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SPATIAL AND TEMPORAL DYNAMICS OF PHYTOPLANKTON ASSEMBLAGES IN TIDEPOOLS: EFFECTS OF THE PHYSICAL ENVIRONMENT, THE NUTRIENT REGIME AND THE GRAZER FIELD

by

Anna Metaxas

Submitted in partial fulfillment of the requirements

for the degree of Doctor of Philosophy

at

Dalhousie University

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by Anna Metaxas

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

This thesis examines the temporal and spatial dynamics of phytoplankton assemblages, and of biotic (e.g. macroalgae, macrofauna, planktonic and benthic micrograzers) and abiotic (e.g. nutrients, temperature, salinity, pH) factors that may regulate these assemblages in tidepools, on a rocky shore, near Halifax, Nova Scotia, Canada. The abundance of phytoplankton changed over the period of tidal isolation of the pools, but these changes varied among phytoplankton groups, and within groups between a time of low phytoplankton abundance and during an autumn bloom in the surrounding seawater. The grazer field and variability in the chemical and physical environment over the period of tidal isolation did not adequately explain the few recorded changes in phytoplankton abundance. Over a period of 16 months, there was little indication of vertical zonation of the phytoplankton assemblages along the intertidal gradient, and differences among zones rarely explained more than 30% of the spatial variability in phytoplankton abundance. However, the abundance of all groups of phytoplankton varied significantly among pools within intertidal zones on most sampling dates, and differences among pools explained up to 96% of the variability in phytoplankton abundance. Furthermore, there was significant variability among pools within zones for all biotic and abiotic characteristics of the pools on most sampling dates. In separate studies, I showed that there also was large variability among pools within intertidal zones in the structure of the macrobenthic and hyperbenthic assemblages. In factorial field manipulations, I examined bottom-up (nutrient availability) and top-down (grazing) effects on the composition of phytoplankton assemblages in tidepools. There were no significant bottom-up or top-down effects on any phytoplankton group in experiments conducted in November 1992 or June 1993. Although there was some variability among pools, both a reduction in grazer density and nutrient enrichment had a positive effect on some groups of phytoplankton but a negative effect on others in experiments conducted in July and August 1993. The strength of top-down effects was greater than that of bottom-up effects for all groups of phytoplankton in July 1993, but only for two groups in August 1993. The results of this thesis suggest that the factors that regulate the temporal and spatial dynamics of phytoplankton assemblages in tidepools probably operate at the scale of the individual pool rather than the intertidal zone. The mechanisms of community regulation in tidepools differ from those on emergent substrata of rocky shores, probably due to differences in the tidal influence on the two habitats.

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This project involved extensive field sampling and I am thankful to a number of people that helped: Emily Chin, Laurence McCook, Todd Minchinton and Ellen Pedersen. However, I could not thank enough Heather Hunt, Don Webb and Brian Dixon who endured the largest number of field trips under my not-always-pleasant "command" (especially when departure time was at 5:30 a.m., or even before 10:00 a.m.) on a few nice, hot days, but also on a lot of long, very cold, wet days, with a bag of 'Chunks Ahoy' for reward: Thanks guys, I could not have done it without you!

I would like to thank a number of other people that helped with various aspects of this work: Pierre Clement at the Marine Chemistry Division of the Department of Fisheries and Oceans at the Bedford Institute of Oceanography (Dartmouth, Nova Scotia, Canada) for analyzing the nutrient samples for nitrate+nitrite, phosphate and silicate; Annamarie Hatcher for sharing some of her knowledge on ammonium analysis (and her automatic pipetor); Charlie Thompson for building the enclosures for the experiments on very short notice; Don Webb for teaching me invertebrate identification; Myriam Barbeau, Heather Hunt, Laurence McCook, Todd Minchinton

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Μανα και πατερα: σας ευχαριστω για την αγαπη σας, την υποστηριξη, τη δυναμη και το κουραγιο που μου δωσατε τα 12 χρονια των σπουδων μου. Επιτελους, οι σπουδες τελειωσαν.

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PREFACE

Some of the research described in this thesis has been published or is in press in the scientific literature. The references to the publications are as follows:

Portions of Chapter 1 are also presented in:

Metaxas, A., and R. E. Scheibling. 1993. Community structure and organization of tidepools. **Marine Ecology Progress Series** 98: 187-198.

The research in Chapter 2 is also described in:

Metaxas, A., H. L. Hunt, and R. E. Scheibling. 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada. **Marine Ecology Progress Series** 105: 89-103.

The research in Chapter 3 is also described in:

Metaxas, A., and R. E. Scheibling. 1994. Spatial and temporal variability of tidepool hyperbenthos on a rocky shore in Nova Scotia, Canada. **Marine Ecology Progress Series** 108: 175-184.

Written permission was obtained from Inter-Research to include the material in these 3 publications in my thesis.

The research described in Chapter 4 is also described in:

Metaxas, A., and R. E. Scheibling. 1994. Changes in phytoplankton abundance in tidepools over the period of tidal isolation. **Botanica Marina** 37: xxx-xxx.

CHAPTER 1: General Introduction

The goal of community ecology is to describe patterns of distribution and abundance of species' assemblages and to understand the processes that give rise to these patterns (Begon *et al.* 1986, Diamond & Case 1986). These processes include biological interactions, such as herbivory, predation and competition, as well as the effect of the physical environment. Community ecologists must understand how and when these regulatory mechanisms operate in community organization, if they are to develop ecological models of broad scope and validity.

A plethora of literature exists on the establishment and organization of communities that inhabit the emergent substrata of rocky intertidal shores. A number of studies have described the general structure of rocky intertidal communities on temperate shores throughout the world (e.g. Pyefinch 1943, Stephenson & Stephenson 1950, 1952, 1954a, b, Underwood 1980, Moore & Seed 1986, Brattstrom 1990, Janke 1990). Other studies have reviewed processes of community organization on rocky intertidal shores (e.g. Connell 1972) and provided models of community regulation (e.g. Lubchenco & Gaines 1981, Connell 1983, Connell & Sousa 1983, Hawkins & Hartnoll 1983, Dayton 1984, Sousa 1984a, Underwood & Denley 1984, Vadas 1985, Menge & Farrell 1989).

The biotic communities of tidepools are less well-studied than those of the emergent substrata of rocky intertidal environments. The literature on tidepool communities has not been reviewed to date and is scattered among several fields such as rocky intertidal ecology, fish biology and natural history. It has even been suggested that pools do not 'represent an intertidal habitat' since 'organisms in pools 'are not emersed during low tide' (Underwood 1981a). Nonetheless, conditions in tidepools, as on emergent substrata, are highly regulated by the tidal cycle. The degree of fluctuations in physical conditions of tidepools will vary greatly with intertidal height, with lower pools being less variable than

higher pools. However, the degree of fluctuation is less than that of the emergent substrata and tidepools are potentially important as refuges from stressful environmental conditions.

This chapter summarizes tidepool community structure and compares the processes that regulate structure between tidepools and emergent substrata. I identify deficiencies in our understanding of community organization and suggest potential uses of these habitats to evaluate general ecological theories. Because of the scarcity of information on some aspects of community organization in marine tidepools, I also have included pertinent studies on freshwater rockpools. Since both habitats represent environments with some similar conditions (e.g. isolated habitats with well-defined boundaries), the regulating factors of community organization may operate in a similar fashion. For the purposes of this chapter, tidepools harbour marine communities and are located on rocky intertidal shores. They receive input from the surrounding sea-water varying from regular submergence (low to high tidepools) to occasional spray during storms (splash pools). In contrast, rockpools harbour freshwater communities and are located higher on the shore between the rocky intertidal and terrestrial habitats.

TIDEPOOLS

Physical environment

The physical environment of tidepools does not fluctuate as much as that of emergent substrata, and the inhabitants of pools remain submerged for the entire tidal cycle; however, the fluctuations are larger than would be encountered under constant submergence in the subtidal zone. Temperature can vary daily by up to 15 °C, depending upon the height of the pool along the intertidal gradient (and, therefore, the extent of isolation from the tide), wave exposure, the degree of shading, and the volume of the pool (Brooker Klugh 1924, Stephenson *et al.* 1934, Pyefinch 1943, McGregor 1965, Green 1971, Daniel & Boyden 1975, Goss-Custard *et al.* 1979, Morris & Taylor 1983, Huggett

& Griffiths 1986). Daily changes in temperature can often result in thermal stratification of the water-column of splash pools (McGregor 1965). Fluctuations in salinity depend upon the height of the pool on the shore (Pyefinch 1943) and may range between 5 and 25 (Lami 1931, Pyefinch 1943, Green 1971, Morris & Taylor 1983). Brooker Klugh (1924) and Daniel & Boyden (1975) found little variability in salinity over a period of at least 1 tidal cycle; however, Brooker Klugh (1924) measured salinity in only 2 tidepools and Daniel & Boyden (1975) monitored salinity for only 9 h after tidal input. Salinity stratification will arise seasonally because of freezing in the winter (Naylor & Slinn 1958, Ganning 1971), evaporation in the summer, and rainfall (Morris & Taylor 1983). Salinity stratification also may occur due to runoff into the pools (Green 1971). Daily fluctuations in oxygen saturation, alkalinity and pH have been recorded, which are due to biological processes in tidepools (Pyefinch 1943, McGregor 1965, Ganning 1971, Green 1971, Daniel & Boyden 1975, Morris & Taylor 1983). Huggett & Griffiths (1986) recorded higher oxygen values in the daytime (when photosynthesis is occurring) and lower values at night. Daniel & Boyden (1975) observed vertical oxygen stratification in the water-column in the daytime but no stratification at night. Daily fluctuations in pO_2 and pCO_2 can vary with season (Morris & Taylor 1983), height of the pool along the intertidal gradient (Daniel & Boyden 1975) or pool depth (Goss-Custard *et al.* 1979). The amplitude of daily fluctuations of temperature, salinity and pH also varies seasonally (Ganning 1971).

The physical environment of the tidepool fluctuates vertically, horizontally, diurnally and seasonally, although not as much as the adjacent emergent rock surfaces. The fluctuations, in turn, will vary with the volume, surface area and depth of the pool, as well as its height on the shore, degree of shading, drainage pattern (which depends upon the aspect) and exposure to waves and splash. It is virtually impossible for 2 natural tidepools to be similar in all these characteristics: individual tidepools are unique in their physical regime.

Community structure

Studies on species assemblages in tidepools have been mostly descriptive and many have examined only 1 or 2 pools on a shore or recorded only presence or absence of the flora and fauna (e.g. Brooker Klugh 1924, Pyefinch 1943, Naylor & Slinn 1958, Ganning & Wulff 1969, Ganning 1971, Aleem 1973, Femino & Mathieson 1980, Preston & Moore 1988, Brattström 1990). The types of organisms recorded have varied from marine diatoms (Metaxas & Lewis 1992) to vascular plants and bryophytes (Haeggström & Skytén 1987), and from invertebrates (Ganning 1971) to fish (Green 1971).

The biological assemblages that inhabit tidepools are generally similar to those described for emergent substrata. Differences between the 2 types of habitats may arise because of smaller fluctuations in physical conditions and/or more intense biological interactions in the pools. Several taxa are more abundant in pools than on emergent substrata. These include algae [e.g. the genera *Ceramium, Spongomorpha, Corallina* and *Rhizoclonium* in Maine, U.S.A. (Johnson & Skutch 1928), *Prionitis* in Washington, U.S.A. (Dethier 1982), and *Fucus distichus* in Nova Scotia, Canada, (Chapman & Johnson 1990)] and gastropods [e.g. the genus *Cellana* in New South Wales, Australia, (Underwood 1976) and *Littorina littorea* in Massachusetts, U.S.A. (Lubchenco 1982)]. Other species are absent or occur in lower densities in pools than on the emergent rock, (e.g. some fucoids such as *Fucus vesiculosus* and *Ascophyllum nodosum* (Lubchenco 1982) and barnacles in New England, U.S.A. (Singletary & Shadlou 1983)) The physically imposed upper limits of the distribution of some organisms are extended in tidepools compared to emergent substrata. For example, macroalgae such as fucoids, *Scytosiphon, Spongomorpha* and *Ulva* occur at higher intertidal levels in tidepools than on the emergent rock surfaces, on the northeast coast of North America (Johnson & Skutch 1928, Femino & Mathieson 1980, Chapman & Johnson 1990). Similar observations have

been made for mussels, chitons, limpets and sea urchins in tidepools in British Columbia, Canada (Green 1971), and for the surfgrass *Phyllospadix* in Washington, U.S.A. (Dethier 1984). Tidepools also provide an extra habitat dimension for their occupants, the water-column. Phytoplankton, zooplankton and fish can be encountered in pools at all times, as opposed to only at high tide for emergent substrata. In particular, pools may provide refuge for fish of varying sizes (Thompson & Lehner 1976, Moring 1990).

A number of studies have documented the zonation of tidepool biota along the intertidal gradient. Droop (1953) classified 9 types of pools in Finland, based on their position along the intertidal gradient: intertidal seawater pools, permanent rockpools in the normal splash zone, stagnant brackish pools, seaweed pools, ephemeral rain pools, permanent rain pools, moss pools, rock sphagneta, and marsh. He examined the phytoplankton communities of these pools and concluded that the lowest abundances of flagellated and non-motile, planktonic microalgae were in the intertidal and splash pools. In British Columbia, Canada, Metaxas & Lewis (1992) found that centric diatom abundance decreased in pools higher on the shore while pennate diatoms tended to increase.

Macroalgae in tidepools also show zonation along the intertidal gradient, with some green algae (e.g. *Enteromorpha, Cladophora* and *Chaetomorpha*) usually dominating higher on the shore while other green algae (e.g. *Spongomorpha*), brown algae (*Fucus, Laminaria, Scytosiphon)* and corallines (*Lithothamnion, Corallina*) being most abundant lower on the shore (Fraser 1936, Green 1971, Daniel & Boyden 1975, Goss-Custard *et al.* 1979, Femino & Mathieson 1980, Dethier 1982, 1984, Sze 1982, Wolfe & Harlin 1988a, Kooistra *et al.* 1989). Gustavsson (1972) used macroalgal zonation to classify tidepools in the littoral fringe and splash zone of the Swedish coast. With increasing distance from the water line, the pools were dominated by *Fucus* and *Chondrus*, *Enteromorpha* and by cyanobacteria, respectively.

The vertical zonation of macroalgae within tidepools was examined in detail by Kooistra *et al.* (1989) in Brittany, France. Using multivariate statistics, they found that macroalgal samples from similar depths in pools grouped together, and that they could allocate algal species to deeper or shallower parts of tidepools in the lower or higher regions of the shore (e.g. *Phymatolithon* in the deeper parts of low and mid intertidal zone pools, *Cladophora* only in the deeper parts of mid pools, and canopy forming species such as *Laminaria* just below the rims of low pools). Kooistra *et al.* (1989) also observed clear borders between particular species (e.g. between *Corallina* and *Phymatolithon*), although the depth of the borders varied between pools.

Many species of benthic invertebrates and fish also show zonation along the intertidal gradient. The periwinkle *Littorina rudis* is mainly found in high pools whereas *L. littorea*, whelks, mussels, sea-urchins and limpets are found in low pools (Fraser 1936, Ganning 1971, Daniel & Boyden 1975, Goss-Custard *et al.* 1979, Femino & Mathieson 1980). Sze (1982) found that the abundance of *L. littorea* increased from low to high pools. However, this discrepancy is probably due to the lower intertidal height of the pools examined in his study compared to others. Huggett & Griffiths (1986) found that pools lower on the shore on Cape Peninsula, South Africa, were dominated by sponges and bivalves while those higher on the shore were dominated by algae and snails. Zonation has also been observed for various meiofaunal groups: flatworms, rotifers, oligochaetes, cladocerans, cyclopoid copepods, ostracods, barnacles, amphipods, isopods and chironomid larvae (Fraser 1936, Ganning 1971, Dethier 1980). Fish zonation in tidepools has been documented extensively, but the results are not quantitative (Green 1971, Nakamura 1976, Gibson 1982, Bennett & Griffiths 1984, Mgaya 1992). Bennett & Griffiths (1984) detected a decrease in the number of fish species with increasing height above low water which they attributed to intolerance to extreme physical conditions.

