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Changes in Planktonic Microbiota

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Introduction

In recent decades, many coastal waters all over the world have experienced remarkable changes from their historical norms. Ecosystems at the land-sea margin are forced by natural and anthropogenic processes originating from the coastal ocean, the atmosphere, and the land. These processes include nutrient enrichment, chemical contamination, hydrologic engineering, aquaculture, fishing, translocation of nonindigenous organisms, and climate change. Unfortunately, it is often not possible to discern a robust functional relationship between ecosystem forcing and response. For example, annual nutrient loading in San Francisco Bay is higher than in Chesapeake Bay, yet it is the latter that responds with high phytoplankton biomass, high primary production and hypoxic bottom waters. Such complexities have given rise to a more refined understanding of coastal ecosystems. This approach explicitly recognizes two important attributes of such ecosystems: first, that each system has specific features that modulate the response, and second, that there is a complex suite of direct and indirect responses (Cloern, 2001).

Halifax Harbour is a "living estuary": it is a functioning ecosystem that has preserved most of its basic functions (Mann, 2000). Although the harbour is apparently less biologically diverse and less productive of fish and shellfish than in the past, there has yet been no rigorous assessment of long-term trends in the lower trophic levels. In recent years, four volumes have summarized the research in Halifax Harbour (Nicholls, 1989a,b, 1991; Ducharme 2000), but there has been no explicit consideration of plankton distributions. Earlier, researchers at Dalhousie University (Riley, 1974; Lewis 1985) made useful contributions in their considerations of biological oceanography with respect to water quality in the habour, but scientific advances in the intervening years have led to the collection of a large volume of

different measurements that are here reviewed. The aim of this paper is therefore to describe the biomass and physico-chemical environment of the plankton microbiota in Halifax Harbour, and then to speculate on whether the long-term annual trends are local to the Harbour or are indicative of larger-scale changes.

Planktonic microbiota

The contemporary view of plankton foodwebs is now solidly grounded on a quarter century of new discoveries of microbial groups and new insights into trophic structures and functions (Kirchman, 2000). The planktonic microbiota span 4 orders of magnitude in size by cell length: they are the femtoplankton (0.02-0.2 μm), the picoplankton (0.2-2 μm), the nanoplankton (2-20 μm) and the microplankton (20-200 μm).

A recent overview of marine microbes has been published by Sherr and Sherr (2000), from which we may extract the following brief summary. The femtoplankton are the viruses. Here, we are not concerned with human and animal pathogenic enteroviruses. Instead, we focus on the large number of virioplankters infecting other plankton - largely bacterioplankton, and to a lesser degree phytoplankton. The picoplankton are a diverse assemblage comprising members from all 3 domains of life: Bacteria, Eukarya and Archaea. In the Bacteria, the dominant members are the heterotrophic prokaryotes and the photoautotrophic cyanobacteria. In the Eukarya, the members include picoalgae and picoheterotrophic flagellates. With exception, very little is presently known about Archaea in surface waters of temperate coastal waters. The nanoplankton include photosynthetic algae, heterotrophic flagellated protists such as chrysomonads, choanoflagellates, as well as mixotrophic forms of prymnesiophytes and prasinophytes. The microplankton include photosynthetic algae, and microzooplankton such as phagotrophic

dinoflagellates and heterotrophic ciliated protists typified by tintinnids. A microplankter of special note is the ciliate *Mesodinium rubrum*, which is photosynthetic by virtue of its chloroplasts "robbed" from cryptophyte algae. This cell chimaera occasionally forms a red-coloured bloom in Bedford Basin.

Earlier descriptions of plankton in Halifax Harbour were predicated on the traditional herbivorous food chain in which diatoms and dinoflagellates are consumed by copepods, which in turn are eaten by larger consumers. It is now evident that marine plankton communities are generally not structured this way, and that the herbivorous food chain is actually one end-member of a continuum of trophic pathways (Legendre and Rassoulzadegan, 1995). Clearly, efforts to monitor long-term change in plankton communities that rely solely on information gathered from nets with large mesh openings are a relic of an earlier era in oceanography and doomed to uncertainty. Statements about the state of the ecosystem cannot be regarded as conclusive without consideration of the significant biomass and turnover of the microbiota.

It is noteworthy that the longest and arguably the best monitoring program in biological oceanography (Continuous Plankton Recorder Survey) has embarked on an effort to enumerate picophytoplankters, bacteria and viruses collected by a towed water sampler in addition to the net-plankton collected by the conventional gauze filtering system (SAHFOS 1999 Annual Report). On the Scotian Shelf, evidence from the CPR surveys indicate that net-phytoplankton (diatoms and dinoflagellates) were higher in the 1990's than in the 1960's and early 1970's (www.meds-sdmm.dfo-mpo.gc.ca/alphapro/zmp/plankton/cpr/scotian_shelf_cpr_e.htm). We have also embarked on a program to monitor the picophytoplankton, bacteria and viruses in these waters.

Annual plankton cycle

The annual cycle of phytoplankton biomass in temperate coastal waters has been documented since the earliest days of biological oceanography, and understood to be regulated by seasonal changes in water column mixing and stratification. Recently, we described the annually recurring events in Bedford Basin from weekly observations made over a 9 year duration (Li and Dickie, 2001).

In Bedford Basin , the cycle is set into motion at week 7 or 8 of the year. This is the time of minimum temperature after which daily solar radiation increases and surface warming begins to stabilise the water column which has been intensely mixed over the winter. These factors initiate the spring bloom of phytoplankton, which may sometimes begin earlier in Bedford Basin than offshore. At this time, nutrients decrease rapidly from their winter maxima to supply the growth of phytoplankton biomass (chlorophyll). This biomass reaches a peak at week 11 or 12 during the spring equinox.

From the spring equinox to the summer solstice (week 25 or 26), there is intense microbial growth, even as bulk chlorophyll decreases. The total number of phytoplankton cells increases, in small part due to cryptophytes, and in spite of a decrease in the cyanobacterium *Synehcococcus*. The picophytoplankton make up an increasingly larger percentage of total chlorophyll biomass (from a low of 15% to a high of 55%) during these weeks. The heterotrophic bacteria and viruses increase at sustained rates to respective maxima at the summer solstice. As well, microzooplankton biovolume increases. Through this period, there is an increased flux of regenerated nutrients, but this is largely balanced by the flux of uptake as spring progresses.

