosum* in New England estuaries also extends the ecological and geographical range of the genus *Islandinium* from cold-climate, high latitudes to warm temperate estuarine environments.

Despite the turbation, so common in estuarine sediments, cyst abundance, species richness, the proportion of cyst produced by heterotrophic and autotrophic dinoflagellates, as well as the composition of cyst assemblages change over time and produce sedimentary cyst records reflecting changes in environmental conditions. The same characteristics of cyst assemblages reflect spatial variations in environmental conditions within a single estuarine system. My results show that dinoflagellate cysts reflect changes in temperature, salinity, nutrient availability and pollution, even at the small spatial (1-10 km) and temporal scales (10-100 yr) that characterize shallow lagoons and embayments, proving the main hypothesis of this thesis that cysts may be used as indicators of environmental conditions in estuarine systems.

In the back-barrier lagoons, the temperature and salinity vary widely from site to site and water quality is affected greatly by the degree of water exchange between lagoon and ocean. These lagoons have no toxic pollution. Multivariate statistical analysis (CCA) of proportions of individual cyst taxa in the assemblages and multi-year measurements of temperature, salinity and nutrients demonstrate that the primary factors influencing dinoflagellate cyst distribution in these sites are temperature and salinity. There is a significant correlation between dinoflagellate cyst species richness and mean summer salinity.

In the Buzzards Bay embayments, gradients of salinity and temperature are shorter than in the lagoons. Thus the role of nutrients is more pronounced in these embayments and cyst assemblages change along a gradient of nutrient enrichment, identified on the basis of the distance from the sewage outfalls. High levels of pollution (high sedimentary concentrations of toxic metals, PCBs and elevated organic carbon) are reflected by a decrease in dinoflagellate cyst concentrations and species richness.

The study of sediment cores from two embayments, New Bedford Harbor and Apponagansett Bay, demonstrates the applicability of dinoflagellate cysts for the assessment of human impact on estuaries. Analyses of the temporal dinoflagellate cyst records along with sediment chemistry and historical data on human activity in the watersheds over the past 500 years reveals the time of the major changes in the aquatic ecosystem. Developments such as the onset of the nutrient enrichment, intensive eutrophication and pollution caused by increasing urbanization and industrialization in the watersheds are reflected in the cyst assemblages. The greatest changes in the dinoflagellate cyst record occur during the 20th century, when New Bedford Harbor was exposed to both toxic pollution and heavy nutrient loading. These conditions are reflected in declining cyst diversity and wide fluctuation in total cyst production. At the same time the composition of dinoflagellate cyst assemblages changes with the increased abundance of Diplopsalidaceae and Polykrikaceae heterotrophic taxa. As impacts of industrialization and urbanization cannot be separated, the cyst response must be interpreted as a cumulative "pollution signal".

Decline in cyst species richness with increasing concentrations of toxins and organic carbon is found in both spatial and historical studies. Although this correlation was not reported in previous studies, my reanalysis of the dinoflagellate cyst records in Norwegian fjords confirms that species richness is the most robust indicator of highly eutrophic and polluted conditions. Because species richness is suppressed in oligohaline environments, species richness will be an indicator of pollution and eutrophication only when salinity >10 psu.

This research advances our understanding of factors affecting dinoflagellate cyst distribution in estuaries, but many questions remain unanswered. There is a need to study estuaries subjected only to eutrophication or toxic pollution in order to separate effects of these factors on dinoflagellate cysts. These signals may, in fact, vary depending on the type of estuary (fjords, embayments, lagoons and river-dominated systems).

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APPENDIX. TAXONOMY

Division: Dinoflagellata (Bütschli, 1885) Fensome et al., 1993
    Subdivision: Dinokaryota Fensome et al., 1993
    Class: Dinophyceae Pascher, 1914

Subclass: Gymnodiniphycidae Fensome et al., 1993
Order: Gymnodiniales Apstein, 1909
Suborder: Gymnodiniineae (Autonym)
    Family: Gymnodiniaceae (Bergh, 1881) Lankester, 1885
    Genus: *Gymnodinium* von Stein, 1878
    Species: *Gymnodinium* spp. indet. (Plate I, fig. 1)
    Family: Polykrikaceae Kofoid & Swezy, 1921
    Genus: *Polykrikos* Bŭtschli, 1873
    Species: *Polykrikos kofoidii* Bŭtschli, 1873 ; *Polykrikos schwartzii* Bŭtschli, 1873 (Plate I, fig. 2).