Biomass and number of algal and invertebrate species decrease in tidepools with increasing height above low water (Femino & Mathieson 1980, Huggett & Griffiths 1986, Wolfe & Harlin 1988b, Kooistra *et al.* 1989). Gustavsson (1972) and Lawrence & McClintock (1987) reached similar conclusions, although the former study only examined high tidepools and splash pools and the latter study only examined 3 mid pools.

Factors affecting community organization

(a) Herbivory

Numerous experimental manipulations have shown that grazers (mainly littorinids and limpets) limit the distribution and abundance of marine algae on the emergent substrata of rocky intertidal shores (e.g. Dayton 1971, Lubchenco & Menge 1978, Raffaelli 1979, Underwood 1980, Underwood & Jernakoff 1981, 1984, Jernakoff 1983, Lubchenco 1983, Petraitis 1983, 1987, Hill & Hawkins 1991, but see Chapman 1989). Herbivory has similar effects in tidepools. Paine & Vadas (1969) showed that removal of sea-urchins resulted in increased macroalgal abundance and diversity in shallow tidepools in Washington, U.S.A. In Massachusetts, U.S.A., Lubchenco (1978) observed the effect of herbivory in 2 mid pools; in one, littorinid snails were absent and the dominant alga was *Enteromorpha,* and in the other, snails were present and the dominant alga was *Chondrus crispus.* Lubchenco (1978) added snails to the first pool and observed a decrease in the cover of the dominant *Enteromorpha.* On the other hand, when she removed snails from the second pool she observed a decrease in cover of the dominant *Chondrus crispus* (Lubchenco 1978). The cover of *Fucus* and ephemerals increased in a number of tidepools in the mid intertidal zone of a protected and a semi-exposed rocky shore in Maine and Massachussetts, U.S.A., when littorinids were excluded (Lubchenco 1982). Negative correlations also have been detected between littorinid abundance and cover of green and red macroalgae, but not fucoids, and between littorinid abundance and macroalgal species

diversity, in tidepools in Rhode Island, U.S.A. (Wolfe & Harlin 1988a). In tidepools located near the littoral fringe of an exposed rocky shore in Nova Scotia, Canada, Chapman (1990) and Chapman & Johnson (1990) found that grazers (mostly littorinids) have a negative effect on the abundance of *Fucus* sporelings, juveniles of *F. distichus*, *F. spiralis* and *F. vesiculosus*, and adults of *F. vesiculosus* and *F. evanescens* (but not *F. distichus*), a positive effect on the abundance of ephemeral algae, and no effect on the cover of the red algal crust *Hildenbrandia*. Dethier (1982) suggested that *Littorina* has a negative effect on the green alga *Collinsiella*, on diatoms, and possibly on the red alga *Rhodomela*, but has no effect on articulated corallines or on the green alga *Cladophora*, in tidepools in Washington, U.S.A. In New South Wales, Australia, Underwood & Jernakoff (1984) showed that cover of non-encrusting algae increased in the absence of grazers (mostly limpets), and Arrontes & Underwood (1991) showed that the starfish *Patiriella exigua* reduced the cover of *Ulva*, in shallow, artificial tidepools.

In a study examining the effects of grazing on bacteria and phytoplankton, Stenton-Dozey & Brown (1992) found that suspended food particles ranging from 1-15 μm (presumably bacteria and microalgae) decreased over a tidal cycle in a tidepool in South Africa. They attributed this decrease in particle density in the field to filter-feeding by the clam *Venerupis corrugatus* (Stenton-Dozey & Brown 1992). In freshwater rockpools in the Baltic Islands in Finland, Ranta *et al.* (1987) showed that the size-structure of phytoplankton communities was altered depending upon the initial density of the cladoceran *Daphnia* in the pools. The authors, however, only examined 3 rockpools, each located on a different island, and their results varied among rockpools (Ranta *et al.* 1987).

(b) Predation

On the emergent substrata of rocky shores, predators, such as starfish and whelks, limit the abundance of barnacles and mussels (Paine 1966, 1984, Connell 1970, Dayton 1971, Menge 1976, Janke 1990) and regulate the overall diversity of species (Paine 1966, 1984, Lubchenco & Menge 1978). Fewer studies have demonstrated the importance of predation in regulating tidepool communities. Fairweather (1987) found that whelks introduced into shallow (3-4 cm deep) tidepools in New South Wales, Australia, reduced the abundance of barnacles, tubeworms and limpets. Lubchenco (1978) suggested that littorinid populations in tidepools in Massachusetts, U.S.A. may be controlled by predation by the green crab, *Carcinus maenas*. In Washington, U.S.A., Dethier (1980) showed that fish, and to a lesser extent sea-anemones, can reduce the abundance of the harpacticoid copepod *Tigriopus californicus* in tidepools in the high zone of rocky shores. She suggested that these copepods are restricted in their distribution to high pools because physical conditions there limit the survival of their predators (Dethier 1980). In Island Bay, New Zealand, Coull & Wells (1983) observed high meiofaunal mortality due to fish predation in tidepools in the absence of *Corallina* spp. which acts as a refuge.

In a detailed study of the effect of predation on rockpool biota in the Baltic Islands, Ranta *et al.* (1987) observed a shift in zooplankton species dominance and size structure, and a decrease in species richness and evenness, after the introduction of predatory fish to the pools. Ranta & Nuutinen (1984) showed that different fish species in these rockpools had different food preferences and, thus, had different impacts on the resident community. In another study of freshwater rockpools in Sweden, Pajunen & Salmi (1991) showed that chironomid larvae increased in numbers in the absence of predatory corixids.

(c) Competition

Competition for space on the emergent substrata of rocky shores has been shown to be an important determinant of zonation and abundance of the dominant space occupiers such as barnacles, mussels and macroalgae, resulting in competitive hierarchies which vary with intertidal height (e.g. Connell 1961, Dayton 1971, Menge 1976, Grant 1977, Lubchenco & Menge 1978, Schonbeck & Norton 1980, Hawkins & Hartnoll 1985, but see Lively & Raimondi 1987, McCook & Chapman 1991). Interspecific competition also may be important in regulating tidepool community structure, but the evidence is sparse. Lubchenco (1982) and Chapman (1990) have documented decreases in fucoid canopy cover due to competition with ephemeral algae and *Chondrus crispus* in tidepools in Massachusetts, U.S.A. and Nova Scotia, Canada, respectively. Chapman & Johnson (1990) suggested that the absence of a canopy of *Ascophyllum nodosum* can enhance recruitment by *Fucus spiralis* in tidepools in Nova Scotia, Canada. Cecchi & Cinelli (1992) found that canopy removal in *Cystoseira*-dominated tidepools on the west coast of Italy had no effect on either encrusting or on articulated corallines (e.g. *Corallina* spp.) or coarsely branched algae (e.g. *Gelidium*), but enhanced the abundance of delicately branched (e.g. *Ceramium*, *Cladophora)* and thickly branched (e.g. *Padina*) algal species. Competitive dominance, as indicated by overgrowth, has been shown for the alga *Halichondria panicea* and thick coralline crusts in tidepools in Brittany, France (Kooistra *et al.* 1989). Arrontes & Underwood (1991) reported a negative correlation between the abundance of the starfish *Patiriella* and the limpet *Cellana* in natural, small tidepools in New South Wales, Australia, although they did not detect an effect of competition in experimental manipulations of the densities of competitors.

In rockpools, Ranta (1982) and Hanski & Ranta (1983) showed that competitive hierarchies involving 3 species of *Daphnia* can lead to competitive exclusion. This system was successfully modelled by Bengtsson (1989).

(d) Recruitment

A number of studies have shown that settlement and recruitment are important factors in determining adult density of sessile invertebrates and algae on the emergent substrata of rocky shores (e.g. Connell 1985, Gaines & Roughgarden 1985, Roughgarden *et al.* 1985, Reed *et al.* 1988, Menge 1991, Minchinton & Scheibling 1991). Recruitment is potentially an important factor in the organization of tidepool communities, although no studies have addressed this directly. The variability in the response of the tidepool community to grazer removal (Paine & Vadas 1969) and recovery from disturbance (Dethier 1984) have been partially attributed to differences in seasonal availability and 'vagaries of recruitment' of algal spores and invertebrate larvae from the surrounding sea-water. Singletary & Shadlou (1983) concluded that although barnacles settle in pools in Rhode Island, U.S.A., heavy post-settlement mortality prevents their establishment. Chapman & Johnson (1990) suggested that differential recruitment success in tidepools in the middle intertidal zone can lead to competitive displacement between *Fucus evanescens* and *F. vesiculosus*.

(e) Physical factors

On emergent substrata, the upper limits of species distributions are mostly determined by tolerance to long periods of desiccation (Lewis 1954, Connell 1961, Paine 1974, Schonbeck & Norton 1978, Denley & Underwood 1979) or freezing (Wethey 1985, Dudgeon *et al.* 1989). Similarly, the abundance of tidepool algae has been correlated with pool elevation (which determines the length of emergence and extent of temperature fluctuations), topography and shading by surrounding rocks (Johnson & Skutch 1928). The number of species present is also correlated with tidepool depth and volume. Several studies have shown that deeper pools may support more plant and invertebrate species

(Droop 1953, Pajunen 1977, Ranta 1982, Fairweather & Underwood 1991). Other studies have shown that fish biomass, species number and abundance may show significant correlations with pool area, depth or volume (Marsh *et al.* 1978, Bennett & Griffiths 1984, Mgaya 1992, but see Richkus 1978).

A number of studies have shown that topographic heterogeneity of emergent substrata can provide refuge from herbivory (Lubchenco 1983, Menge *et al.* 1985, but see Jernakoff 1985), predation (McGuinness & Underwood 1986) and desiccation (Menge *et al.* 1985, Fairweather 1988, Gosselin & Bourget 1989). In contrast, Lubchenco (1982) and Chapman (1990) found that substrate heterogeneity is apparently unimportant in the development of a fucoid canopy in tidepools. Increased biogenic structure, due to the presence of coralline algae (presumably a refuge from predators), has been shown to increase abundance of harpacticoid copepods, but not amphipods or polychaetes, in tidepools (Coull & Wells 1983).

As on emergent substrata (Menge 1976, 1978, 1983, Lubchenco & Menge 1978, Underwood & Jernakoff 1981), algal cover and the abundance of littorinids and fish in tidepools are correlated with wave exposure. Sze (1982) showed that some algae such as *Enteromorpha*, *Spongomorpha* and *Scytosiphon* are more abundant in tidepools on exposed shores where littorinids are absent, whereas fucoids are more abundant in pools on protected shores. Dethier (1984) also found that the cover of the dominant algal species varied between pools of different wave exposures. For example, the green alga *Collinsiella* and the red alga *Rhodomela* were found in pools higher on the shore in more exposed habitats (Dethier 1982). Some of the variability in macroalgal species composition observed by Wolfe & Harlin (1988a, b) among pools in Rhode Island, U.S.A., also can be attributed to differences in wave exposure. Grossman (1982) found that the abundance of fish in tidepools decreases with increased wave action, possibly because few species can adapt to higher turbulence in exposed pools (Gibson 1982). Green (1971) and Bennett &

Griffiths (1984) also found that the vertical distribution of cottid fish was related to the degree of wave exposure in tidepools, with fewer fish found in lower pools on more exposed shores. Some species, however, showed increased abundance at higher exposure levels.

(f) Physical disturbance

On emergent substrata, physical disturbance can greatly affect species composition and richness, depending upon the magnitude and frequency of the disturbance (Sousa 1979a, b, 1984b, Farrell 1989, but see McGuinness 1987a, b). However, there is little information on the effect of disturbance in organizing the communities of tidepools. In tidepools in Washington, U.S.A., Dethier (1984) used an operational definition of disturbance as the destruction of biomass over a period of less than 6 mo which she subjectively categorized as severe, moderate or minimal (affecting most, some, or 1-2 species of a pool, respectively). Freezing and heat stress were types of physical disturbances for the surf-grass *Phyllospadix*; bashing by logs and rocks, were types of disturbance for mussels, anemones and *Cladophora*. More disturbances were recorded in low than in high zone pools, and the frequency of disturbance was the same in wave-exposed as in more protected sites. The rate of recovery from disturbance varied with species and depended upon the magnitude of the disturbance. In the Aland archipelago in Finland, Ostman & Rönnberg (1991) showed that physical disturbance by ferryboat wash induced an increase in *Enteromorpha* cover in tidepools, although the magnitude of the effect varied among pools and among months. Changes in fish abundance have been associated with changes in the topography of tidepools through the movement of boulders by waves (Richkus 1978). Thompson & Lehner (1976) found that short-term disturbances, such as winterkills due to severe drops in temperature, changed the species composition of fish communities in 2 tidepools in the Gulf of California.

Variability in tidepools

The ubiquitous zonation of organisms along the intertidal gradient is perhaps the most striking characteristic of communities of the emergent substrata of rocky intertidal shores (Stephenson & Stephenson 1950, 1952, 1954a, b, Dayton 1971, Lubchenco & Menge 1978, Underwood 1981a, Janke 1990). In tidepools, however, the relationship between the distribution of organisms and their height on the shore is less clear. Marked spatial variability in species abundance has been recorded among pools that are at similar heights and close to each other on the shore. For example, on Cape Peninsula, South Africa, Stephenson *et al.* (1934) studied 3 pools at the same height on the shore and within 150 m of each other. One was characterized by large plant abundance, another by large animal abundance, and the third by intermediate abundances of both plants and animals. Similarly, Pyefinch (1943) found considerable variability in species composition between paired pools at the same height, in both the mid and the high zone, in North Wales, United Kingdom. Dethier (1982) measured 95% confidence intervals nearly equal to the mean percentage cover of the green alga *Collinsiella* and the red alga *Rhodomela* in pools at the same intertidal height. Lawrence & McClintock (1987) found that macrofloral and macrofaunal species abundance on the island of Kerguelen, in the southern Indian Ocean, varied markedly among 3 pools of similar size, intertidal height (within a maximum distance of 50 cm) and wave exposure. Wolfe & Harlin (1988a, b) detected differences of up to 60% in average percentage cover of dominant algal groups, and up to 30% in species diversity among pools of similar heights, volumes and exposures. Arrontes & Underwood (1991) detected statistically significant pool effects on algal abundance, demonstrating large among-pool compared to within-pool variability. Wilson *et al.* (1992) attributed the variability in species composition among 15 tidepools in New Zealand within a maximum vertical distance of 25 cm, to random processes. Green (1971) found that the vertical

zonation of cottid fish varied horizontally along the shore. Beckley (1985) recorded variability in fish abundance in 3 pools in East Cape, South Africa, in the lower balanoid zone within 100 m of each other. An apparent zonation in fish abundance in tidepools of different intertidal zones in British Columbia, Canada, was not detected statistically by Mgaya (1992), because of high interpool variability within zones. Pajunen (1990) recorded variation in corixid abundance of up to 100% of the mean in freshwater rockpools in the Tvärminne area, Finland, and attributed variability in species dominance among rockpools to differences in pool size.