The summer, from the solstice to the autumn equinox (week 37 or 38) is perhaps the most interesting part of the year from a microbial point of view. The thermocline is fully formed and surface nitrate approaches undetectable limits, but ammonium is available as a result of microbial regeneration. Both bacteria and viruses fall off slightly from their maxima but remain relatively abundant throughout the summer. This is also the time of year when the ratio of viruses to bacteria is highest. The weekly average concentration of chlorophyll increases, building up to a peak (the fall bloom) in September. Throughout the summer, primary production is at levels almost as high as in the spring. Short-lived blooms of dinoflagellates are not unusual, but they do not recur with annual regularity. One such bloom in 1993 led to the highest value of chlorophyll recorded in this basin (109 mg m^{-3}).

Summer culminates in the autumn equinox when water temperature is at its highest average value for the year. This is the time of maximum phytoplankton abundance, and accounts for the peak of the fall bloom as measured by bulk chlorophyll . It is also the time of maximum tintinnid abundance, maximum microzooplankton biovolume, and maximum microbial biomass as measured by particulate ATP.

From the autumn equinox to the winter solstice, the stratification of the water column begins to be eroded by lower air temperatures and stronger winds, bringing nutrients to the surface. However, increased discharge from the Sackville River and lower surface salinity retard the destratification to some extent. Before the solar radiation becomes too low, there is an opportunity for moderate phytoplankton renewal; for example as a short-lived bloom of the dinoflagellate *Ceratium longipes*. After the winter solstice, the water column is completed destratified and the microbial populations, excepting *Synechococcus*, reach their annual minima.

In summary, the surface waters of Bedford Basin exhibit general features common to many coastal plankton systems dominated by phytoplankton biomass and production. A major bloom of phytoplankton biomass in spring is fueled by nitrate, a lower but sustained level of phytoplankton biomass in summer is fueled by recycling activities of bacteria and viruses, a secondary bloom of phytoplankton biomass develops in autumn, and a return to lowest community biomass occurs in winter.

Spatial gradients

The physical setting of the Halifax inlet system (Fig. 1) has been well-described in previous volumes (Nicholls, 1989a,b, 1991; Ducharme 2000). Very briefly, the innermost part of the system is Bedford Basin, which is 6 km long, 17 square km in area, and 70 m in maximum depth. Seaward of the Basin is a shallow sill marking the inner portion of Halifax Harbour, which is 8 km long, 0.5 to 1.5 km wide, and only 20 m in depth. The outer portion of the Harbour is also about 6 km long, but much wider at 7 km, and 20 to 30 m deep. A line drawn from Chebucto Head to Devil's Island is usually taken to demarcate Halifax Harbour from the continental shelf.

The physical oceanography of the inlet system is also quite well-understood (Ruddick, 1985a,b). Essentially, Halifax Harbour is an estuary in which the mixing, dispersion and flushing of seawater are affected by freshwater discharge from the Sackville River entering the head of the Basin, by tidal currents, by winds, and by occasional intrusions of dense shelf water forced by upwelling.

A transect of 11 stations extending from the head of the inlet at Bedford Bay to the continental shelf beyond Chebucto Head (Fig. 1), sampled at 1,5 and 10 m depths, reveals the

zonation of the 3 areas: Bedford Basin, inner harbour, and outer harbour. On October 1, 1996, temperature, freshwater content, inorganic nutrients (nitrate, phosphate, silicate), dissolved organic carbon, particulate organic carbon and particulate organic nitrogen were all highest in Bedford Basin (Fig 2). The inner and outer harbours were similar to each other in their cooler and saltier waters, but the outer harbour was much lower in nutrients and slightly lower in POC and PON (Fig. 2).

The zonation was also evident in phytoplankton composition (Fig. 3) and microbial abundance (Fig. 4). The general decrease of total phytoplankton biomass (Chl *a*) from inshore to offshore was reflected to varying degrees by diatoms (fucoxanthin), dinoflagellates (peridinin), cryptophytes (alloxanthin) and cyanobacteria (zeaxanthin). However, the "green" algae (Chl *b*) and especially the prymenesiophytes (19'-hexanoyloxyfucoxanthin) were more favoured offshore than inshore (Fig. 3). Presumably, these latter groups are the taxa comprising many of the picophytoplankters and nanophytoplankters whose total abundance increased from inshore to offshore (Fig. 4). Bacteria were distributed fairly uniform across the transect, except perhaps at Georges Island where they were not only most abundant, but also appeared to have a larger genome (Fig. 4). Viruses were more abundant in Bedford Basin than in the inner and outer harbours (Fig. 4).

Although the dataset for October 1, 1996 has been chosen to illustrate the inshore-offshore gradients, it is necessary to note that the conditions on this week in Bedford Basin were a departure from their long-term climatological averages. In particular, the temperature and nutrient concentrations were significantly higher from weeks number 37 to 40 in 1996 than the long-term averages. In other words, the gradients we display for week 40 in 1996 were not

typical for the average week 40. It will be pointed out later that the average conditions in Bedford Basin are the same as on the adjacent continental shelf areas.

Long-term trends

Since late 1991, weekly observations have been made at the Compass Buoy station in Bedford Basin. This monitoring program provides a unique dataset to examine plankton changes at weekly, monthly, seasonal and annual scales (www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/BedfordBasin.htm). For example, the time series (Fig. 5) has been used to compute the weekly averages on which the earlier description of annual plankton cycles was based (Li and Dickie, 2001).

In this section, we examine the long-term trends by considering data averaged at the annual time scale. Generation times of microbial plankton are of course much shorter and the community undergoes many successional events over the period of a year. However, the cycle of seasonal change returns the community to a state more or less similar to that from which it started 12 months previously. The question we pose is whether all the events that occur over a 12 month period, taken together, lead to a systematic change in the net state as the years go by.

Data prior to 1992 were extracted from a collection of 11 technical reports referenced in Li et al. (1998). Measurements of water temperature, nutrients and chlorophyll were available for a number of years back to 1967, but the record is not continuous (Fig. 6). The data give an impression that in the 1990's, the winters have become warmer, and that the concentrations of nitrate and phosphate have become greater (Fig. 6).