Subclass: Peridiniphycidae Fensome et al., 1993
Order: Gonyaucales Taylor, 1980
Suborder: Gonyaulacineae (Autonym)
    Family: Gonyaulacaceae Lindeman, 1928
    Subfamily: Cribroperidinioideae Fensome et al., 1993
    Genus: *Lingulodinium* Wall 1967 emend. Dodge 1989
    Species: *Lingulodinium machaerophorum* (Deflandre & Cookson, 1955) Wall, 1967 (Plate I, fig. 3)
    Genus: *Operculodinium* Wall 1967 emend. Matsuoka et al., 1997
    Species: *Operculodinium centrocarpum* sensu Wall & Dale, 1966 (Plate I, figs. 4-5); *Operculodinium centrocarpum* sensu Wall & Dale, 1966 var. *truncatum* (Plate I, fig. 6); *Operculodinium israelianum* (Rossignol, 1962) Wall, 1967 (Plate I, fig. 7)

Subfamily: Gonyaulacoideae (Autonym)

Genus: *Impagidinium* Stover & Evitt, 1978

Genus: *Nematosphaeropsis* Deflandre & Cookson, 1955 emend. Wrenn, 1988

Species: *Nematosphaeropsis* spp. indet. (Plate I, figs. 8-9)

Genus: *Spiniferites* Mantell, 1850 emend. Sarjeant, 1970

Species: *Spiniferites bentorii* (Rossignol, 1964) Wall & Dale, 1970 (Plate II, figs. 2-3); *Spiniferites elongatus* Reid, 1974 (Plate II, fig. 4); *Spiniferites membranaceus* (Rossignol, 1964) Sarjeant, 1970 (Plate II, figs. 5-6); *Spiniferites* cf. *delicatus* (Plate II, fig. 7); *Spiniferites* spp. indet. (Plate II, figs. 8-9; Plate III, fig. 1)

Genus: *Tectatodinium* Wall, 1967 emend. Head, 1994

Species: *Tectatodinium pellitum* Wall, 1967 emend. Head, 1994 (Plate III, fig. 2)

Suborder: Goniodomineae Fensome et al., 1993

Family: Goniodomaceae Lindemann, 1928

Subfamily: Helgolandinioideae Fensome et al., 1993

Genus: *Alexandrium* Halim, 1960 emend. Balech, 1990

Species: *Alexandrium tamarense* (Lebour, 1925) Balech 1990 (Plate III, figs. 3-4)

Genus: *Tuberculodinium* Wall, 1967

Species: *Tuberculodinium vancampoae* (Rossignol, 1962) Wall, 1967 (Plate III, fig. 5)

Order: Peridiniales Haeckel, 1894

Suborder: Peridiniineae (Autonym)

Family: Peridiniaceae Ehrenberg, 1831

Subfamily: Calciodinelloideae Fensome et al., 1993

Genus: *Pentapharsodinium* Indelicato & Loeblich III, 1986 emend. Montresor et al., 1993

Species: *Pentapharsodinium dalei* Indelicato & Loeblich III, 1986 (Plate III, fig. 6)

Family: Protoperidiniaceae Balech, 1988

Subfamily: Diplopsalioideae Abe, 1981

Genus: *Dubridinium* Reid, 1977

Species: *Dubridinium* spp. indet. (Plate III, figs. 7-9)

Subfamily: Protoperidinioideae Balech, 1988

Genus: *Brigantedinium* Reid, 1977 ex Lentin & Williams, 1993

Species: *Brigantedinium cariacoense* (Wall, 1967) Lentin & Williams, 1993 (Plate IV, fig. 1); *Brigantedinium simplex* Wall, 1965 ex Lentin & Williams, 1993 (Plate IV, fig. 2); *Brigantedinium* spp. indet.