Some studies also have shown considerable variability among tidepools at the same height in response to experimental manipulation. For example, Paine & Vadas (1969) showed that sea urchin removal resulted in initial differences in species composition among tidepools in the low zone in Washington, U.S.A., although these differences gradually diminished within 2 yr. In contrast, Dethier (1984) found that species composition in tidepools from which the dominant species, the surfgrass *Phyllospadix*, was removed were initially similar but became largely variable after 2 to 4 yr.

It has been argued that differences in wave exposure can result in variability among tidepool communities at the same intertidal height. Sze (1980) characterized the macroalgal communities in tidepools in the high intertidal zone, along a gradient of wave exposures in Maine, U.S.A.. He found that at the least exposed site, pools were dominated either by cyanobacteria, *Hildenbrandia* or *Enteromorpha*, whereas there was no distinct pattern of dominance at the most exposed site (unless dominated exclusively by cyanobacteria). Bennett & Griffiths (1984) observed differences in fish zonation among sites on different South African coasts which they partly attributed to differences in wave exposure.

The structure of tidepool communities may exhibit large temporal variability, mostly related to season. Microalgal abundance varies seasonally with a maximum in spring and minimum in summer (Aleem 1950, Dethier 1982). Macroalgae in tidepools also vary

seasonally (Underwood & Jernakoff 1984) but this variability may be more species-specific than in the microalgae. Femino & Mathieson (1980) found *Ulva* in tidepools throughout the year but *Spongomorpha* spp. were only present in the spring and *Fucus distichus* was absent in late summer. Dethier (1982) observed seasonality in cover of *Collinsiela* and *Rhodomela* which she attributed to seasonality in wave action and herbivory by littorinids. Wolfe & Harlin (1988a, b) found that the different macroalgal species in tidepools peaked at different times of the year but there was also seasonal variation in species diversity and richness. Fish that are either permanent inhabitants or transient species in pools show seasonal changes in abundance that usually are inversely related to temperature (Thompson & Lehner 1976, Grossman 1982, Yoshiyama *et al.* 1986, Moring 1990).

Synthesis and perspectives for future research

A number of similarities and differences exist in community organization between tidepools and emergent substrata of rocky shores. Biologically, the two habitats are similar since many of the same species are common to both. However, certain differences in the physical regime can result in differences in species composition between the two habitats. On one hand, the amplitude of the fluctuations in the physical regime tends to be smaller in some tidepools, particularly those located lower on the shore, making them more benign habitats. As a result, the vertical range of many intertidal organisms is extended in tidepools. Tidepools may be an important refuge from the extreme environmental fluctuations of the rocky intertidal habitat, although this has not as yet been quantitatively demonstrated. However, grazing and predation may be more intense in tidepools where both food and favourable foraging conditions (due to continuous submergence) are provided for extended periods. In addition, tidepools that are high on the shore and infrequently flushed can become stagnant, resulting in harsh conditions because of lack of

nutrients and food, and pronounced deleterious changes in physical parameters such as pH, salinity and temperature. Low tolerance of a large number of species to harsh conditions in high tidepools can probably account for the observed decrease in species diversity with increasing intertidal height.

The variability in community structure between pools is larger than that on emergent substrata, with pools at the same height on the same shore showing large variability in species composition and abundance. Despite the large variability, some general patterns of species' distribution in tidepools along the intertidal gradient have emerged. Most studies have shown that the dominant space occupiers in lower tidepools are fucoid and coralline algae and mussels, whereas higher pools are dominated by green algae. However, a number of physical factors interact to determine the tidepool environment and this may be what sets different pools apart, rather than intertidal height per se. It is difficult to even define the intertidal height of pools, since tidepools at the same absolute height might have very different periodicities of flushing and emergence. Differences in community structure among studies arise because of differences in the determination of intertidal height of the pools. These factors should be carefully considered when replicate tidepools are selected for study or when comparisons are made between studies in different areas.

The amount of information available on community organization of tidepools is much more limited than that for emergent substrata of rocky shores. The information on tidepools is highly descriptive and measurements between pools are at times poorly replicated. However, some generalizations can be made. Although several studies have examined herbivory as a regulating factor of tidepool community organization, its effect has varied among studies for some taxa. All studies, despite their limitations, have suggested that grazers have a negative effect on fucoid abundance and most studies have invoked a negative grazer effect on the abundance of green algae. The positive effect of grazers on ephemeral algae noted by Chapman (1989) and Chapman & Johnson (1990) was for pools

near the littoral fringe on an exposed shore, where grazer activity may have been reduced relative to lower pools or wave-protected areas. Therefore, although it can be suggested that herbivory is a potentially important regulating factor in tidepool communities, the evidence is either correlative (Wolfe & Harlin 1988a) or based on studies with low replication (Lubchenco 1978), and sometimes yields inconsistent results (e.g. Chapman 1989). In a few studies, it has been suggested that predation limits species abundance in tidepools, although as yet there is little direct evidence of this effect. Therefore, unless further studies are conducted, the importance of predation in the regulation of tidepool communities will remain unknown. The importance of competition in organizing tidepool communities has been consistently demonstrated for macroalgae but further studies are necessary to determine the importance of competition among tidepool fauna. Studies of competition probably have been biased towards macroalgae because of the low abundance of animals in pools. For example, the percentage cover of mussels in tidepools may vary between 10 and 30% (Dethier 1984) whereas on emergent substrata mussels form continuous mats (e.g. Dayton 1971, Paine & Levin 1981). Recruitment also has not been sufficiently well-studied to evaluate its importance in regulating community structure and dynamics in tidepools, and further studies are required. Some studies have suggested correlations between species abundance and physical factors such as pool topography, substrate heterogeneity, pool elevation and exposure to waves, although experimental manipulations have not been conducted to examine causal mechanisms for the observed correlations. The importance of physical disturbance has been addressed in 4 studies. However, in the most detailed study (Dethier 1984) disturbance was defined as its most dramatic end result (i.e. destruction of biomass) which limits interpretation of the importance of the frequency and magnitude of specific agents of disturbance in regulating tidepool communities. The other 3 studies strongly suggest that disturbance is important but their conclusions are largely inferential or based on low replication.

It can be argued that tidepools represent an intermediate habitat type between the subtidal and the emergent substrata of the rocky intertidal habitats. Because of this, caution is advised when applying models that are developed for either subtidal or intertidal systems to the tidepool habitat. Menge & Sutherland (1976, 1987) proposed a model of rocky intertidal community organization that predicted that the relative importance of physical factors, competition and predation in community regulation varied with environmental conditions and the magnitude of recruitment. Menge & Farrell (1989) concluded that this model may not apply to subtidal systems because it was developed for habitats with large environmental fluctuations which are not present in the subtidal. Similar arguments could be raised about the applicability of the Menge-Sutherland model to tidepool communities. In any event, more information on the community organization of tidepools is required before the applicability of any model can be properly evaluated.

Individual tidepools may be unique habitats of the rocky intertidal environment which support distinct communities, depending upon their physical setting. Tidepools may be particularly useful systems in which to test ecological models and theories because they have well-defined boundaries, they can be easily manipulated, and they are of manageable size. For species that can actively migrate between pools, pools have been considered as harbouring metapopulations (Bengtsson 1989). For assemblages where active migration is not possible (e.g. macroalgae, sessile invertebrates), the theory of island biogeography (MacArthur & Wilson 1967) can be tested, with the open ocean acting as the 'mainland' and the individual pools as 'islands'. Rockpools and tidepools also can be used as model systems for examining founder effects (Sale 1977, 1979, Sale & Douglas 1984). For example, initial densities of grazers can control the final structure of the phytoplankton community (Ranta *et al.* 1987). The intermediate disturbance hypothesis, relating the magnitude and frequency of disturbance to species diversity (Connell & Sousa 1983, Sousa 1984a), may be assessed for pools at different heights along the intertidal gradient.

In order for such theories to be tested, however, the mechanisms that regulate the organization of the pools must be better known.

PURPOSE AND OUTLINE OF THE RESEARCH

My thesis examines the structure and organization of phytoplankton assemblages in tidepools. Phytoplankton occupy a position at the base of food-webs, and in tidepools provide an important food source for sessile filter-feeders, planktonic micrograzers, and possibly motile macrofauna such as littorinids. Despite the potential importance of phytoplankton in this habitat, little is known about their community dynamics. Phytoplankton are introduced into tidepools with the incoming tide and their assemblages may change over the period of tidal isolation of the pools due to various biotic and abiotic factors. The composition of the assemblages may be completely reset during the following rise of the tide or changes may persist and become cumulative over longer periods of time. The frequency of tidal input into the pools will affect the extent to which the composition of the phytoplankton assemblages in the pools differs from that in the surrounding seawater. In pools with long isolation times, the structure of the assemblages may change over periods of months due to processes particular to those pools.

Specifically this thesis addresses the following questions:

(1) On what temporal scale do processes that determine the structure of phytoplankton assemblages in tidepools occur?

(2) What are the sources of spatial variability in the structure of phytoplankton assemblages in tidepools?

(3) What are the sources of spatial variability in the biotic and abiotic factors that can affect the abundance of phytoplankton in tidepools? Is there a relationship between the sources of spatial variability in phytoplankton abundance and the potential regulating factors?

(4) What is the relative importance of nutrients and herbivory in regulating the abundance of phytoplankton in tidepools?

In Chapter 2, I describe the tidepools in terms of their macroalgal and macrofaunal assemblages, in order to provide a measure for comparison between the habitat in my study and that in previous studies. In Chapter 3, I provide a description of the hyperbenthic assemblages of the tidepools since most members of the hyperbenthos are micrograzers of phytoplankton. In Chapter 4, I examine whether the composition of phytoplankton assemblages vary more over the period of tidal isolation of the tidepools or over periods of months. In the same chapter, I also examine relationships between changes in the abundance of phytoplankton and the biological (density of grazers) and physical/chemical (e.g. concentration of nutrients, temperature, salinity, pH) factors that can affect phytoplankton. In Chapter 5, I examine the sources of vertical and horizontal variability of the phytoplankton assemblages over a period of 15 months, to assess whether the phenomenon of intertidal zonation is evident in these assemblages or whether horizontal variability masks pattens of zonation. I also describe the sources of spatial variability in the biotic and abiotic characteristics of the pools to determine whether they can explain the variability in the abundance of phytoplankton. In Chapter 6, I present an experimental study that examines the relative importance of nutrients and grazers in regulating the phytoplankton assemblages in the tidepools. In the final chapter (Chapter 7), I integrate the results of these studies into the context of community organization in the rocky intertidal environment.

CHAPTER 2: Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada

INTRODUCTION

Biological zonation along the intertidal gradient is a prominent feature of the emergent substrata of rocky shores around the world (Stephenson & Stephenson 1950, 1952, 1954a, b, Dayton 1971, Lubchenco & Menge 1978, Underwood 1981a, Janke 1990). In tidepools, however, zonation patterns are less clear due to large variability in species abundance among tidepools at similar tidal heights (see Chapter 1 for review). Nevertheless, some algal forms (e.g. *Spongomorpha*, fucoids, and coralline algae such as *Corallina*) tend to be found mainly in pools located lower on the shore, whereas other forms (e.g. *Enteromorpha*) dominate in pools higher on the shore (Fraser 1936, Green 1971, Daniel & Boyden 1975, Goss-Custard *et al.* 1979, Femino & Mathieson 1980, Dethier 1982, 1984, Sze 1982, Wolfe & Harlin 1988a, Kooistra *et al.* 1989). Moreover, species diversity tends to decrease in pools with increasing intertidal height (Femino & Mathieson 1980, Huggett & Griffiths 1986, Wolfe & Harlin 1988b, Kooistra *et al.* 1989).

Variability in the biological communities has been attributed to differences in the physical characteristics of tidepools (e.g. area, volume and depth) which provide a greater range of physical settings than the emergent substrata (Johnson & Skutch 1928, Droop 1953, Marsh *et al.* 1978, Bennett & Griffiths 1984, Fairweather & Underwood 1991). Also, because a number of factors determine the extent of tidal exchange into the pools (e.g. orientation, wave exposure, height of the surrounding rocks, and drainage patterns) vertical distance above chart datum probably does not sufficiently describe the tidal position of a tidepool. Tidepools separated by a small vertical distance may receive different tidal inputs and, thus, harbour different biological communities. Because of the large variability

in their algal communities, tidepools are often characterized by the dominant algal groups rather than their height on the shore, in contrast to the communities on emergent substrata (e.g. Stephenson *et al.* 1934, Gustavsson 1972, Sze 1982).

In this chapter, I examine spatial and temporal patterns in the distribution and abundance of macroalgal and macrofaunal communities of tidepools across an intertidal gradient on a rocky shore in Nova Scotia, Canada. I compare the spatial variability of these communities among pools within the same intertidal zone to spatial variability among zones, over a period of 15 mo. I also examine the relationship between macroalgal abundance patterns and various biological and physical characteristics of the tidepools. In order to examine processes responsible for community organization in any system, the potential sources of variability for that system should be described. This study provides a basis for assessing existing hypotheses (and generating new ones) to account for the large variability in macrobenthic communities that is observed in tidepools on rocky shores.

MATERIALS AND METHODS

Four tidepools at each of 3 intertidal zones (mid, high and splash, determined by the period of isolation of the pools) were sampled at Cranberry Cove, an exposed rocky shore near Halifax, Nova Scotia (44°28'N, 63°56'W) in June, August and October 1991, and at monthly intervals between May and September 1992. The shoreline consists of gradually sloping granite platforms and large rock outcrops (10 to 30% grade), has a southern exposure to the Atlantic Ocean and receives up to 10 m swells especially in the fall. The pools were irregularly shaped with the maximum dimension ranging from 2 to 14 m and maximum depth ranging from 0.21 to 0.75 m. Transect lines were set at 0.5 m intervals along the length of each pool to either side of a central line. Length was measured along each transect line and width was measured at 0.5 m intervals along the central line. This provided a map of the pool perimeter which was then digitized to estimate surface area. Pool depth was measured at 0.3 m intervals along each of the 0.5 m transects, subdividing the pool into a grid of 0.5 x 0.3 m subunits (units around the perimeter were smaller). Average depth within each subunit was estimated by averaging the depths at each corner, and the volume of each tidepool estimated by summing the subunit volumes. The period of isolation of each pool was determined on 17 dates (June 1990, and at about 2 to 6 wk intervals between March 1991 and July 1992) as the period between tidal recession and subsequent tidal input, including spray. The height above chart datum of each pool was measured using a transit level in July 1991 and 1992. Flushing rate of each pool was determined as the percentage decrease in concentration of a fluorescent red dye (Rhodamine B, SIGMA® chemicals), added to the pools in known concentration, over the period between slack low and high tides (i.e. per tidal cycle). Flushing rate was measured on 9 July 1992, when wave height was between 2 to 3 m and it was raining lightly, and on 30 August 1993 when wave height was ~1 m and it was not raining.

In June, August and October 1991, and May and June 1992, 2 60-mL samples were collected at mid-depth of each pool for nutrient analysis with an acid-washed (1N HCL) syringe. These samples were pressure-filtered through a 0.8-μm Millipore® filter and frozen for subsequent analysis. Nitrate+nitrite and phosphate concentrations were measured with a Technicon AA2 autoanalyzer and ammonium concentration was determined spectrophotometrically according to Parsons *et al.* (1984).

In each tidepool, percentage cover of the upper visible layer of macroalgae and macrofaunal density were measured in 5 0.2 x 0.2 m quadrats (except for littorinid abundance which was measured in 5 0.1 x 0.1 m quadrats). The quadrats were randomly assigned for each sampling date. Percentage cover of macroalgae was estimated by placing a plastic quadrat with 60 randomly placed holes on the substratum and counting the number of holes overlying each species.