The computed annual average temperatures indicate that the water has warmed a remarkable 2^{o}C over 33 years (Fig. 7). On an annual average basis, nutrients and chlorophyll, however, do

not display any convincing, systematic trends (Fig. 7). In recent years, nitrate, phosphate and chlorophyll appear higher, while silicate appears lower than 3 decades ago - but these trends, with the exception of phosphate, do not satisfy the generally accepted criterion for statistical significance. On the other hand, the nutrient trends, weak though they may be, occur in opposite fashion for silicate versus nitrate and phosphate. For this reason, there is a downward trend in the ratios of silicate:nitrate and silicate:phosphate.

In other coastal waters, such as the Irish Sea, the Mississippi River, the Bay of Brest and the German Bight, the Si:N ratio has also shown decadal-scale decreases (Cloern, 2001). Since silicate is required as a macronutrient only by diatoms, other phytoplankters are at a competitive advantage when nutrient ratios shift towards silicate limitation. In the German Bight from 1962 to 1984, long-term reductions in the silicate ratios were accompanied by increases in phytoflagellates and decreases in diatoms. In Bedford Basin, full-year records for floristic composition are available only for recent periods. From 1993 to 2000, there has been a substantial increase in the abundance of nanophytoplankters as well as the picoplankter *Synechococcus* (Fig. 7); unfortunately, the information for diatom abundance is yet unavailable. At present, it is not possible to say whether the recent apparent increase in non-diatom phytoplankters is a long-term trend; and if so, whether it is a response to increased temperature, to altered nutrient ratios or to other factors.

The abundance of heterotrophic bacteria in Bedford Basin appears to have remained invariant at an annual average value of 2 million cells per mL from 1992 to 2000 (Fig. 7). A global survey of annual average bacterial abundance has demonstrated that 79% of its variance in temperate and polar waters can be explained by annual average temperature (Li, 1998). The abundance of bacteria in Bedford Basin is almost exactly that which is predicted by this relationship.

Bedford Basin and the Scotian Shelf

Bedford Basin is connected to the adjacent continental shelf through a sill and a long channel. The exchange of shelf and inshore water, largely caused by alongshore winds driving Ekman transport, exerts strong control of the nutrient and chlorophyll regimes in the Basin. At a certain time scale, Bedford Basin loses its autonomy as an independent ecological unit because external physical forces dominate the intrinsic biological dynamics (Lewis and Platt, 1982). From considerations of physiography and water exchange at the inlet mouth, it has been estimated that the length of time required to flush the upper layers of Bedford Basin may typically be as few as 3 to 5 days (Lewis and Platt, 1982), or may be susbtantially longer (Ruddick, 1985a,b). At shorter time scales, aperiodic events occur in which local biological signals may override general seasonal patterns. These include exceptional events of red-water discolouration attributed to the dinoflagellates *Gonyaulax digitale* and *Dinophysis norvegica*.

At the time scale of one week, the computed climatologies in Bedford Basin may in fact be reasonable exemplars of the adjacent shelf (Fig. 8). Indeed, weekly average temperatures and nutrient concentrations in Bedford Basin might be used to interpolate monthly average values on the central Scotian Shelf, which have been published by Petrie et al. (1996, 1999). The coupling of Bedford Basin to the adjacent continental shelf at longer time scales suggests that there may be close similarities in the annual sequence of recurring biological events in these areas. To date, measurements of microbiota on the Scotian Shelf in the Atlantic Zone Monitoring Program confirm a similar annual cycle of microbial events, such as the emergence of picophytoplankton in the autumn (Fig. 9).

Conclusions

Since 1967, the surface waters of Bedford Basin have increased in temperature by about 2^{o}C on an annual average basis. During this period, there appears to have been a weak shift in the ratios of the dissolved inorganic macronutrients favouring nitrate and phosphate over silicate. Although total phytoplankton biomass as indexed by chlorophyll *a* appears not to have changed systematically, there has been an increase in the number of smaller cells (nano- and picophytoplankton) since at least 1993. At the monthly and seasonal scales, Bedford Basin and the adjacent area on the Scotian Shelf are similar with respect to temperature, nutrient concentrations and microbial standing stocks. It remains to be seen whether the long-term trends in these two areas are concordant.