Genus: *Islandinium* Head et al., 2001

Species: *Islandinium brevispinosum* Pospelova et Head, 2002 (Plate IV, fig. 3); *Islandinium*? *cezare* Head et al., 2001 (Plate IV, fig. 4); *Islandinium minutum* Head et al., 2001 (Plate IV, fig. 5)

Genus: *Lejeunecysta* Artzner & Dorhofer, 1978 emend. Lentin & Williams, 1996

Species: *Lejeunecysta oliva* (Reid, 1977) Turon & Londeix, 1988 (Plate IV, fig. 6); *Lejeunecysta sabrina* (Reid, 1977) Bujak, 1984

Genus: *Protoperidinium* Bergh, 1881

Species: *Protoperidinium minutum* (Kofoid, 1907) Loeblich, 1970 (Plate IV, fig. 7); *Protoperidinium oblongum* (Aurivillius, 1898) Cleve, 1990 (Plate IV, fig. 8); *Protoperidinium* spp. indet. (Plate IV, fig. 9)

Genus: *Quinquecuspis* Harland, 1977

Species: *Quinquecuspis concreta* (Reid, 1977) Harland, 1977 (Plate V, fig. 1)

Genus: *Selenopemphix* Benedek, 1972 emend. Head, 1993

Species: *Selenopemphix nephroides* Benedek, 1972 emend. Bujak in Bujak et al., 1980 (Plate V, fig. 2); *Selenopemphix quanta* (Bradford, 1975) Matsuoka, 1985 (Plate V, fig. 3)

Genus: *Stelladinium* Bradford, 1975

Species: *Stelladinium stellatum* (Wall in Wall & Dale, 1968) Reid, 1977 (Plate V, fig. 4)

Genus: *Trinovantedinium* Reid, 1977

Species: *Trinovantedinium applanatum* (Bradford, 1977) Bujak & Davies, 1983 (Plate V, fig. 5)

Genus: *Votadinium* Reid, 1977

Species: *Votadinium calvum* Reid, 1977 (Plate V, fig. 6); *Votadinium spinosum* Reid, 1977 (Plate V, fig. 7)

Cyst type E (Plate V, figs. 8-9)