Macroalgae were assigned to each of the functional/form groups suggested by Littler (1980), and Littler & Littler (1980, 1984): sheets, filamentous, coarsely-branched, thick-leathery, jointed-calcareous and crustose forms. Macrofauna consisted mainly of mussels (*Mytilus edulis* and/or *M. trossulus*), littorines (*Littorina littorea, L. obtusata* and *L. rudis*) and whelks (*Nucella lapillus*). For each sampling date, abundances of each macroalgal and macrofaunal species or group, as well as the cover of bare rock, were compared among intertidal zones, and among pools within zones, using 2-factor analyses of variance. The effect of the nested factor (Pool) was examined within each zone (mid, high and splash).

Backwards elimination stepwise multiple regressions (Sokal & Rohlf 1981, Kleinbaum *et al.* 1988) were done to examine the relationship of each macroalgal functional group with littorine and mussel abundance, the physical characteristics of the pools (height above chart datum, flushing rate, volume and surface area) and the nutrient regime (nitrate+nitrite, phosphate, and ammonium concentrations and the nitrogen to phosphorus

ratio). Regressions were carried out for the entire sampling period and for each sampling date. The α-to-remove value was 0.150.

I examined spatial and temporal variability in the macroalgal and macrofaunal assemblages of the tidepools in two ways. Firstly, the Shannon Diversity Index (H') (Pielou 1969) was calculated separately for macroalgae and macrofauna for each tidepool and each sampling date as $H' = - \sum_{i=1}^{n} P_i \ \ln P_i$, where P_i is the proportion of the *i*th species in each tidepool. Comparisons of H' among intertidal zones for the entire sampling period were done using 2-factor analyses of variance (Zone and Date). Secondly, I used the Bray Curtis measure of dissimilarity (Field *et al.* 1982), calculated separately for macroalgae and macrofauna, in a cluster analysis by average linkage of pools at each sampling date.

For all statistical analyses, macroalgal percentage cover was arcsine[square root (x+0.5)]-transformed and macrofaunal density was ln (x+1)-transformed to successfully remove heterogeneity of variance when detected using Cochran's test. *A posteriori* multiple comparisons of treatment means were done using Student-Newman-Keuls (SNK) tests. All analyses were carried out using SYSTAT v. 5.1 (Wilkinson 1989) on a Macintosh SE 30 computer.

RESULTS

Physical and chemical environment

The physical characteristics of the tidepools at Cranberry Cove are summarized in Table 2.1. Pools with 3-8 h average periods of isolation over the 17 sampling dates were assigned to the mid zone, those with 10-12 h periods to the high zone, and those that were not reached by splash on most dates, or received tidal input only during storms, were assigned to the splash zone.

Nutrient concentrations were highly variable among pools within zones and no general trends were apparent in nutrient concentration among zones (Table 2.2). Nitrate+ nitrite concentrations were greatest in the high zone in August 1991 and May 1992, whereas the concentrations of phosphate and ammonium were similar on all sampling dates. None of the nutrients varied significantly among zones on any sampling date (in all cases, $F_{2,9} < 4.26$, $p > 0.05$).

Temporal patterns of abundance

Most functional groups of macroalgae (Table 2.3) were present on more than one sampling date in the tidepools (Figs. 2.1, 2.2, 2.3 & 2.4). Sheets were present in all pools in all zones (mainly *Enteromorpha intestinalis* and *Scytosiphon lomentaria*) and their percentage cover, averaged over all pools, was greatest in May and June of both years (Fig. 2.1). Filamentous forms (mainly *Cladophora* and *Spongomorpha* spp.) also were present in most pools on most dates and their cover decreased with the increase in cover of sheets. Coarsely branched forms (mainly *Chordaria flagelliformis*) were rare, occuring only in mid pools between June and September (Fig. 2.2). Jointed calcareous forms (*Corallina officinalis*) were found mostly in 1 mid pool with maximal cover in September (Fig. 2.2). No consistent temporal changes in percentage cover of thick leathery (mainly *Fucus vesiculosus*) and crustose forms (mainly *Phymatolithon* sp. in mid pools, and

Hildenbrandia rubra in high and splash pools) were observed over the sampling period. The cover of bare substratum appeared to increase in high and splash pools in June (i.e. after the decrease in sheets) and in October.

The 3 most abundant groups of macrofauna present in the pools on most sampling dates were: mytilid mussels, littorinid snails and whelks. The density of mussels was highly variable among pools, but tended to increase in early summer (Fig. 2.5). Two species of *Mytilus* are found in Nova Scotia, *Mytilus edulis* and *M. trossulus* (Pedersen 1991), although I did not differentiate these species in this study. Littorinid snails were abundant in all pools except in 1 splash pool where they were never recorded (Fig. 2.6). Temporal patterns in littorinid abundance were similar to those of mussels. *Littorina littorea* was found in mid and high pools whereas *L. obtusata* and *L. rudis* were found in all zones, with *L. rudis* being the most abundant species in high and splash pools. Whelks (*Nucella lapillus*) were abundant in 2 of the mid pools where they increased in density in summer of both years, but absent in 2 of the 4 pools in both the high and the splash zone. Anemones (*Metridium senile*), barnacles (*Semibalanus balanoides*), limpets (*Tectura testudinalis*) and urchins (*Strongylocentrotus droebachiensis*) were recorded in a few pools on some sampling dates (mainly in 2 mid pools in summer), but were not included in any statistical analysis because of their rarity.

Spatial patterns of abundance

Percentage cover of some of the functional form groups of macroalgae, especially the tougher in texture, varied significantly among intertidal zones on some sampling dates (Table 2.4). For example, percentage cover of thick leathery forms was greater in mid pools than in high and splash pools in June, August and October 1991 and May 1992, and it was greater in mid than in high pools (but not splash pools) in June 1992 (SNK tests, $p < 0.05$). Percentage cover of crustose forms was greater in the mid pools than in the

splash pools in June and August 1991 (SNK tests, $p < 0.05$). In contrast, percentage cover of sheets, filamentous, coarsely branched and jointed calcareous forms did not vary significantly among intertidal zones. Percentage cover of bare substratum was less in the mid pools than in the high and splash pools in June and October 1991, and in June, and September 1992 (SNK tests, $p < 0.05$).

Percentage cover of most macroalgal functional groups varied significantly among pools within intertidal zones on most sampling dates (Table 2.4). Percentage cover of sheets varied significantly among splash pools on all sampling dates, among high pools in May 1992, and among mid pools from June to October 1991 and from May to July 1992. Percentage cover of filamentous forms varied significantly among pools in all zones on all sampling dates, except in June 1992 when it did not vary significantly among high pools. Percentage cover of coarsely branched forms varied significantly among mid pools in June 1991 (although the overall Pool effect was not significant) and in August 1992. Percentage cover of thick leathery forms varied significantly among mid pools on all sampling dates (although the overall Pool effect was not significant from June 1991 to May 1992). Percentage cover of jointed calcareous algae varied significantly among mid pools from August 1991 to September 1992 (although the overall Pool effect was not significant in May 1992). Percentage cover of crustose forms varied significantly among high pools in June and October 1991 and in June, August and September 1992, and among mid pools in June 1991 and in July and August 1992. The amount of bare substratum varied significantly among splash pools in August and October 1991 and from May to September 1992, among high pools from June to October 1991, in May 1992 and from July to September 1992, and among mid pools in June 1991.

In summary, only the thick leathery and crustose macroalgal groups varied in percentage cover among intertidal zones. However, high variability among pools within

intertidal zones may mask differences among zones in the abundance of most macroalgal forms.

As with the macroalgae, the density of the three major macrofaunal groups varied among intertidal zones only on a few sampling dates (Table 2.4). Mussels were significantly more abundant in mid pools than in high and splash pools in August 1991 and 1992 (SNK tests, $p < 0.05$). The few mussels which occurred in high and splash pools were found mostly in cracks and crevices. Littorines were significantly more abundant in high pools than in mid and splash pools in June and October 1991 and in September 1992 (SNK tests, $p < 0.05$). Littorines also were more abundant in high pools than in splash pools in May 1992, and in high pools than in mid pools in August 1992 (SNK tests, $p < 0.05$). At the species level, only *Littorina obtusata* was more abundant in mid than high and splash pools in May 1992 ($F_{2,9} = 5.64$, $p < 0.05$, SNK test, $p < 0.05$). Whelks were significantly more abundant in mid pools than in high and splash pools in July 1992 (SNK tests, $p < 0.05$).

The density of the major macrofaunal groups also varied among pools within zones on most sampling dates (Table 2.4). Mussels varied significantly among mid pools on all sampling dates, among high pools in August and October 1991 and from May to August 1992, and among splash pools in June 1991, May, July and September 1992. Littorines varied significantly among mid pools in June and August 1991, and in May and June 1992, among high pools in August and October 1991 and from May to September 1992, and among splash pools from June to October 1991 and from June to September 1992. Whelks varied significantly among mid pools from June to October 1991 and from June to September 1992, and among splash pools in June 1991.

The few significant differences in the density of macrofauna among intertidal zones that I observed were not consistent for any group. As for the macroalgae, high variability among pools within zones appears to mask differences among zones.

Correlates of macroalgal abundance

Percentage cover of macroalgae did not vary consistently with grazer and mussel abundance, the nutrient regime and the physical characteristics of the pools for the different functional groups (Table 2.5). The number of significant regressions was smallest for sheets and larger for the thick leathery and crustose macroalgal forms. Sheets varied significantly with all the factors in the model, but only in June 1991. Filamentous forms varied significantly with the physical characteristics of the pool in 3 regression models, with snail abundance and nutrient concentrations in 2 models, and with mussel abundance in 1 model. Coarsely branched forms varied significantly with mussel abundance in 2 regression models and with nutrient concentration and the physical characteristics of the tidepools in 1 model. Thick leathery forms varied significantly with physical characteristics of the pools in 8 regression models, with nutrient concentrations in 4 models and with snails and mussels in 1 model. Jointed calcareous macroalgae varied significantly with mussel abundance in 3 regression models, with the physical characteristics of the pools in 2 models and with snail abundance and nutrient concentration in 1 model. Crustose forms varied significantly with the physical characteristics of the pool in regression models, with mussel abundance and nutrient concentration in 3 models and with snail abundance in 1 model.

For most macroalgal functional groups, the regression models that were obtained for each individual sampling date explained a greater proportion of the variance than the models for the entire sampling period. Overall, the number of significant relationships between macroalgal abundance and the physical and biological characteristics of the pools was greater for the tougher thick leathery and crustose groups than for sheets and filamentous algae.

Patterns of species diversity and community similarity

The Shannon Diversity Index (H') calculated for the macroalgal assemblages of the pools was highest in mid pools and lowest in splash pools ($F_{2,72} = 107.6$, $p < 0.001$; SNK test, $p < 0.05$); H' calculated for the macrofaunal assemblages was greater in mid pools than high and splash pools ($F_{2,72} = 30.99$, $p < 0.001$; SNK test, $p < 0.05$) (Figs. 2.8 & 2.9). H' for both the macroalgal and macrofaunal assemblages did not vary significantly over the entire sampling period ($F_{7,72} = 1.69$ and 1.32, respectively, $p > 0.05$) and there was no significant interaction between Date and Zone effects ($F_{14,72} = 0.477$, 1.23, respectively, $p > 0.05$).

Cluster analyses based on the macroalgal assemblages of tidepools showed that the mid pools clustered in pairs in June 1991, but by August 1991 all 4 mid pools belonged to the same cluster, which was maintained in October 1991 (Fig. 2.10). Similarly, in 1992, the mid pools were in separate clusters in May, but grouped more closely from June through September. The only other cluster of pools that was evident in August 1991 and from July to September 1992 was a high pool (Pool 3) and a splash pool (Pool 1); the remaining high and splash pools usually belonged to the same cluster. Cluster analysis based on the macrofaunal assemblages gave less clear results, although mid pools usually clustered closer to high pools than splash pools (Fig. 2.11). Certain high and splash pools were frequently dissimilar to the other pools. For example, one splash pool (Pool 2) was highly dissimilar to any other pool on any sampling date.

Table 2.1: Physical characteristics of 4 tidepools (Pool 1-4) located in each of 3 intertidal zones (mid, high and splash), at Cranberry Cove, Nova Scotia, Canada. C.D. = chart datum; - = no recorded input during 12 h tidal cycle; S.D. = standard deviation.

INTERTIDAL ZONE	SURFACE AREA (m^2)	MAXIMUM DEPTH (m)	VOLUME (m^3)	ISOLATION PERIOD (h)	HEIGHT ABOVE C.D. (m)	FLUSHING RATE PER 1/2 TIDAL CYCLE (%)	
						July 1992	August 1993
MID							
POOL 1	3.20	0.15	0.19	3	1.2	100	100
POOL 2	10.91	0.45	2.03	5	1.4	100	100
POOL 3	14.36	0.36	1.81	7	2.3	75	94
POOL 4	8.94	0.46	2.27	8	1.2	37	48
MEAN ± S.D.	9.35 ± 4.67	0.36 ± 0.14	1.58 ± 0.94	6 ± 2	1.5 ± 0.5	78 ± 30	86 ± 25
HIGH							
POOL 1	10.04	0.19	0.92	12	3.0	15	21
POOL 2	15.75	0.27	1.49	11	2.5	66	99
POOL 3	24.23	0.64	7.28	12	2.6	23	0
POOL 4	11.84	0.13	0.68	10	2.9	40	8
MEAN ± S.D.	15.47 ± 6.31	0.31 ± 0.23	2.59 ± 3.14	11 ± 1	2.8 ± 0.2	36 ± 23	32 ± 46
SPLASH							
POOL 1	0.68	0.13	0.05	-	2.8	0	11
POOL 2	8.85	0.31	1.15	-	3.4	37	4
POOL 3	7.47	0.32	0.71	-	3.9	36	7
POOL 4	3.94	0.43	0.94	-	4.5	52	0
MEAN ± S.D.	5.24 ± 3.67	0.30 ± 0.12	0.71 ± 0.48	-	3.7 ± 0.7	31 ± 22	6 ± 5

Table 2.2: Nutrient concentrations (in μM) and ratios (mean ± standard deviation) in 4 tidepools in each of 3 intertidal zones at Cranberry Cove, Nova Scotia, Canada.

NUTRIENT	ZONE	5 JUNE 1991	8 AUGUST 1991	27 OCTOBER 1991	12 MAY 1992	15 JUNE 1992
NO_3+NO_2	MID	1.10±0.41	1.46±1.20	1.68±2.37	1.82±0.92	1.75±0.67
	HIGH	0.77±0.38	4.15±6.01	0.39±0.32	6.75±11.9	0.63±0.27
	SPLASH	1.44±0.84	1.89±2.07	1.03±1.46	2.32±1.53	2.13±3.28
NH_4	MID	0.32±0.44	0.00±0.00	0.15±0.19	0.00±0.00	0.36±0.25
	HIGH	0.07±0.14	0.04±0.09	0.17±0.31	0.02±0.04	0.00±0.00
	SPLASH	0.29±0.35	0.31±0.62	0.88±0.83	0.00±0.00	0.57±1.06
PO_4	MID	0.37±0.26	0.41±0.22	0.47±0.18	0.52±0.27	0.51±0.56
	HIGH	0.33±0.18	0.39±0.28	0.51±0.26	0.42±0.47	0.37±0.19
	SPLASH	0.40±0.15	0.53±0.39	0.22±0.23	0.34±0.41	0.97±0.98
N:P	MID	3.92±1.02	3.26±1.29	2.32±2.19	3.34±0.72	6.72±2.05
	HIGH	2.41±0.40	13.7±19.2	1.56±1.48	9.78±10.7	1.75±1.04
	SPLASH	4.15±1.99	6.15±5.21	8.75±7.86	16.4±19.0	2.71±1.55

Table 2.3: List of species of macroalgae and macroinvertebrates present in the tidepools on at least 1 sampling date between June 1991 and September 1992.