Acknowledgements

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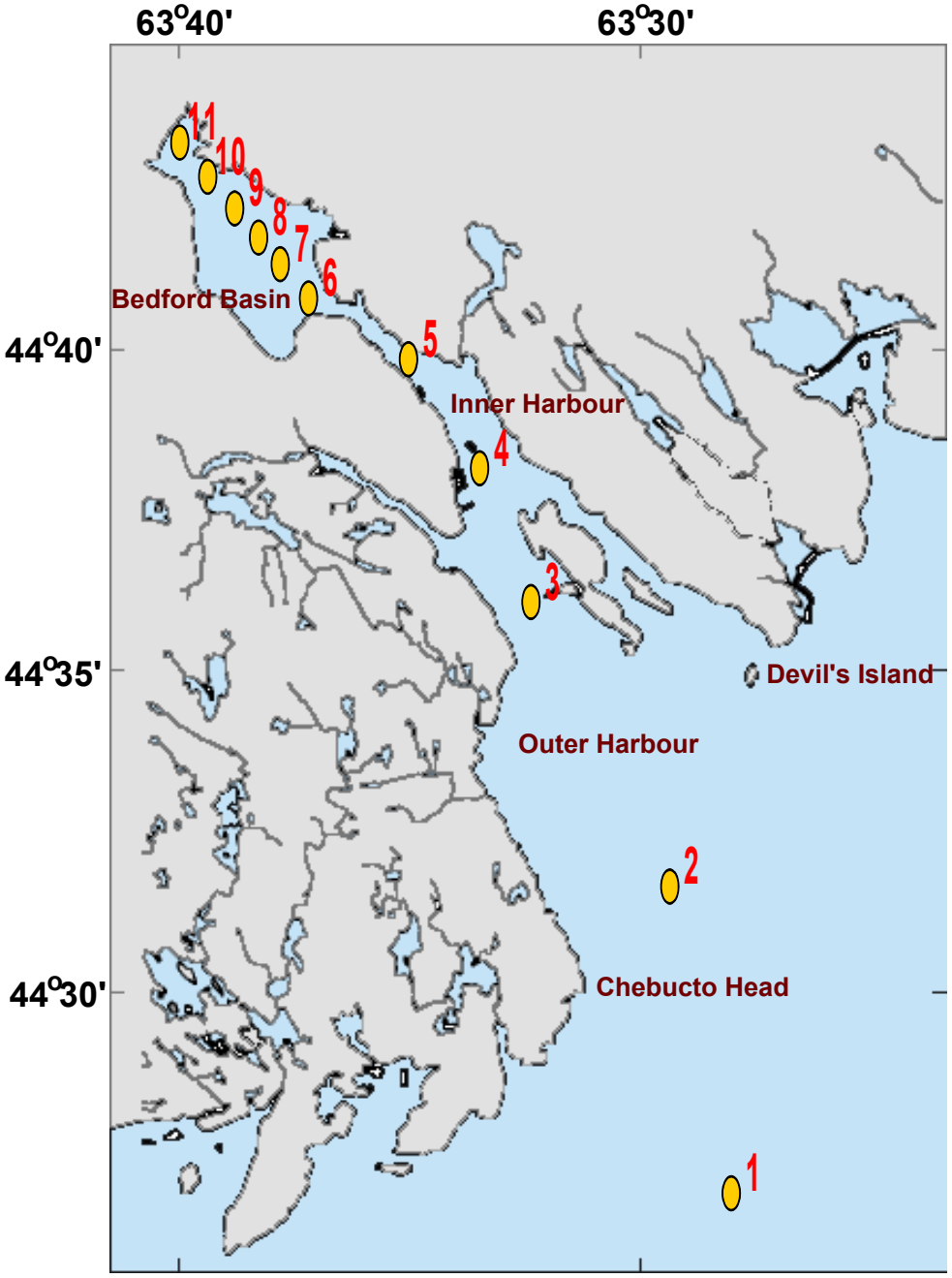
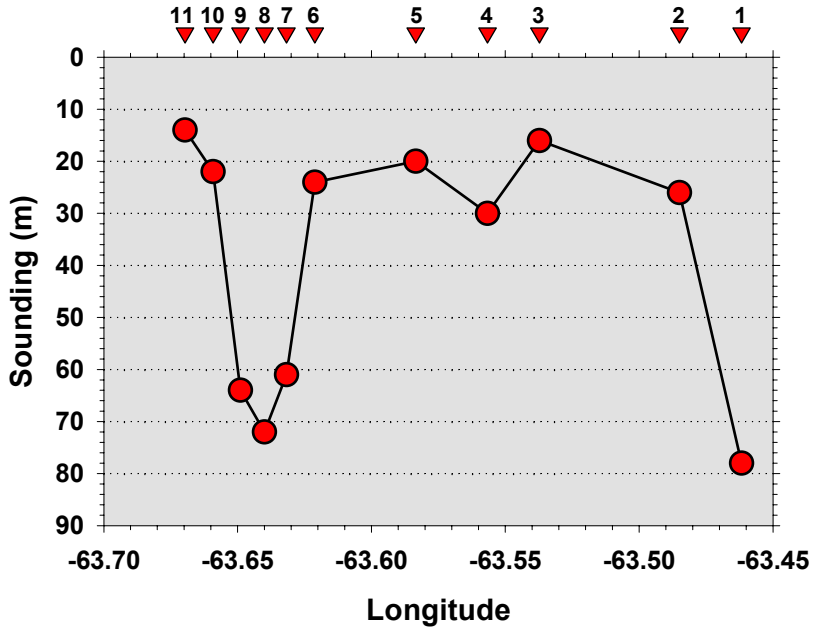
Figure 1 Sampling stations along Halifax Harbour transect: October 1, 1996





11 Bedford Bay
10 Downey Bluff
9 Magazine Jetty
8 Compass Buoy
7 Birch Cove
6 MacKay Bridge
5 MacDonald Bridge
4 Georges Island
3 York Redoubt
2 Portuguese Cove
1 Chebucto Head

Figure 2 Physico-chemical variables along Halifax Harbour transect: October 1, 1996