Genus: *Peridinium* Ehrenberg, 1830

Species: *Peridinium wisconsinense* Eddy, 1930

PLATE I

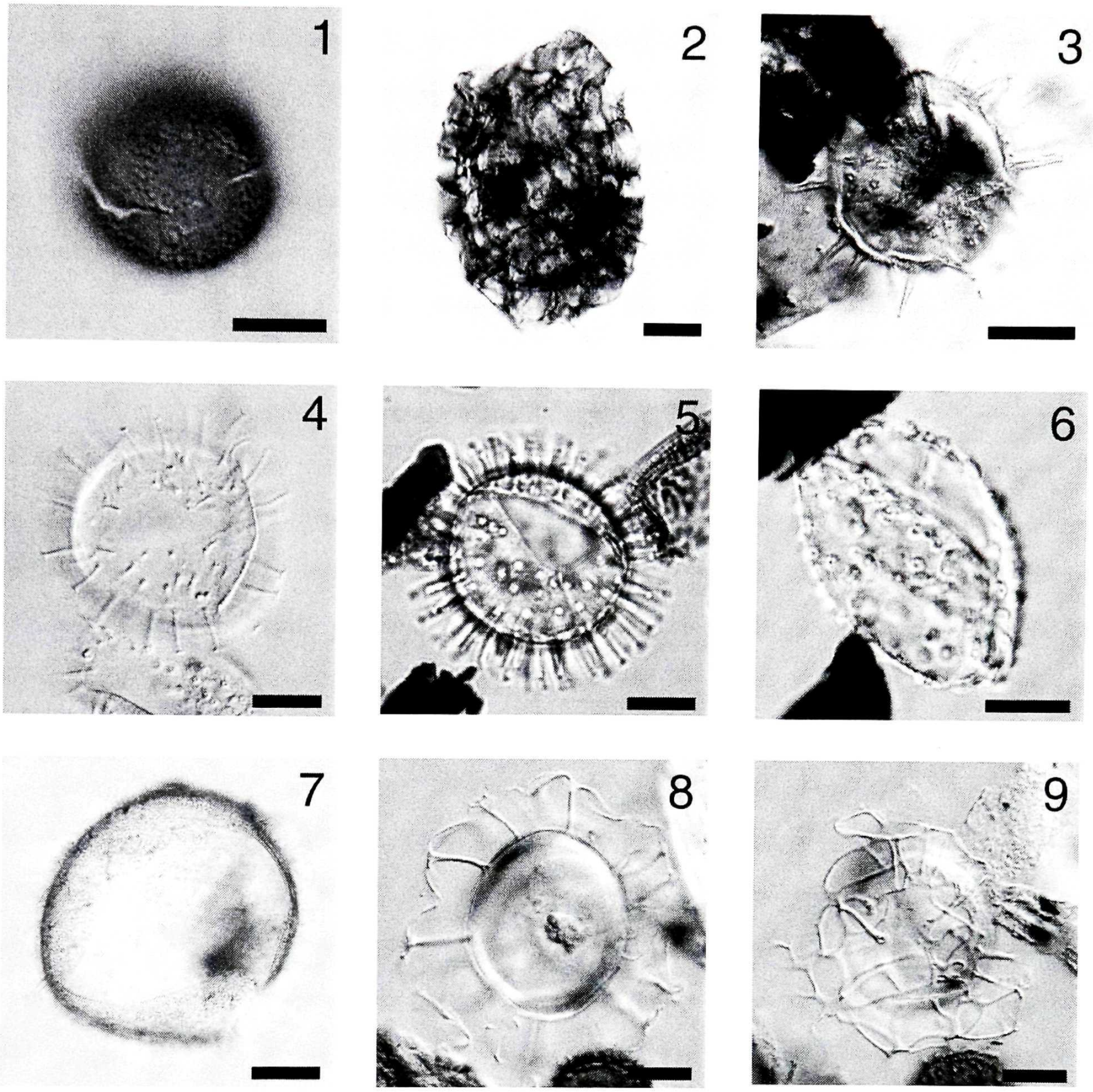

Plate I. Photomicrographs are bright field images. Scale bar 10 μm.
1. *Gymnodinium* spp., NBH325, slide x, W53/2, lateral surface.
2. *Polykrikos schwartzii*, NBH346, slide 1, O29/3, equatorial view.
3. *Lingulodinium machaerophorum*, NBH247, slide 1, L391/2, orientation uncertain.
4-5. *Operculodinium centrocarpum* sensu Wall & Dale (1966), NBH325, slide 1, M51/4, dorsal surface (4); NBH325, slide 1, dorsal surface (5).
6. *Operculodinium centrocarpum* var. *truncatum*, NBH204, slide 2, S58/3, orientation uncertain.
7. *Operculodinium israelianum*, AB2, slide 1, R41/1, dorsal surface.
8-9. *Nematosphaeropsis* spp. indet, CPE, slide 1, V38/0, optical section (8), ventral surface (9).