TAXON	MID POOLS				HIGH POOLS				SPLASH POOLS			
	1	2	3	4	1	2	3	4	1	2	3	4
SHEETS												
Enteromorpha intestinalis			✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Petalonia fascia	✔	✔										
Scytosiphon lomentaria	✔	✔	✔	✔	✔	✔	✔	✔	✔			✔
Ulva lactuca	✔	✔										
FILAMENTOUS												
Bonnemaisonia hamifera	✔											
Ceramium rubrum	✔											
Chaetomorpha melagonium	✔											
Cladophora sp.	✔	✔	✔	✔								
Ectocarpus / Pilayella spp.	✔											
Spongomorpha sp.	✔	✔	✔	✔	✔	✔	✔	✔		✔	✔	✔
COARSELY BRANCHED												
Chordaria flagelliformis	✔	✔										
Devaleraea ramentacea	✔											
THICK LEATHERY												
Ascophyllum nodosum				✔				✔				
Fucus vesiculosus	✔	✔		✔	✔			✔				
Laminaria digitata / L. saccharina	✔	✔										
Palmaria palmata	✔											
JOINTED CALCAREOUS												
Corallina officinalis	✔	✔					✔					
CRUSTOSE												
Hildenbrandia rubra	✔	✔	✔	✔	✔		✔	✔	✔		✔	✔
Phymatolithon sp.	✔	✔	✔	✔	✔		✔	✔	✔			✔
Ralfsia sp.					✔			✔				

Table 2.3 (continued)

TAXON	MID POOLS				HIGH POOLS				SPLASH POOLS			
	1	2	3	4	1	~	3	4	1	2	3	4
MUSSELS												
Mytilus edulis / *M. trossulus*	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
LITTORINES												
Littorina littorea	✔	✔	✔	✔	✔	✔	✔	✔				
L. obtusata	✔	✔	✔	✔	✔		✔	✔	✔		✔	✔
L. rudis	✔	✔	✔	✔	✔	✔	✔	✔	✔		✔	✔
WHELKS												
Nucella lapillus	✔	✔	✔	✔			✔	✔		✔	✔	✔
ANEMONES												
Metridium senile	✔	✔										
BARNACLES												
Semibalanus balanoides		✔										
URCHINS												
Strongylocentrotus droebachiensis	✔	✔					✔					
LIMPETS												
Tectura testudinalis	✔	✔										

Table 2.4: Analyses of variance of percentage cover of different functional forms of macroalgae and bare substratum, and of the density of macroinvertebrates (individuals . m^{-2}) for 8 sampling periods, between June 1991 and September 1992. Factors are Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)} = 9, 48$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 57$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * - $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

VARIABLE	FACTOR	5 JUNE 1991			8 AUGUST 1991		
		MS	F,	p	MS	F,	p
MACROALGAE							
SHEETS	P(Z):	430	4.65,	0.000***	0.01	5.52,	0.000***
	Z:	2003	0.26,	NS	0.06	0.54,	NS
FILAMENTOUS	P(Z):	500	10.46,	0.000***	441	16.15,	0.000***
	Z:	5235	0.21,	NS	7127	0.01,	NS
COARSELY BRANCHED	P(Z):	0.002	1.56,	NS		ABSENT	
	Z:	0.003	1.86,	NS		ABSENT	
THICK LEATHERY	P(Z):	268	1.93,	NS	129	2.07,	NS
	Z:	515	6.70,	*	266	7.82,	0.011*
JOINTED CALCAREOUS	P(Z):	IN ONE POOL			0.005	4.65,	0.000***
	Z:	MID ZONE			0.02	1.79,	NS
CRUSTOSE	P(Z):	0.12	5.34,	0.000***	0.04	1.31,	NS
	Z:	0.63	6.96,	*	0.04	4.03,	*
BARE ROCK	P(Z):	0.10	7.94,	0.000***	445	11.97,	0.000***
	Z:	0.76	6.78,	*	5346	1.08,	NS
MACROFAUNA							
MUSSELS	P(Z):	3.15	5.23,	0.000***	1.70	6.87,	0.000***
	Z:	16.47	3.71,	NS	11.70	8.75,	0.008**
LITTORINES	P(Z):	2.54	5.22,	0.000***	1.72	18.96,	0.000***
	Z:	13.23	7.31,	0.013*	32.51	1.69,	NS
WHELKS	P(Z):	1.37	12.31,	0.000***	2.85	14.81,	0.000***
	Z:	16.87	1.33,	NS	42.16	1.94,	NS

Table 2.4 (continued)

VARIABLE	FACTOR	27 OCTOBER 1991			12 MAY 1992		
		MS	F,	p	MS	F,	p
MACROALGAE							
SHEETS	P(Z):	0.02	4.27,	0.000***	0.10	9.62,	0.000***
	Z:	0.10	0.76,	NS	1.00	0.83,	NS
FILAMENTOUS	P(Z):	456	10.10,	0.000***	0.04	12.56,	0.000***
	Z:	4615	0.83,	NS	0.45	0.05,	NS
COARSELY BRANCHED	P(Z):		ABSENT			ABSENT	
	Z:		ABSENT			ABSENT	
THICK LEATHERY	P(Z):	310	1.63,	NS	227	1.12,	NS
	Z:	506	7.80,	0.000***	364	2.73,	NS
JOINTED CALCAREOUS	P(Z):	13.70	5.53,	0.000***	0.01	1.61,	NS
	Z:	75.74	0.85,	NS	0.02	8.13,	0.01*
CRUSTOSE	P(Z):	0.05	2.18,	*	208	1.17,	NS
	Z:	0.11	1.95,	NS	213	0.92,	NS
BARE ROCK	P(Z):	457	6.58,	0.000***	0.05	13.76,	0.000***
	Z:	3008	8.13,	0.01*	0.75	3.74,	NS
MACROFAUNA							
MUSSELS	P(Z):	2.52	5.33,	0.000***	3.49	4.76,	0.000***
	Z:	13.41	1.99,	NS	16.61	3.89,	NS
LITTORINES	P(Z):	1.68	11.39,	0.000***	72.32	5.38,	0.000***
	Z:	19.14	4.65,	*	389	5.01,	*
WHELKS	P(Z):	0.42	2.66,	0.014*	0.40	1.31,	NS
	Z:	1.12	1.93,	NS	0.42	1.51,	NS

Table 2.4 (continued)

VARIABLE	FACTOR	15 JUNE 1992 MS	15 JUNE 1992 F, p	27 JULY 1992 MS	27 JULY 1992 F, p
MACROALGAE					
SHEETS	P(Z):	0.04	5.24, 0.000***	36.48	5.21, 0.000***
	Z:	0.20	2.07, NS	190	1.27, NS
FILAMENTOUS	P(Z):	745	5.77, 0.000***	361	323, 0.000***
	Z:	4295	0.03, NS	8255	0.03, NS
COARSELY BRANCHED	P(Z):		ABSENT		IN ONE POOL
	Z:		ABSENT		MID ZONE
THICK LEATHERY	P(Z):	200	116, 0.000***	0.02	10.81, 0.000***
	Z:	1229	0.93, NS	0.22	1.36, NS
JOINTED CALCAREOUS	P(Z):	0.0001	6.13, 0.000***	0.004	9.51, 0.000***
	Z:	0.06	5.81, *	0.05	3.88, NS
CRUSTOSE	P(Z):	0.06	3.79, 0.001**	0.03	2.62, *
	Z:	0.21	0.51, NS	0.08	1.04, NS
BARE ROCK	P(Z):	0.11	4.97, 0.000***	0.05	17.15, 0.000***
	Z:	0.52	8.78, 0.008**	0.92	2.98, NS
MACROFAUNA					
MUSSELS	P(Z):	2.76	7.30, 0.000***	2.78	7.30, 0.000***
	Z:	20.10	2.91, NS	20.32	3.71, NS
LITTORINES	P(Z):	1.01	17.17, 0.000***	39.76	10.70, 0.000***
	Z:	17.25	2.93, NS	425	3.11, NS
WHELKS	P(Z):	0.82	4.44, 0.000***	1.05	4.99, 0.000***
	Z:	3.64	3.46, NS	5.24	4.94, *

Table 2.4 (continued)

VARIABLE	FACTOR	24 AUGUST 1992 MS	F, p	26 SEPTEMBER 1992 MS	F, p
MACROALGAE					
SHEETS	P(Z):	0.0?	3.95, 0.001**	0.01	3.19, 0.004**
	Z:	0.08	0.86, NS	0.04	0.90, NS
FILAMENTOUS	P(Z):	789	6.65, 0.000***	848	6.34, 0.000***
	Z:	5244	0.06, NS	5379	0.69, NS
COARSELY BRANCHED	P(Z):	0.02	2.25, *	IN ONE POOL, MID ZONE	
	Z:	0.04	1.41, NS		
THICK LEATHERY	P(Z):	0.01	18.85, 0.000***	37.32	36.89, 0.000***
	Z:	0.23	1.06, NS	582	1.07, NS
JOINTED CALCAREOUS	P(Z):	0.003	16.89, 0.000***	0.01	15.59, 0.000***
	Z:	0.05	4.59, NS	0.18	3.78, NS
CRUSTOSE	P(Z):	0.04	3.63, **	0.03	4.69, 0.000***
	Z:	0.13	0.49, NS	0.14	0.72, NS
BARE ROCK	P(Z):	0.11	5.47, 0.000***	696	4.06, 0.001**
	Z:	0.60	3.88, NS	2823	6.22, *
MACROFAUNA					
MUSSELS	P(Z):	2.21	6.69, 0.000***	3.42	6.36, 0.000***
	Z:	14.77	7.20, 0.014*	21.78	2.69, NS
LITTORINES	P(Z):	68.28	10.39, 0.000***	45.11	5.33, 0.000***
	Z:	709	4.53, *	241	6.34, *
WHELKS	P(Z):	500	6.47, 0.000***	229	5.14, 0.000***
	Z:	3233	2.71, NS	1177	2.56, NS

Table 2.5: Significant backwards elimination multiple regressions for percentage cover of 6 functional groups of macroalgae against the biological and physical characteristics of tidepools for the entire sampling period and 8 separate sampling times between June 1991 and September 1992. Independent variables are: S=snail abundance; M=mussel abundance; H=height above chart datum; A=surface area; V=volume; F=flushing rate; PO= phosphate concentration; NO=nitrate+nitrite concentration; NH=ammonium concentration; N:P= dissolved nitrogen to phosphorus ratio. Within each multiple regression, independent variables with significant partial F-values are shown in bold.

DEPENDENT VARIABLE	DATE	N	MODEL	R^2	F, p
SHEETS	5-6-91	12	=**-77.47** +0.011(**S**) +0.026(**M**) +7.890(**H**) -6.605(**A**) +15.74(**V**) -0.438(**F**) +315(**PO**) -82.08(**NO**) -625(**NH**) +33.47(**N:P**)	0.998	666, *
FILAMENTOUS	ALL DATES	96	=-10.34 +11.51(**H**) +0.369(**F**)	0.101	6.24, *
	5-6-91	12	=**452** -0.017(**S**) +4.361(**A**) -28.01(**V**) +0.752(**F**) -884(**PO**) +140(**NO**) +1242(**NH**) -101(**N:P**)	0.938	21.69, *
	8-8-91	12	=-36.65 +0.017(**S**) -0.210(**M**) +1.304(**F**) +103(**PO**) -5.230(**NO**)	0.765	8.14, *
COARSELY BRANCHED	ALL DATES	96	=-0.348 +0.004(**M**)	0.344	50.71, ***
	5-6-91	12	=**-1.747** +0.051(**A**) +0.013(**F**) +0.456(**NO**) +13.20(**NH**)	0.875	20.77, **
	24-8-92	12	=-0.491 +0.009(**M**)	0.721	29.43, ***
THICK LEATHERY	ALL DATES	96	=**20.77** -6.154(**H**) -1.685(**A**) +4.204(**V**) +0.271(**F**)	0.728	64.48, ***

Table 2.5 (continued)

DEPENDENT VARIABLE	DATE	N	MODEL	R^2	F, p
	5-6-91	12	=**40.60** -0.004(**S**) -0.009(M) -11.23(**H**) +0.313(**F**) +8.558(**NO**) -6.168(**N:P**)	0.888	15.53, **
	8-8-91	12	=**32.57** +0.023(**M**) -0.023(**H**) -1.731(**A**) +3.796(**V**) -0.058(**F**) +13.64(**PO**) -1.163(**NO**) -123(**NH**) +0.655(**N:P**)	0.999	910, **
	27-10-91	12	=**37.07** +0.074(M) -4.507(**A**) +9.688(**V**) +0.314(**F**) -8.518(**NO**) -125(**NH**) -2.078(**N:P**)	0.367	11.07, *
	12-5-92	12	=**33.64** +0.009(S) +0.055(**M**) -5.642(**H**) -1.384(**A**) -69.99(PO) +12.48(NO) -2885(NH) -0.860(N:P)	0.954	29.35, **
	15-6-92	12	=**149** -18.79(**H**) -7.644(**A**) +17.19(**V**) +0.699(**F**) -125(**PO**) +37.87(**NO**) +13.62(NH) -15.53(**N:P**)	0.959	32.93, **
	24-7-92	12	=-9.105 +0.333(**F**)	0.354	7.03, *
	24-8-92	12	=-15.38 +0.010(S) -2.892(**A**) +9.196(**V**) +0.631(**F**)	0.661	6.36, *
	26-9-92	12	=-2.829 -1.554(A) +4.431(V) +0.356(**F**)	0.604	6.59, *
JOINTED CALCAREOUS	ALL DATES	96	=-1.566 -0.266(A) +1.046(**V**) +0.087(**F**)	0.229	10.39, ***
	8-8-91	12	=-0.297 +0.011(**M**)	0.682	24.57, **
	12-5-92	12	=0.242 +0.013(**M**) -0.740(V)	0.596	9.10, **
	15-6-92	12	=**78.90** -0.003(S) -0.012(**M**) -8.504(**H**) -3.107(**A**) +7.153(**V**) +0.390(**F**) -87.61(**PO**) +27.55(**NO**) +14.92(**NH**) -11.20(**N:P**)	0.999	1744, *

Table 2.5 (continued)

DEPENDENT VARIABLE	DATE	N	MODEL	R^2	F, p
CRUSTOSE	ALL DATES	96	=0.306 +0.016(**M**) +2.673(**V**)	0.308	22.18, ***
	5-6-91	12	=42.77 +0.021(M) -18.88(**H**) -4.541(A) +16.21(V) +160(**PO**) -736(NH)	0.771	7.19, *
	8-8-91	12	=1.493 -0.001(S) +0.040(**M**) +0.829(**A**) -0.170(**F**)	0.643	5.96, *
	27-10-91	12	=1.646 -0.003(**S**) -4.392(**V**) +66.17(**PO**) -8.703(**NO**)	0.634	5.76, *
	15-6-92	12	=**-6.154** +0.005(M) +6.235(**V**) +4.990(**NH**)	0.885	29.18, ***
	24-7-92	12	=0.040 +0.009(**M**) +1.218(V)	0.604	9.40, **
	24-8-92	12	=1.962 +2.553(**V**)	0.365	7.33, *
	26-9-92	12	=2.673 +0.005(M) +4.518(**V**) -0.120(**F**)	0.853	22.25, ***

Figure 2.1: Mean percentage cover of 6 functional forms of macroalgae and of bare substratum in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992 (n = 4).