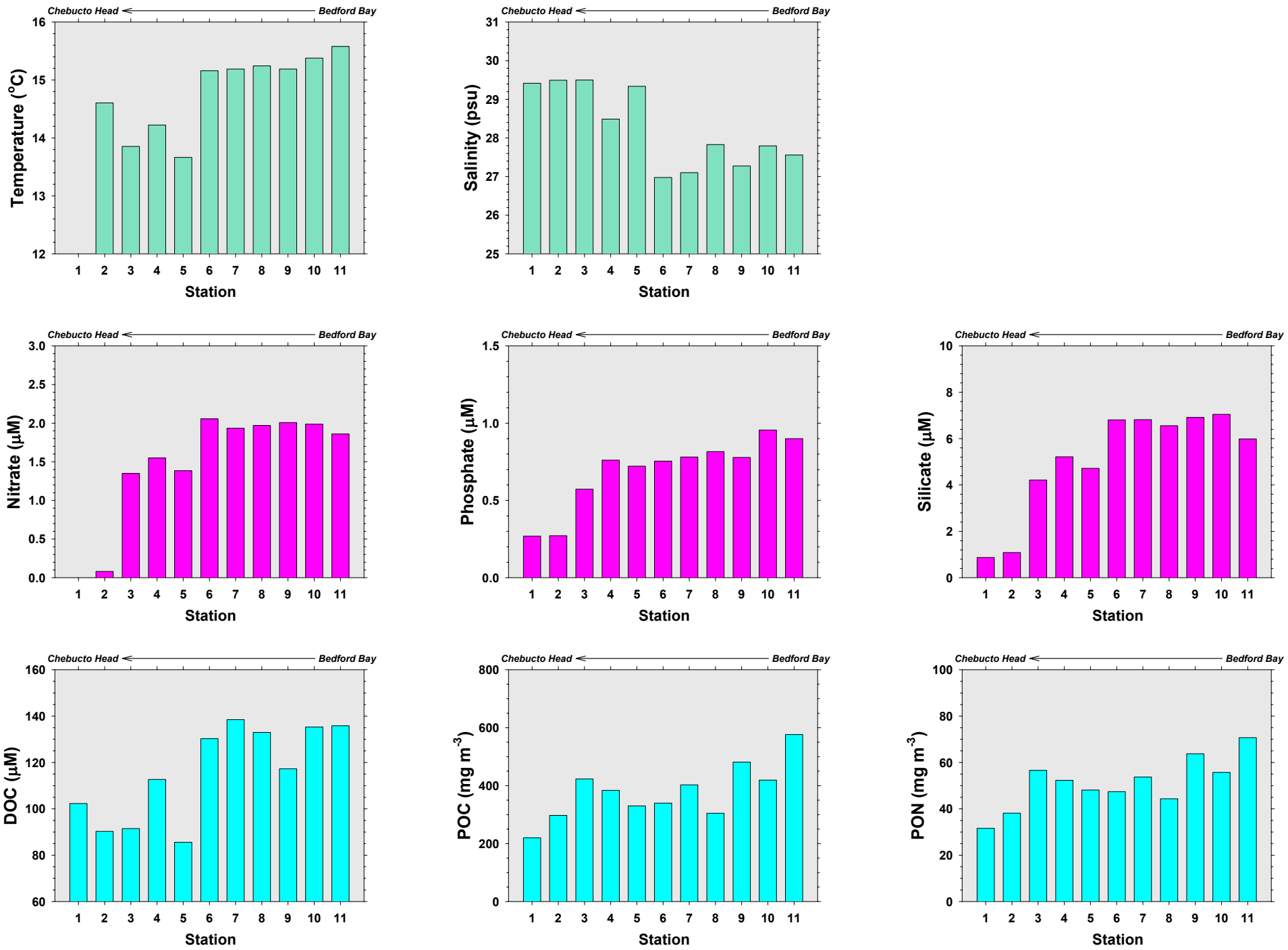


Figure 3 Photosynthetic pigments along Halifax Harbour transect: October 1, 1996

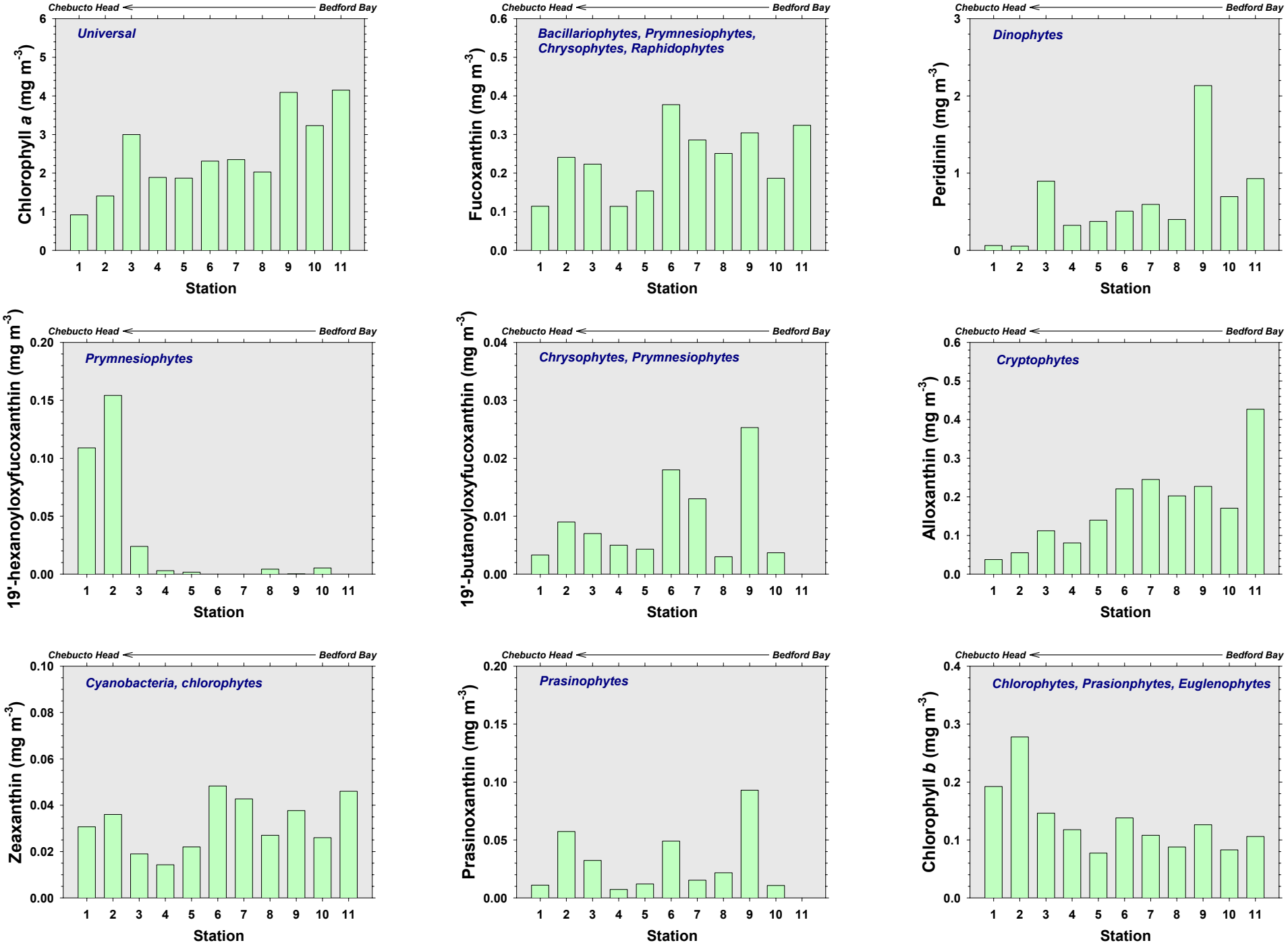