PLATE II

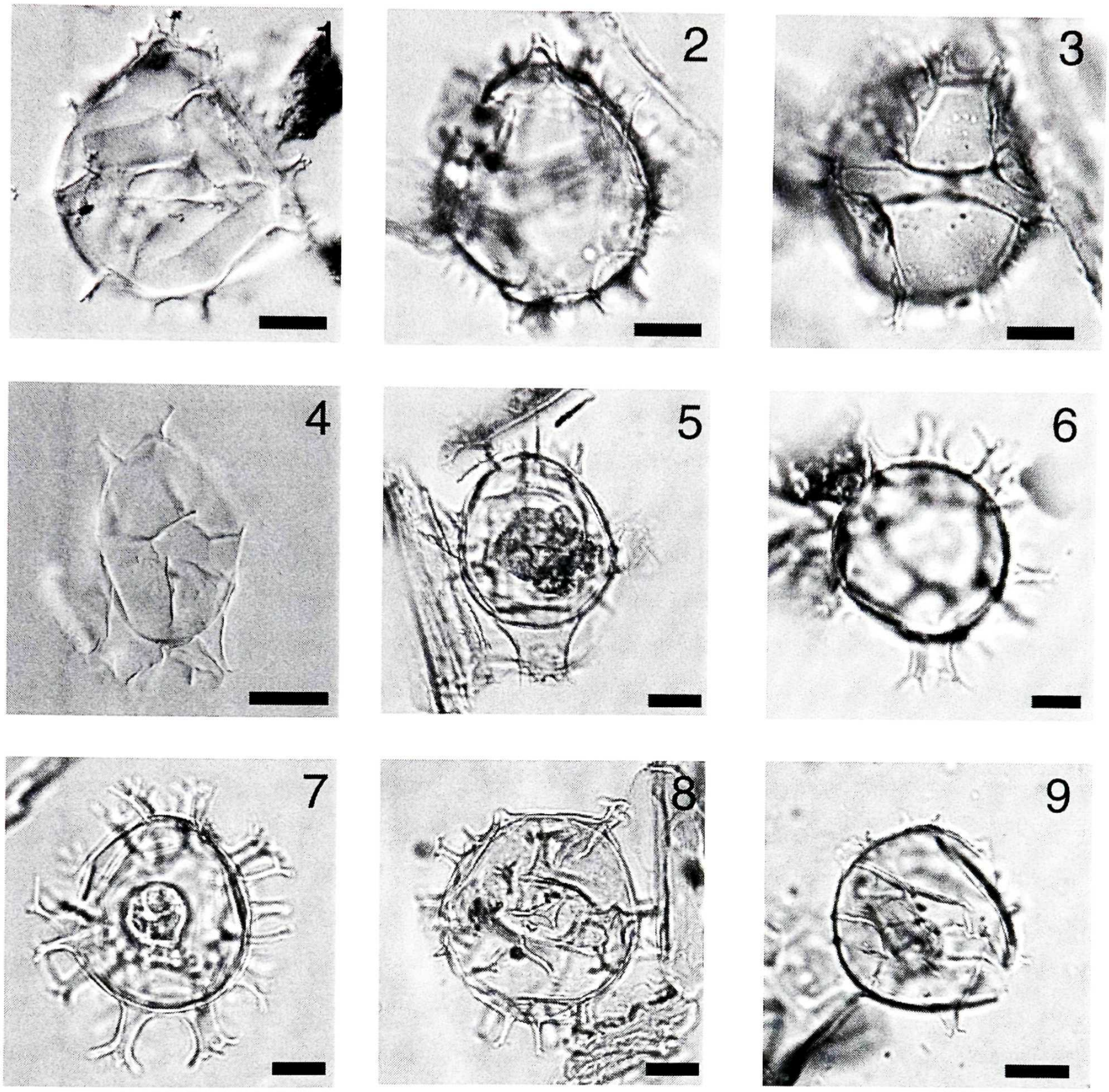

Plate II. Photomicrographs are bright field images. Scale bar, 10 μm.

1-3. *Spiniferites bentorii*, CPC, slide 1, V38/0, lateral surface (1); NBH317, slide 2, optical section (2), ventral surface (3).

4. *Spiniferites elongatus*, NBH325, slide 1, X36/1, ventral surface.

5-6. *Spiniferites membranaceus*, NBH236, slide 1, optical section (5); AB5, slide 3, optical section.

7. *Spiniferites* cf. *delicatus*, NBH324, slide 2, optical section.

8-9. *Spiniferites* spp. indet, NBH325, slide 1, lateral surface (8); NBH204, slide 1, optical section (9).