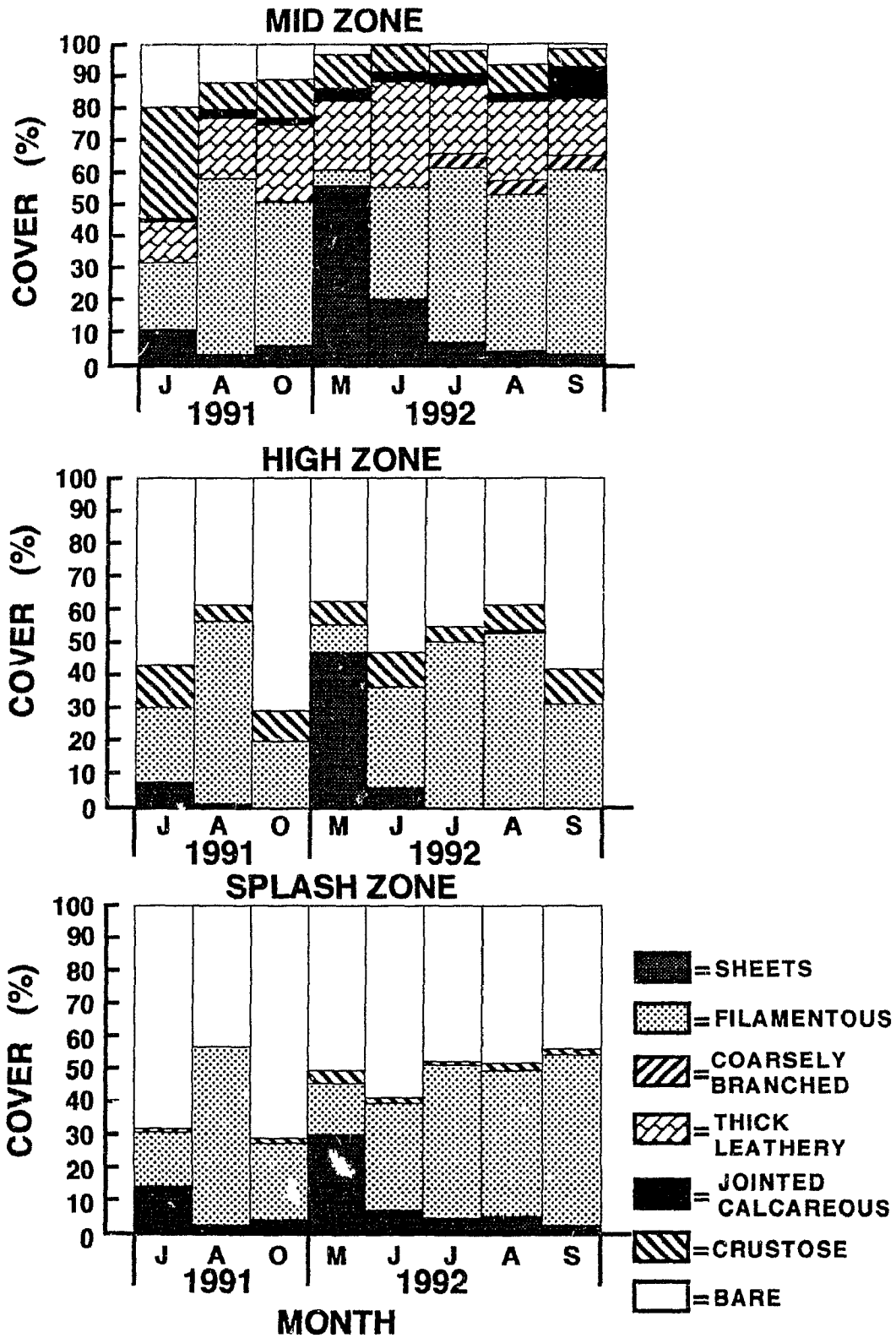
MID ZONE
HIGH ZONE
SPLASH ZONE
COVER (%)
100
90
80
70
60
50
40
30
20
10
0
J A O M J J A S
1991
1992
MONTH
=SHEETS
=FILAMENTOUS
=COARSELY BRANCHED
=THICK LEATHERY
=JOINTED CALCAREOUS
=CRUSTOSE
=BARE

Figure 2.1

Figure 2.2: Mean percentage cover of 6 functional forms of macroalgae and of bare substratum in 4 tidepools in the mid intertidal zone at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992 (n = 5).

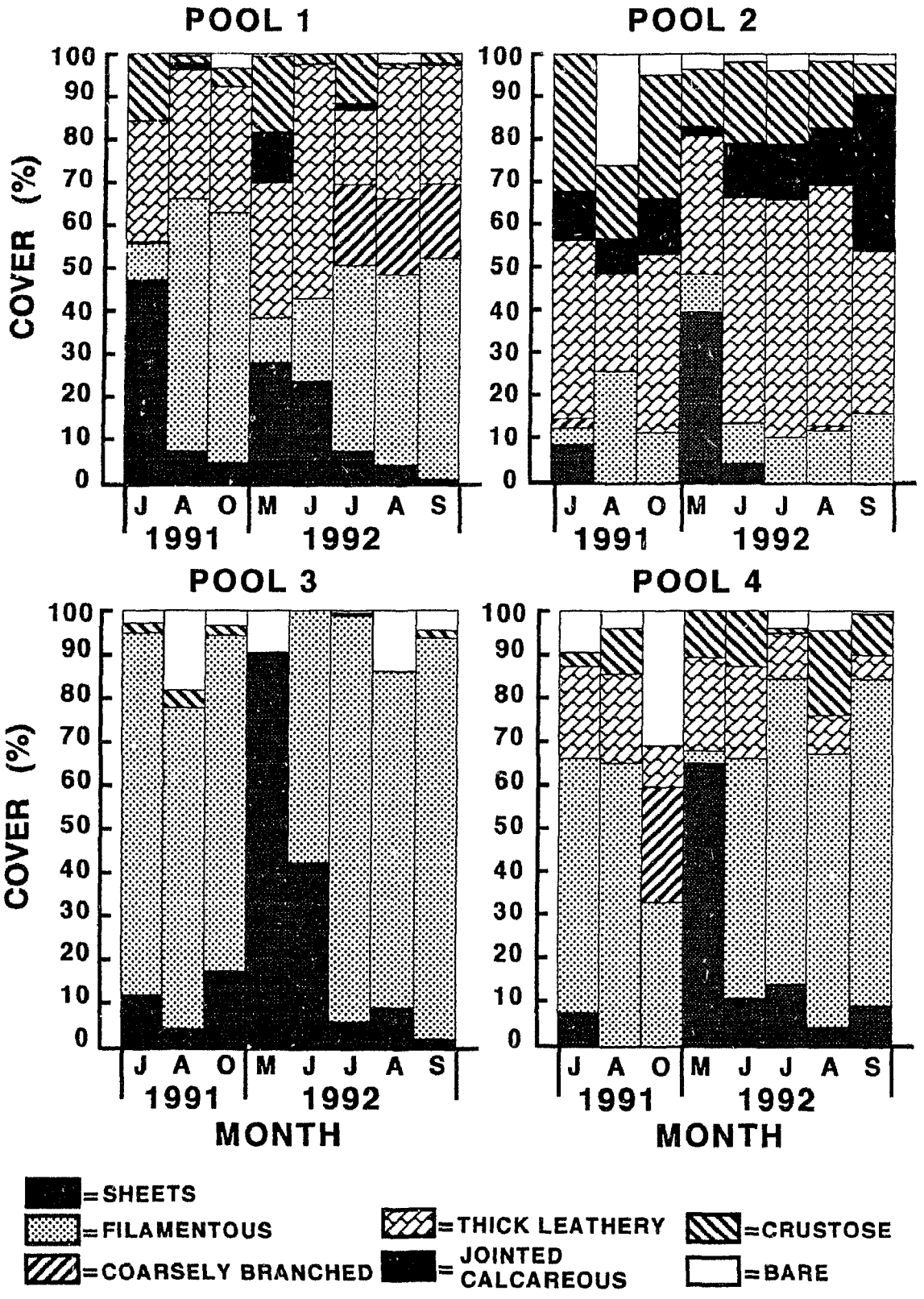
POOL 1
POOL 2
POOL 3
POOL 4
COVER (%)
100
90
80
70
60
50
40
30
20
10
0
J A O M J J A S
1991
1992
MONTH
=SHEETS
=FILAMENTOUS
=COARSELY BRANCHED
=THICK LEATHERY
=JOINTED CALCAREOUS
=CRUSTOSE
=BARE

Figure 2.2

Figure 2.3: Mean percentage cover of 6 functional forms of macroalgae and of bare substratum in 4 tidepools in the high intertidal zone at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992 (n = 5).

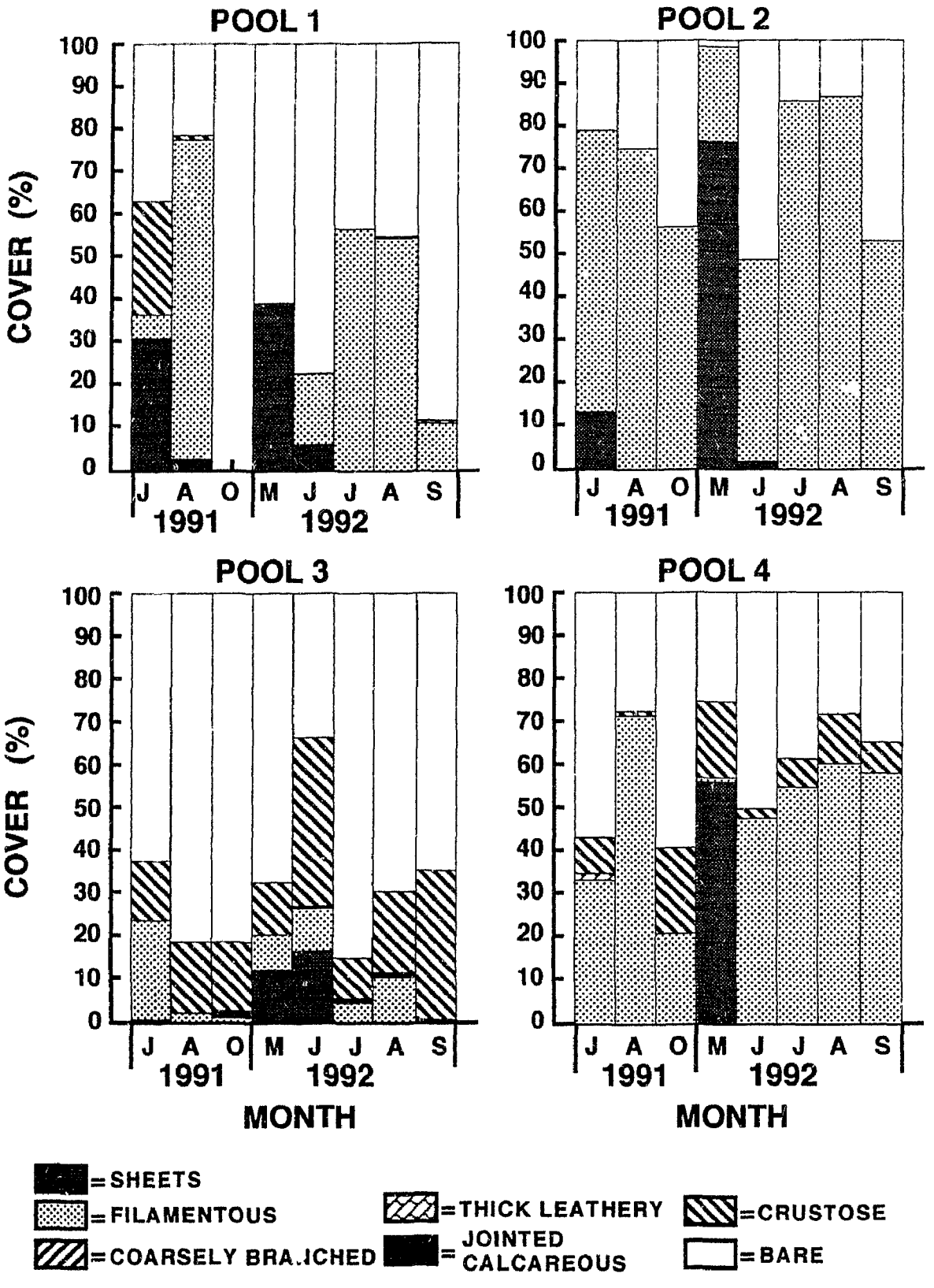
POOL 1
POOL 2
POOL 3
POOL 4
COVER (%)
100
90
80
70
60
50
40
30
20
10
0
J A O M J J A S
1991
1992
MONTH
=SHEETS
=FILAMENTOUS
=COARSELY BRANCHED
=THICK LEATHERY
=JOINTED CALCAREOUS
=CRUSTOSE
=BARE

Figure 2.3

Figure 2.4: Mean percentage cover of 6 functional forms of macroalgae and of bare substratum in 4 tidepools in the splash zone at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992 (n = 5).

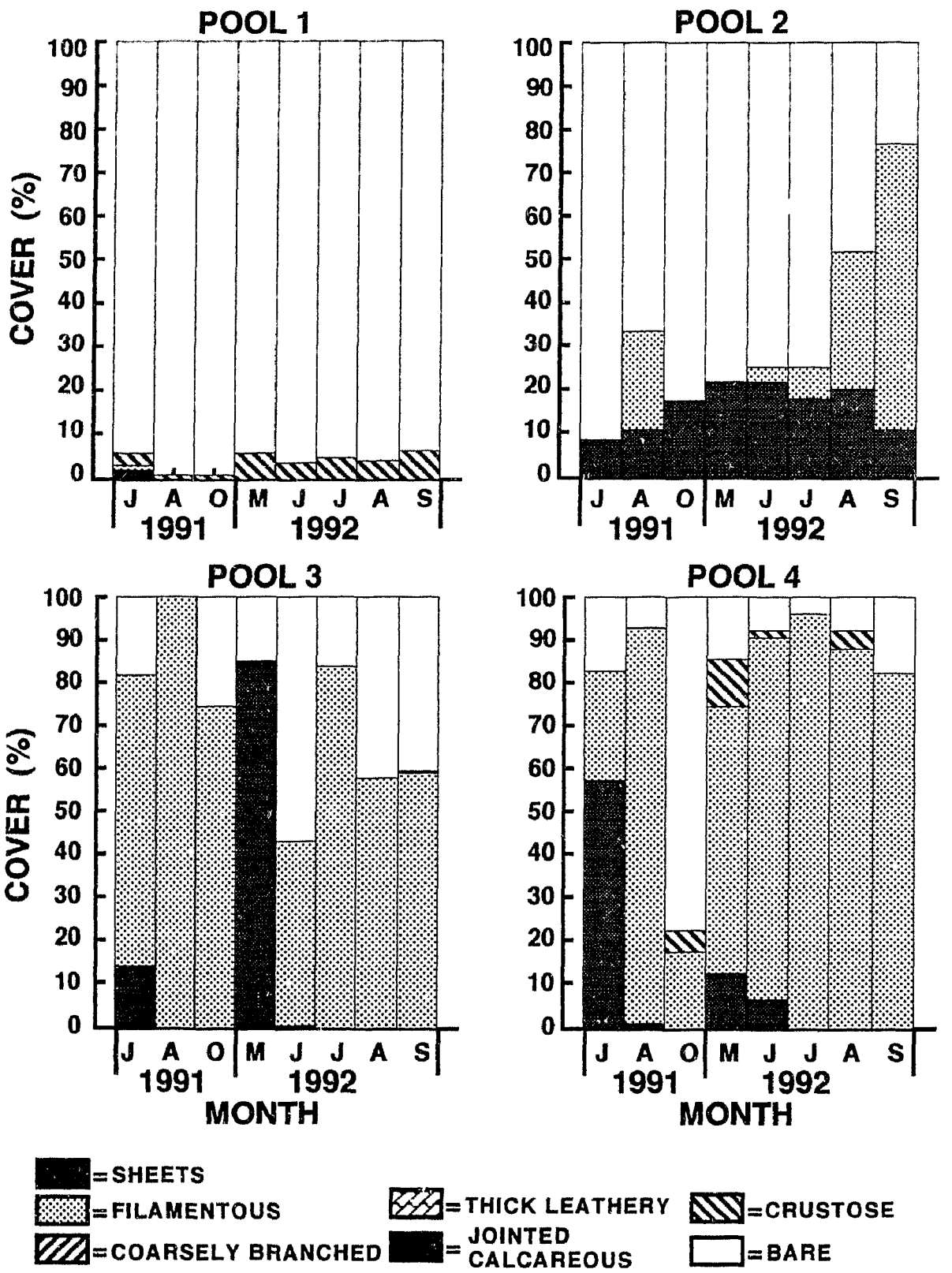
POOL 1
POOL 2
POOL 3
POOL 4
COVER (%)
100
90
80
70
60
50
40
30
20
10
0
J A O M J J A S
1991
1992
MONTH
=SHEETS
=FILAMENTOUS
=COARSELY BRANCHED
=THICK LEATHERY
=JOINTED CALCAREOUS
=CRUSTOSE
=BARE

Figure 2.4

Figure 2.5: Density of mussels in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992. The top 3 panels show mean density in each tidepool, at each zone (n = 5). The bottom panel shows mean density in each intertidal zone (4 tidepools).