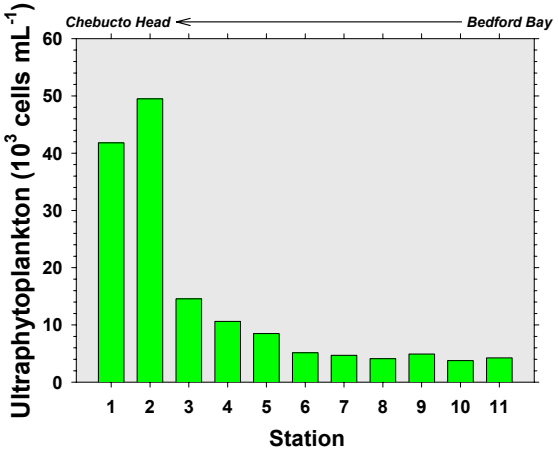
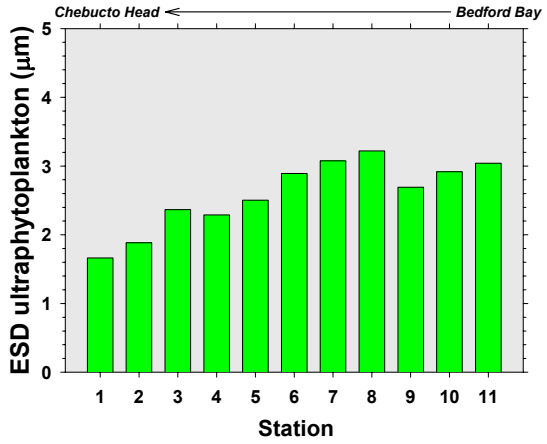
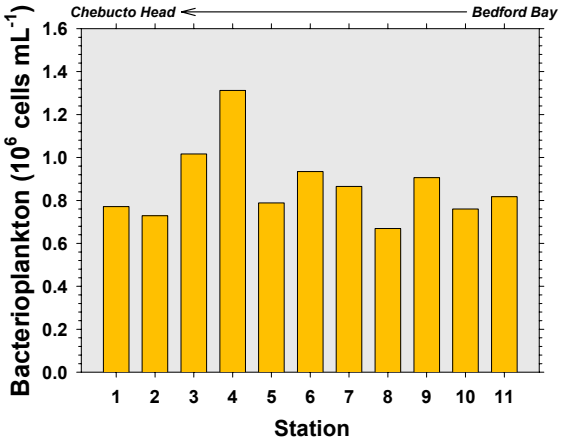
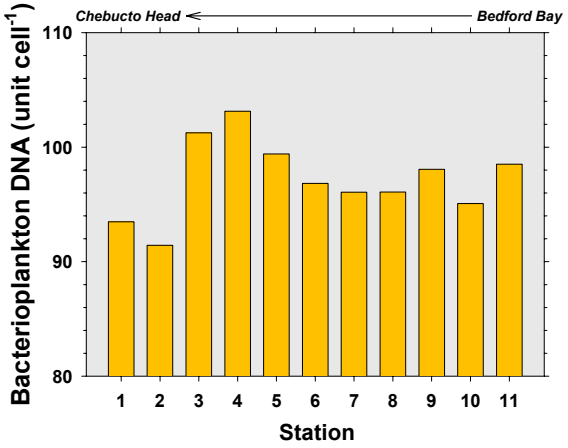