PLATE III

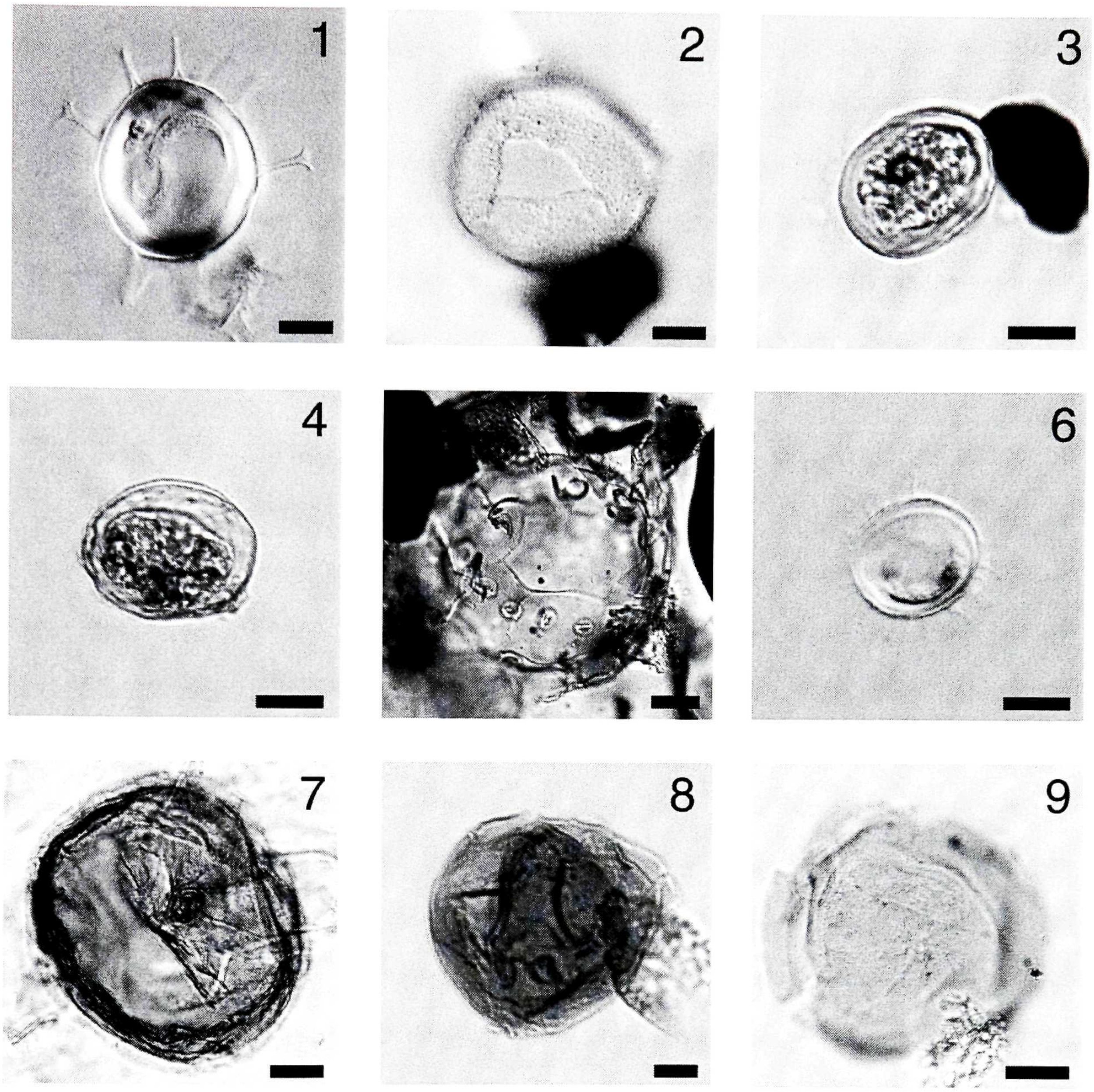

Plate III. Photomicrographs are bright field images. Scale bar, 10 µm.

1. *Spiniferites* spp. indet, CPG, slide 1, optical section.

2. *Tectatodinium pellitum,* CPE, slide 1, X48/1, dorsal surface.

3-4. *Alexandrium tamarense,* NBH247, slide 1, optical section; NBH247, slide 2, optical section.

5. *Tuberculodinium vancampoae*, NBH317, slide 1, T43/1, apical surface.

6. *Pentapharsodinium dalei*, CPE, slide 1, F613/4, optical section.

7-9. *Dubridinium* spp. indet, NBH324, slide 1, D38/1, apical view (7); CPB, slide 2, apical surface (8); NBH236, slide 4, apical surface (9).