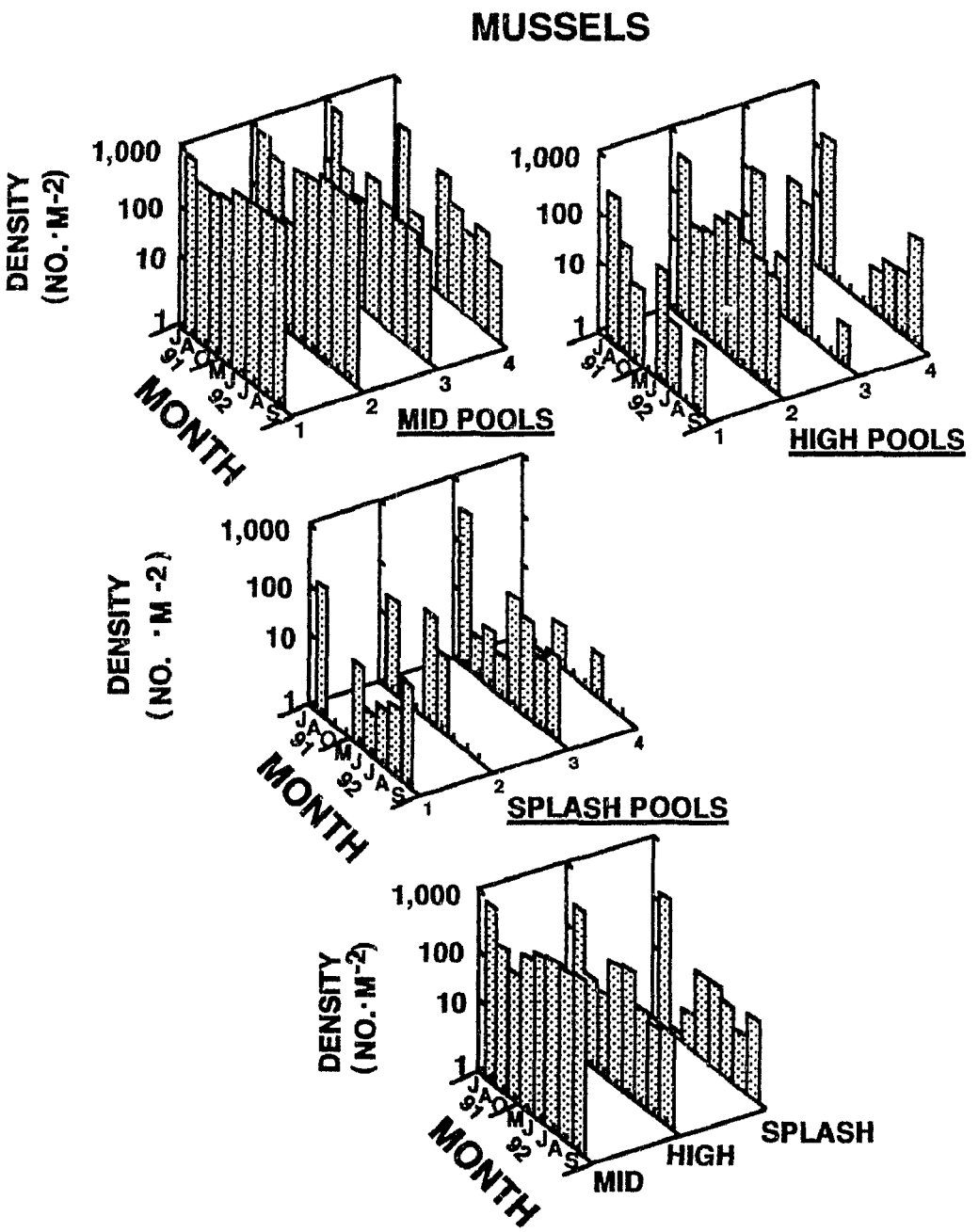
MUSSELS
DENSITY (NO. · M-2)
1,000
100
10
1
J A O 91 M J J A S 92
MONTH
1
2
3
4
MID POOLS
HIGH POOLS
SPLASH POOLS
MID
HIGH
SPLASH

Figure 2.5

Figure 2.6: Density of littorinid snails in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992. The top 3 panels show mean density in each tidepool, at each zone (n = 5). The bottom panel shows mean density in each intertidal zone (4 tidepools).

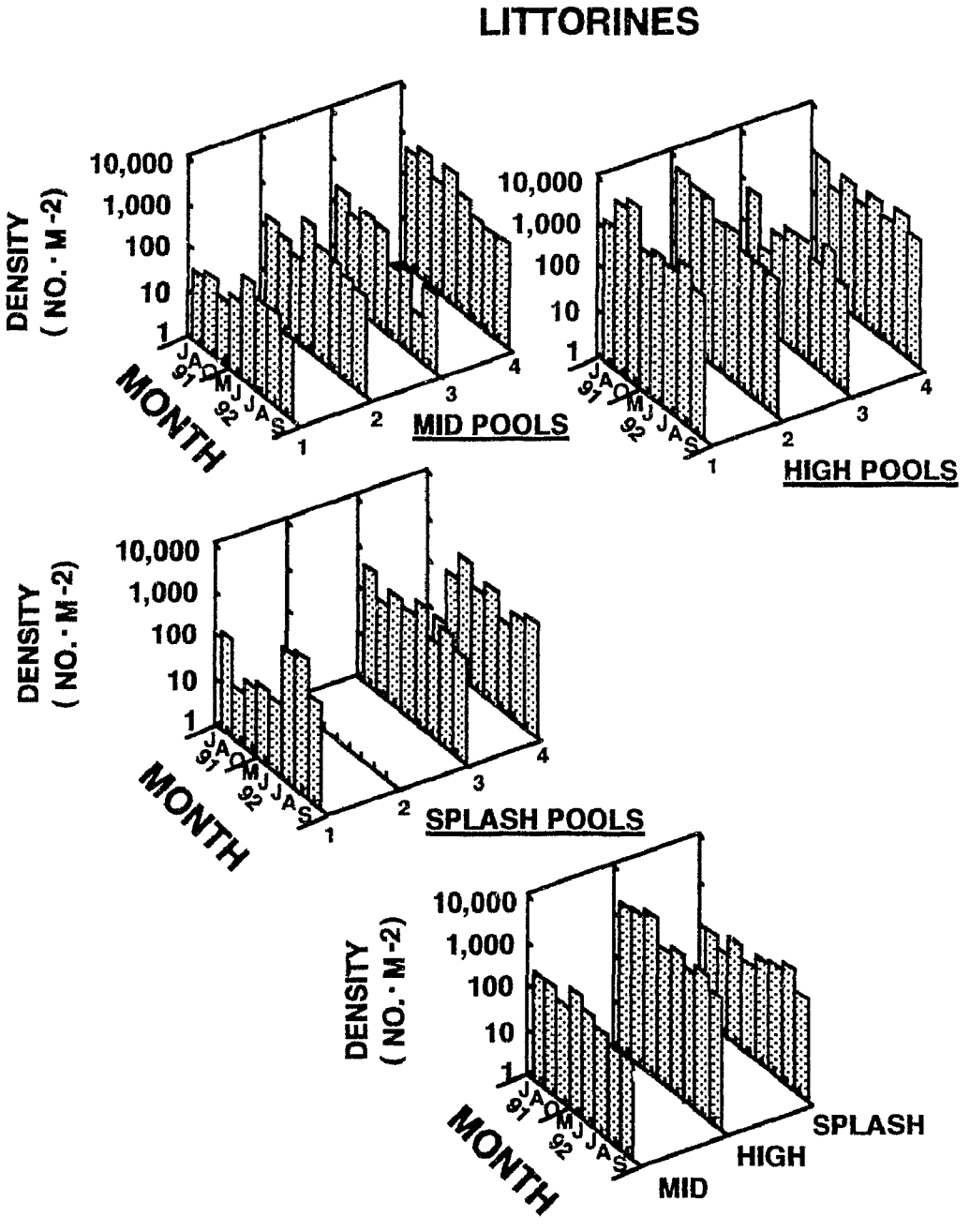
LITTORINES
DENSITY
(NO. · M -2)
10,000
1,000
100
10
1
MONTH
J A O
91
M J J A S
92
1
2
3
4
MID POOLS
HIGH POOLS
SPLASH POOLS
SPLASH
HIGH
MID

Figure 2.6

Figure 2.7: Density of whelks in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992. The top 3 panels show mean density in each tidepool, at each zone (n = 5). The bottom panel shows mean density in each intertidal zone (4 tidepools).

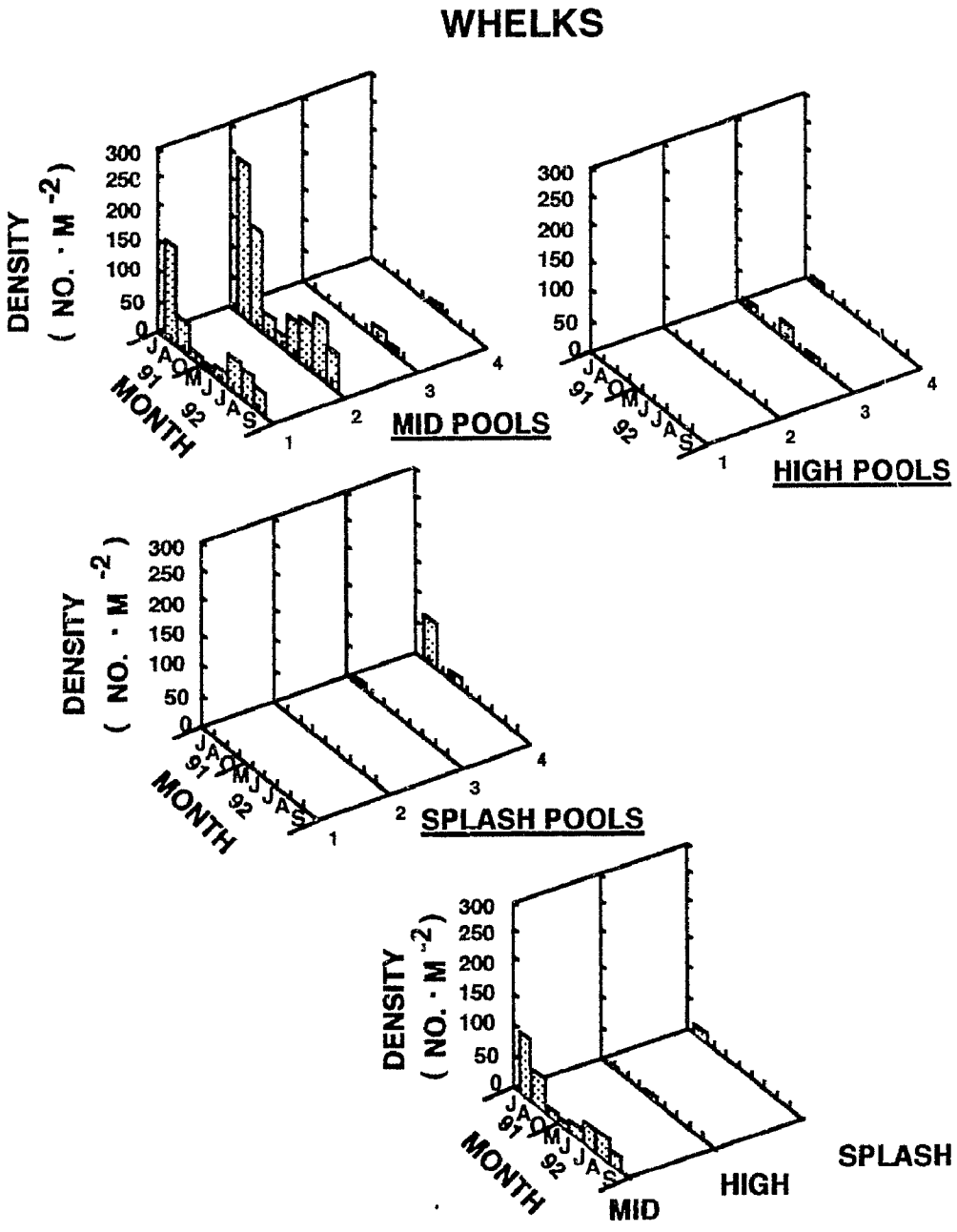
WHELKS
DENSITY
(NO. · M -2)
300
250
200
150
100
50
0
J A O
91
M J J A S
92
MONTH
1
2
3
4
MID POOLS
HIGH POOLS
SPLASH POOLS
SPLASH
HIGH
MID

Figure 2.7

Figure 2.8: Shannon Diversity Indices of the macroalgal communities in tidepools in 3 intertidal zones (mid, high and splash), at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992. Error bars are standard deviations (n = 4).