Figure 4 Microbial plankton abundance and cell properties along Halifax Harbour transect: October 1, 1996









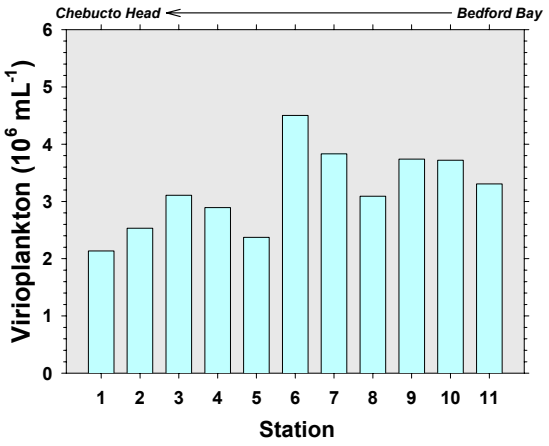


Figure 5 Time series of temperature amd microbiota at the Compass Buoy, 1992-2000.

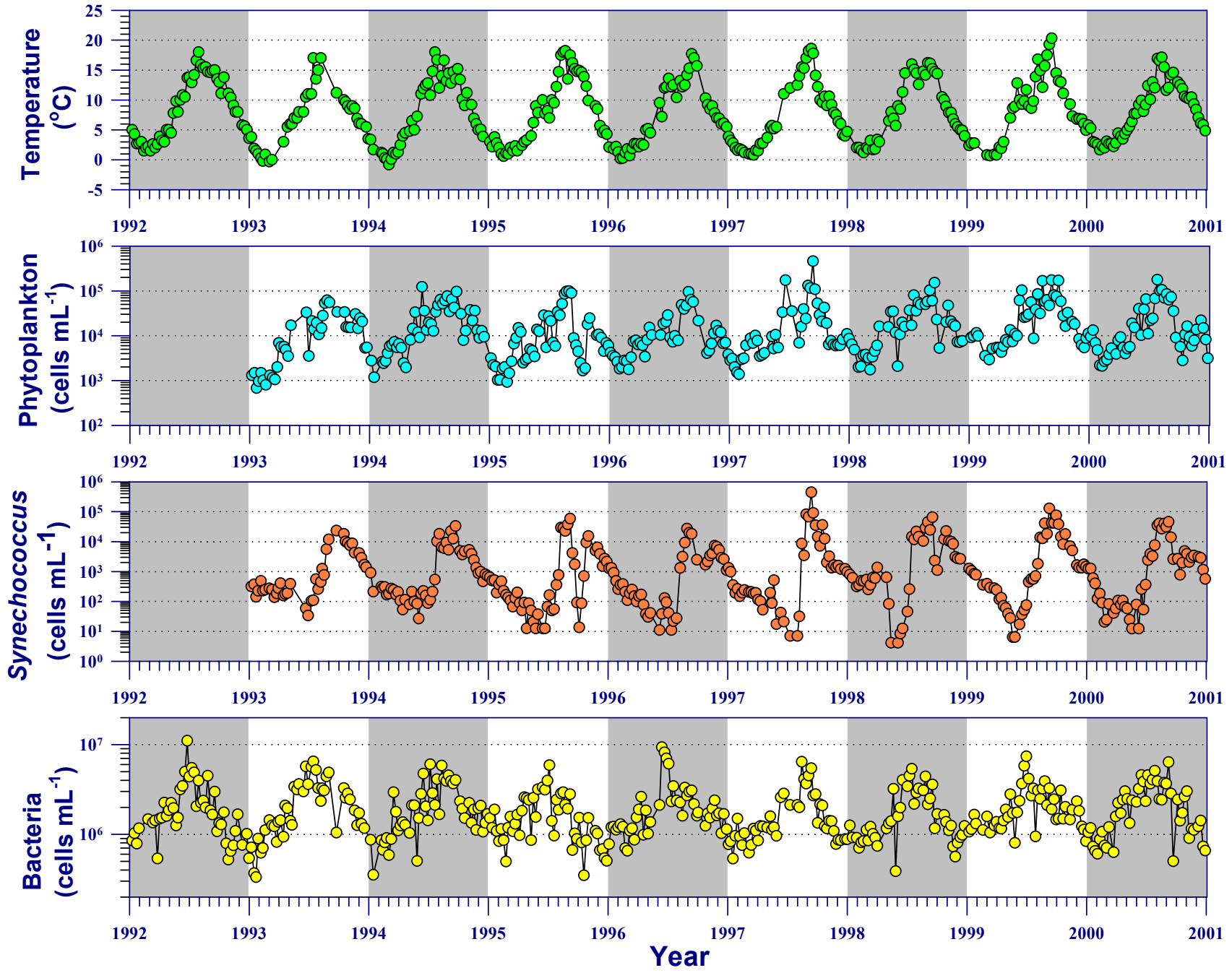


Figure 6 Time series of temperature and nutrients at the Compass Buoy, 1967-2000

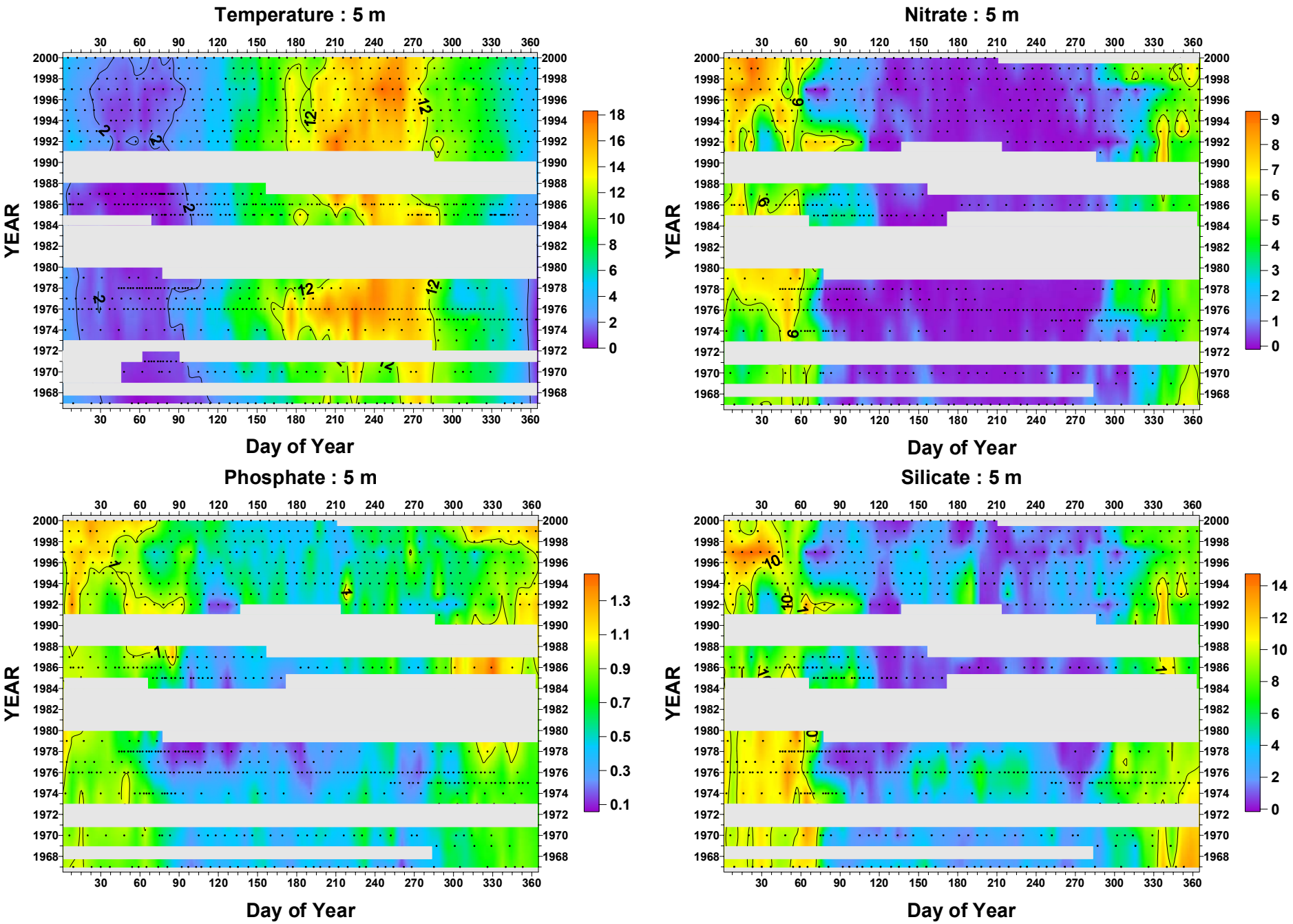


Figure 7 Annual averages of temperature, nutrients, chlorophyll and microbiota at the Compass Buoy, 1967-2000