PLATE IV

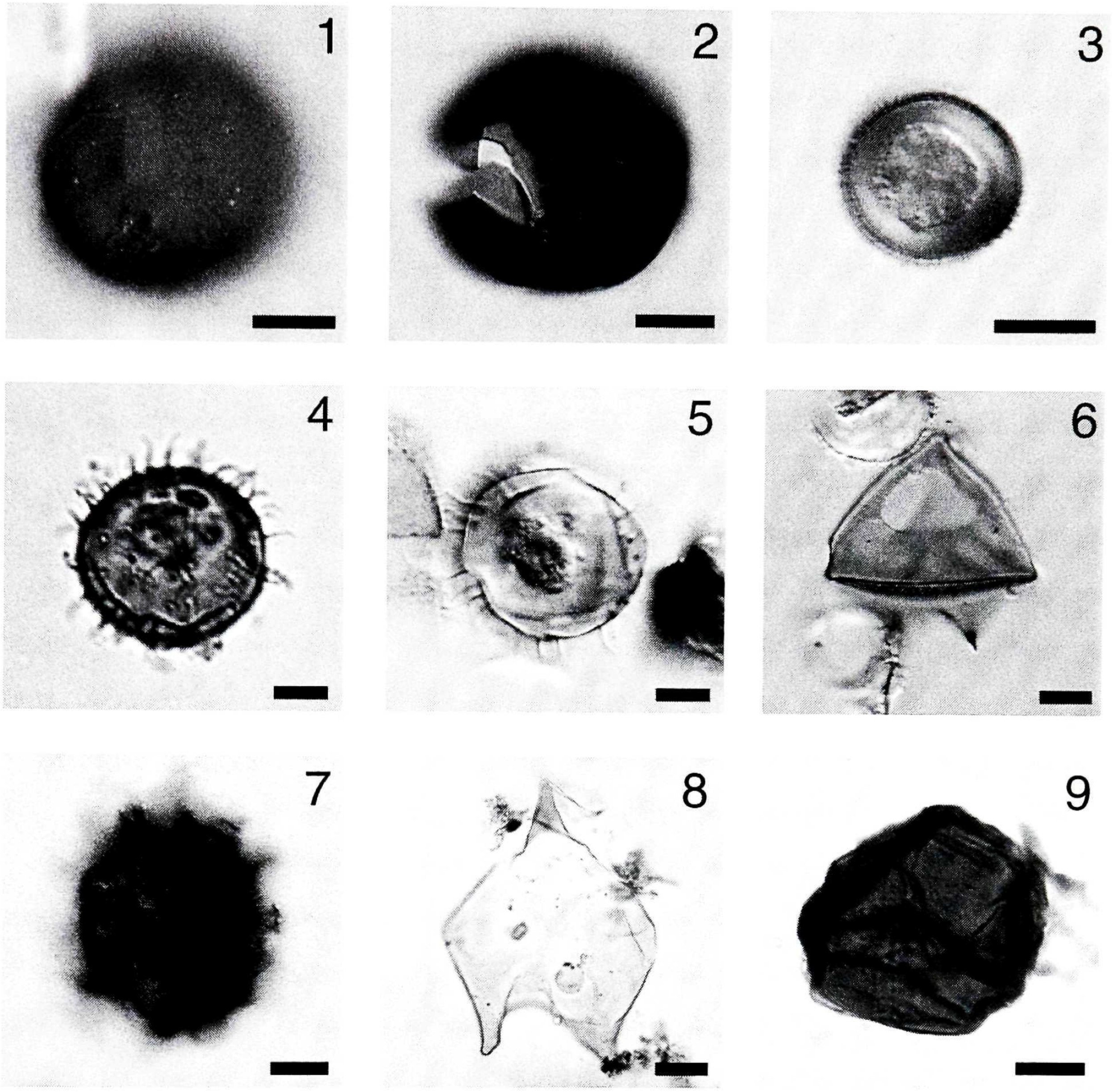

Plate IV. Photomicrographs are bright field images. Scale bar, 10 μm.
1. *Brigantedinium cariacoense*, CPG, slide 1, F55/4, lateral surface.
2. *Brigantedinium simplex*, NBH325, slide 1, L51/1, dorsal surface.
3. *Islandinium brevispinosum*, CPG, slide 1, D48/4, orientation uncertain.
4. *Islandinium? cezare*, NBH204, slide 1, orientation uncertain.
5. *Islandinium minutum*, NBH317, slide 1, F41/4, optical section.
6. *Lejeunecysta oliva*, CPC, slide 1, V56/4, dorsal surface.
7. *Protoperidinium minutum*, CPE, slide 1, T46/2, orientation uncertain.
8. *Protoperidinium oblongum*, CPG, slide 2, dorsal surface.
9. *Protoperidinium* spp. indet, NBH325, slide 2, orientation uncertain.

PLATE V

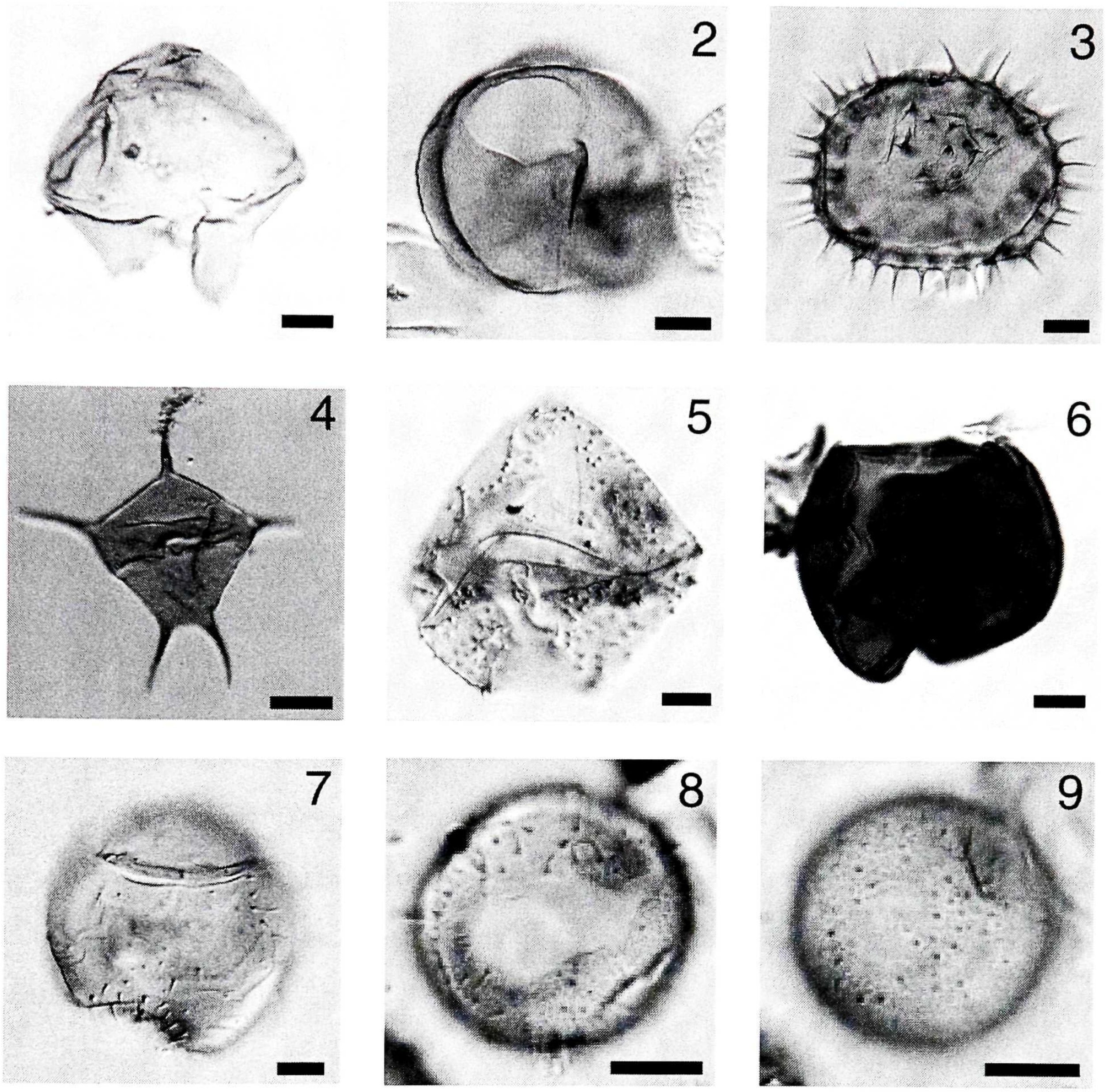

Plate V. Photomicrographs are bright field images. Scale bar, 10 μm.

1. *Quinquecuspis concreta*, NBH324, slide 2, N51/1, ventral surface.
2. *Selenopemphix nephroides*, CPE, slide 1, C49/0, apical surface.
3. *Selenopemphix quanta*, NBH346, slide 1, X58/4, apical surface.
4. *Stelladinium stellatum*, CPC, slide 1, Y59/2, dorsal surface.
5. *Trinovantedinium applanatum*, CPG, slide 1, O62/3, dorsal surface.
6. *Votadinium calvum*, NBH317, slide 1, dorsal surface.
7. *Votadinium spinosum*, CPG, slide 1, O62/3, dorsal surface.

8-9. Cyst type E, CPC, slide 2, dorsal surface (8), ventral surface (9).