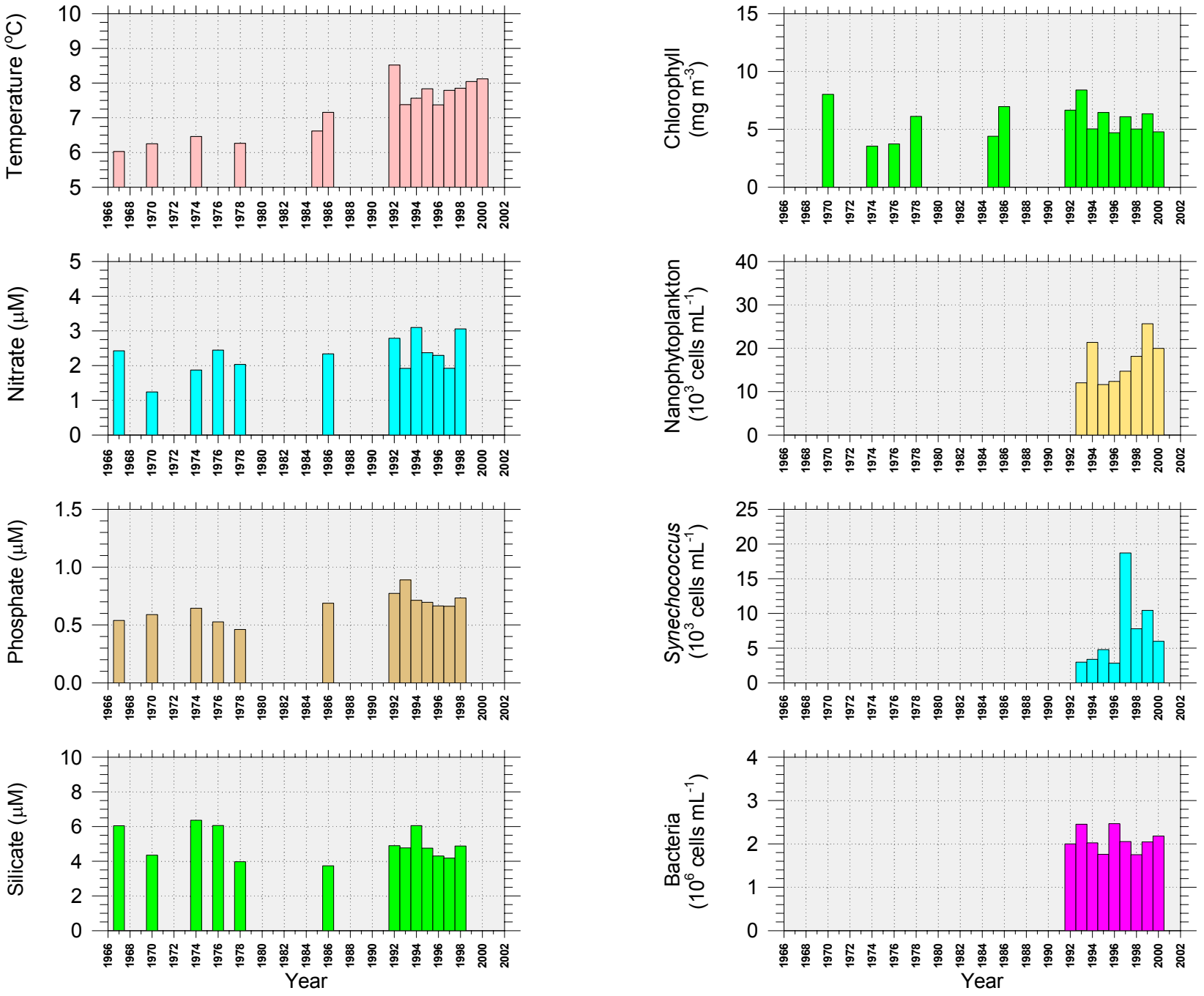


Figure 8 Nutrients and their ratios: weekly averages in Bedford Basin compared with monthly averages on the central Scotian Shelf

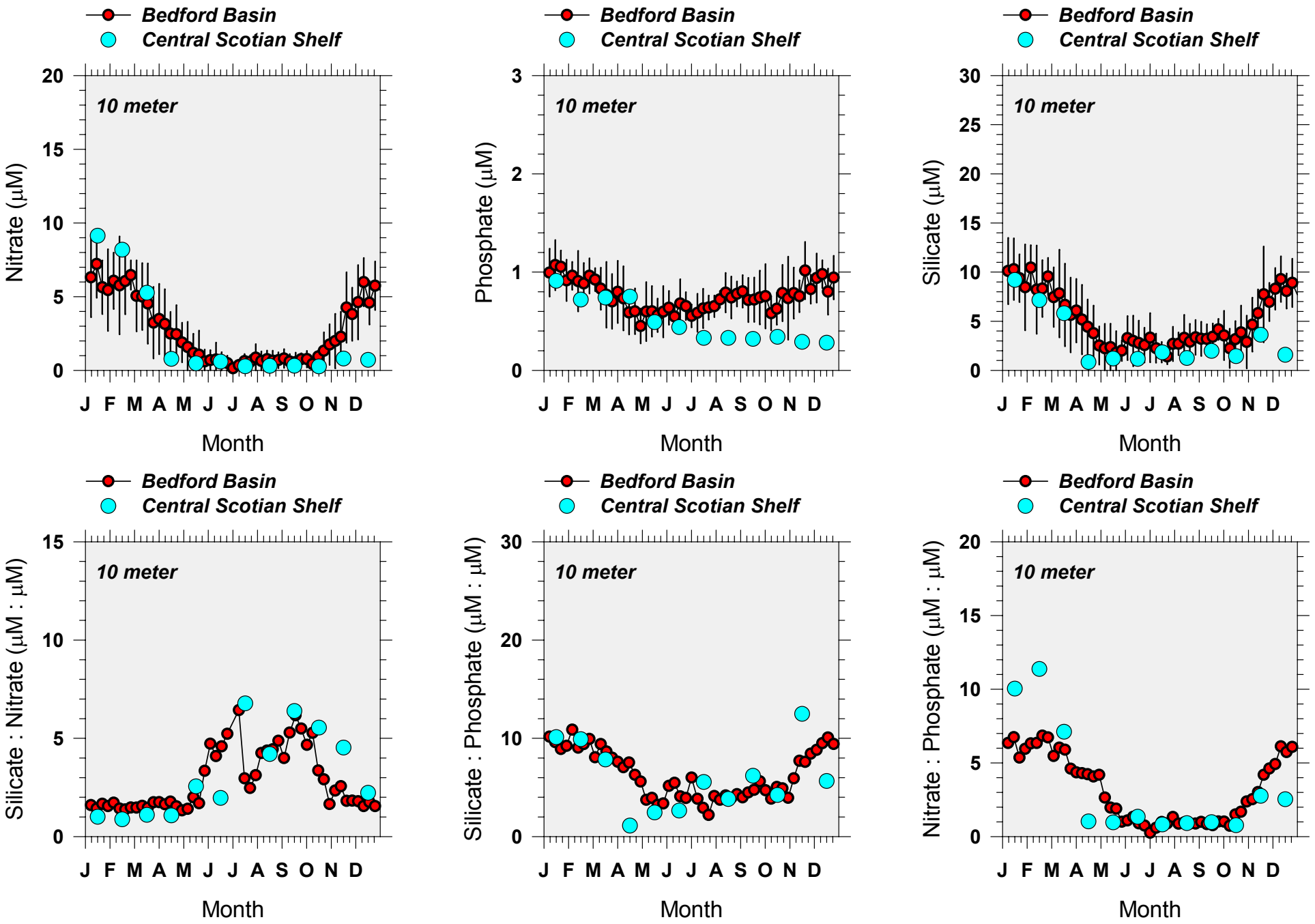


Figure 9 Microbial standing stocks along the "Halifax Line" stations 1 to 7, spring (IV) and fall (X) 1997-2000