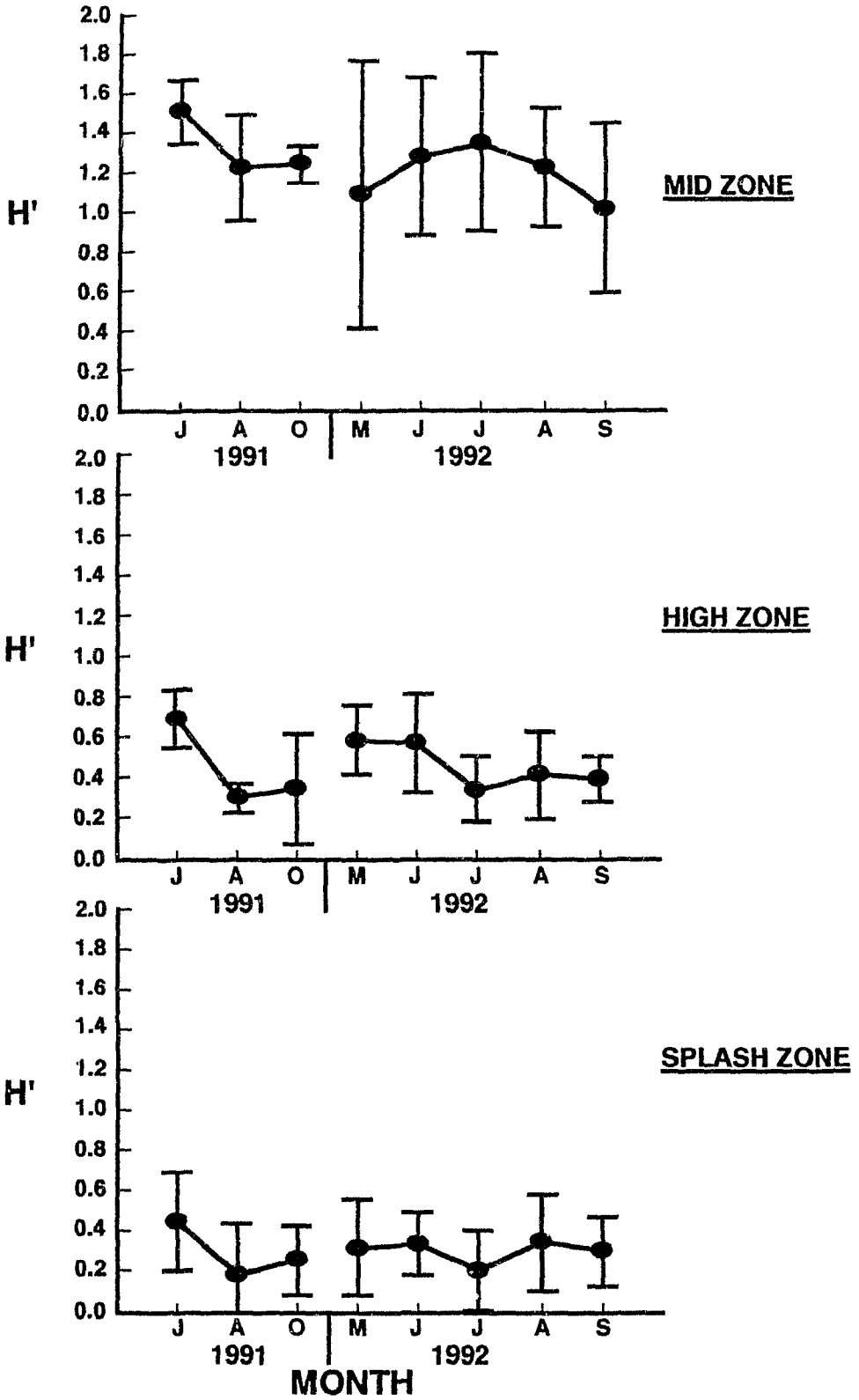
H'
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
J A O M J J A S
1991
1992
MID ZONE
HIGH ZONE
SPLASH ZONE
MONTH

Figure 2.8

Figure 2.9: Shannon Diversity Indices of the macroinvertebrate communities in tidepools in 3 intertidal zones (mid, high and splash), at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992. Error bars are standard deviations (n = 4).

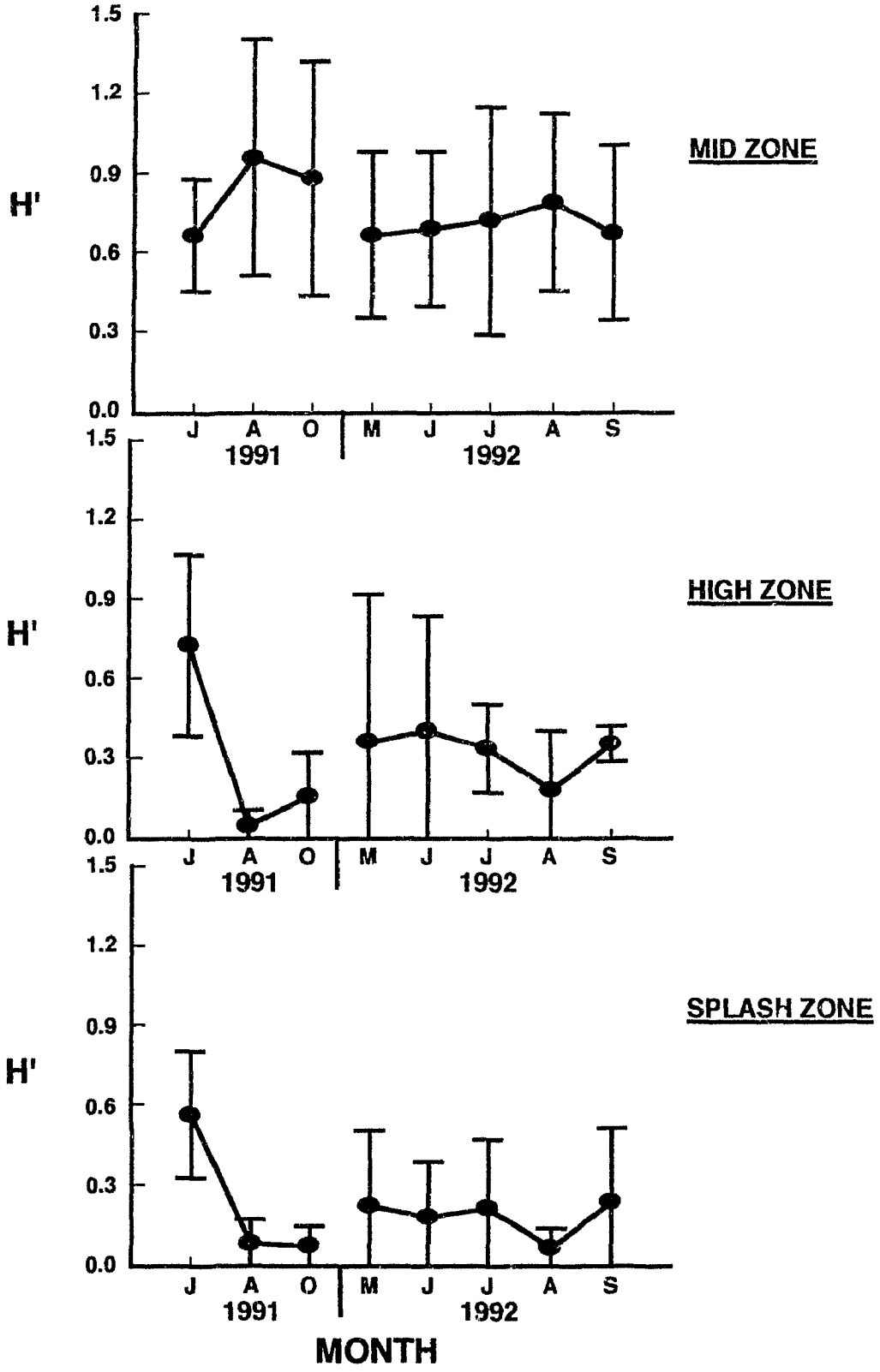
H'
1.5
1.2
0.9
0.6
0.3
0.0
MID ZONE
HIGH ZONE
SPLASH ZONE
J A O M J J A S
1991
1992
MONTH

Figure 2.9

Figure 2.10: Cluster analyses of the macroalgal communities in 4 tidepools (1, 2, 3, 4) at each of 3 intertidal zones (M=mid, H=high and S=splash), at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992.

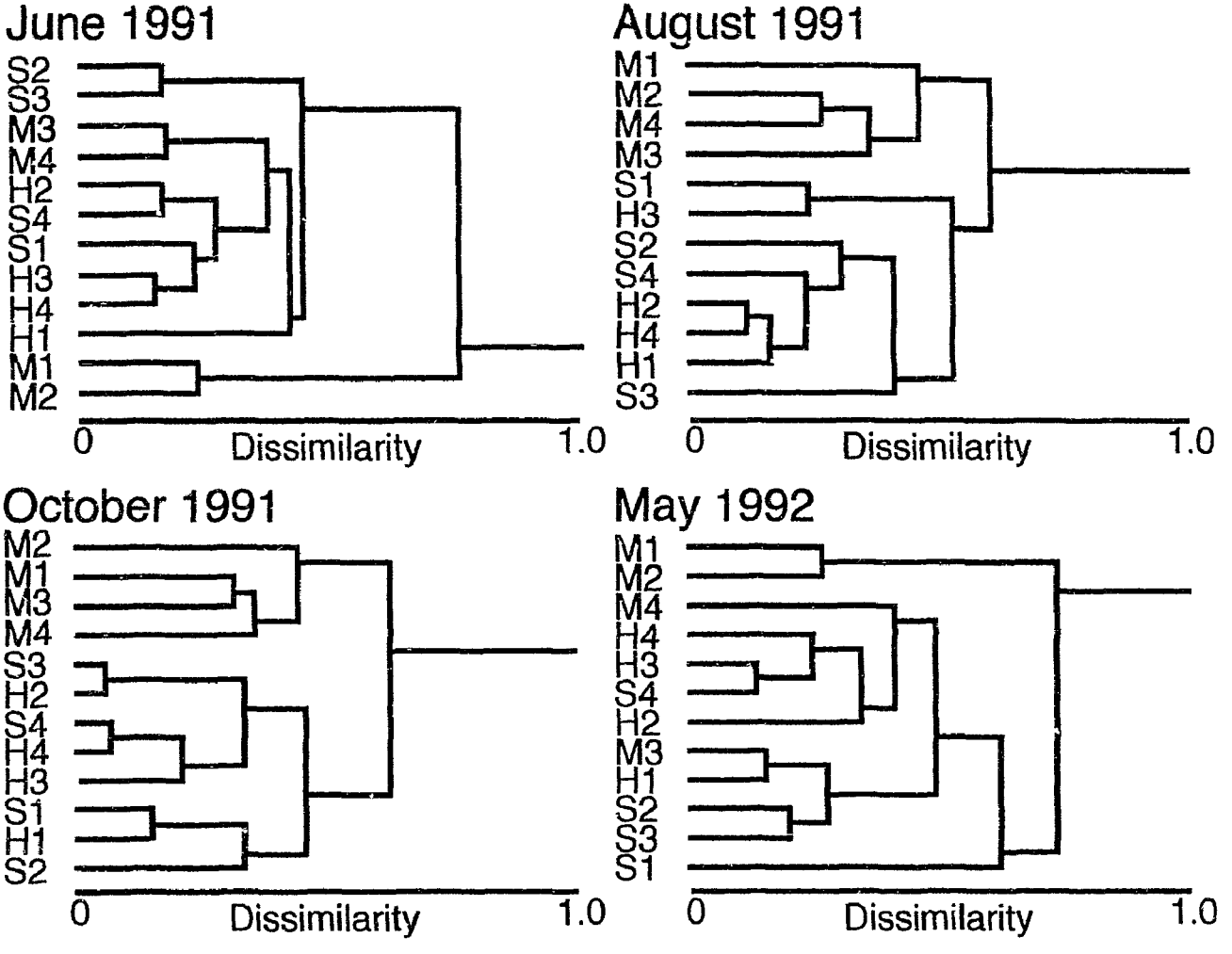
June 1991
S2
S3
M3
M4
H2
S4
S1
H3
H4
H1
M1
M2
0
Dissimilarity
1.0
August 1991
M1
M2
M4
M3
S1
H3
S2
S4
H2
H4
H1
S3
0
Dissimilarity
1.0
October 1991
M2
M1
M3
M4
S3
H2
S4
H4
H3
S1
H1
S2
0
Dissimilarity
1.0
May 1992
M1
M2
M4
H4
H3
S4
H2
M3
H1
S2
S3
S1
0
Dissimilarity
1.0

Figure 2.10

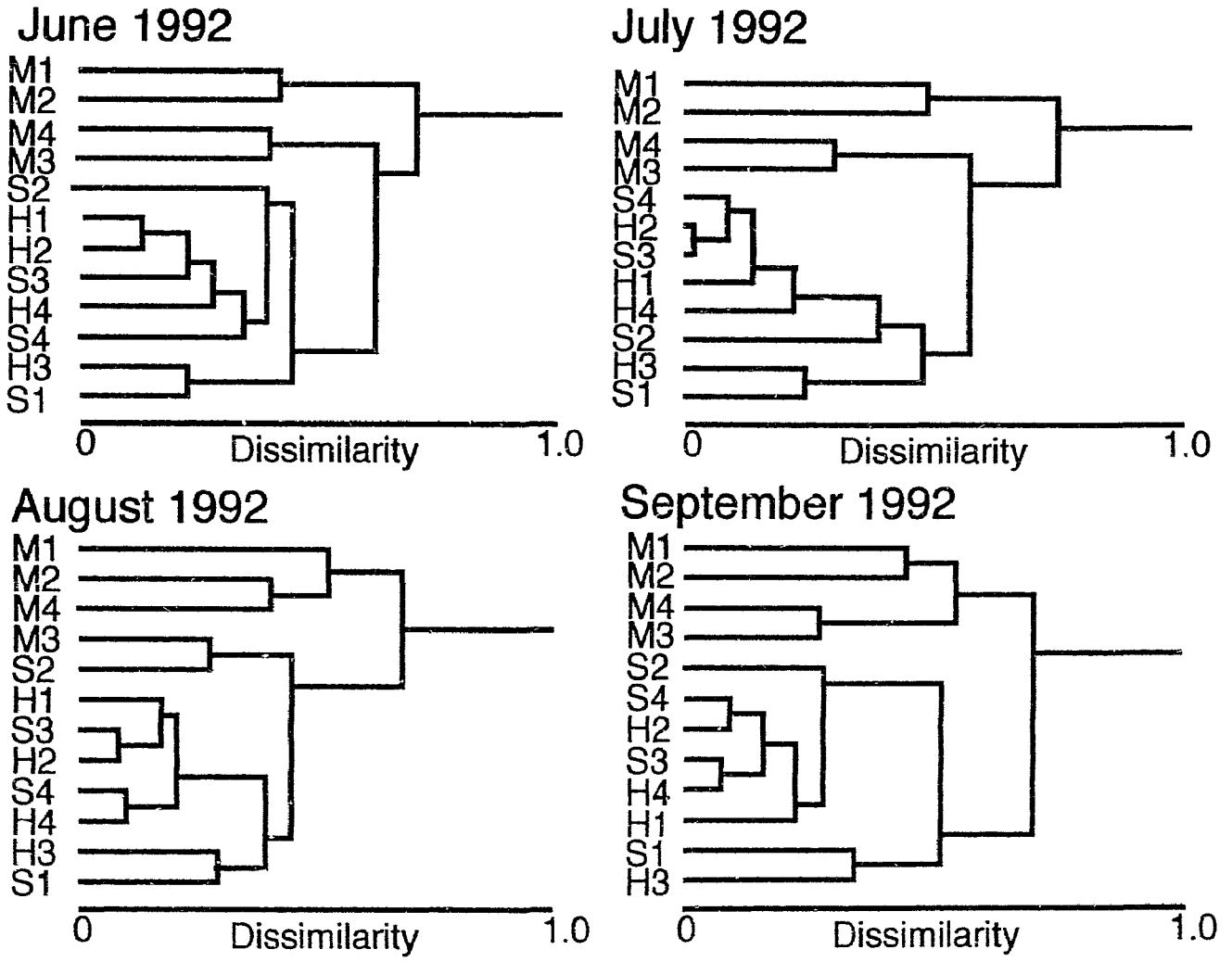

Figure 2.10 (continued)

Figure 2.11: Cluster analyses of the macroinvertebrate communities in 4 tidepools (1, 2, 3, 4) at each of 3 intertidal zones (M=mid, H=high and S=splash), at Cranberry Cove, Nova Scotia, sampled in June, August and October 1991, and at monthly intervals between May and September 1992.

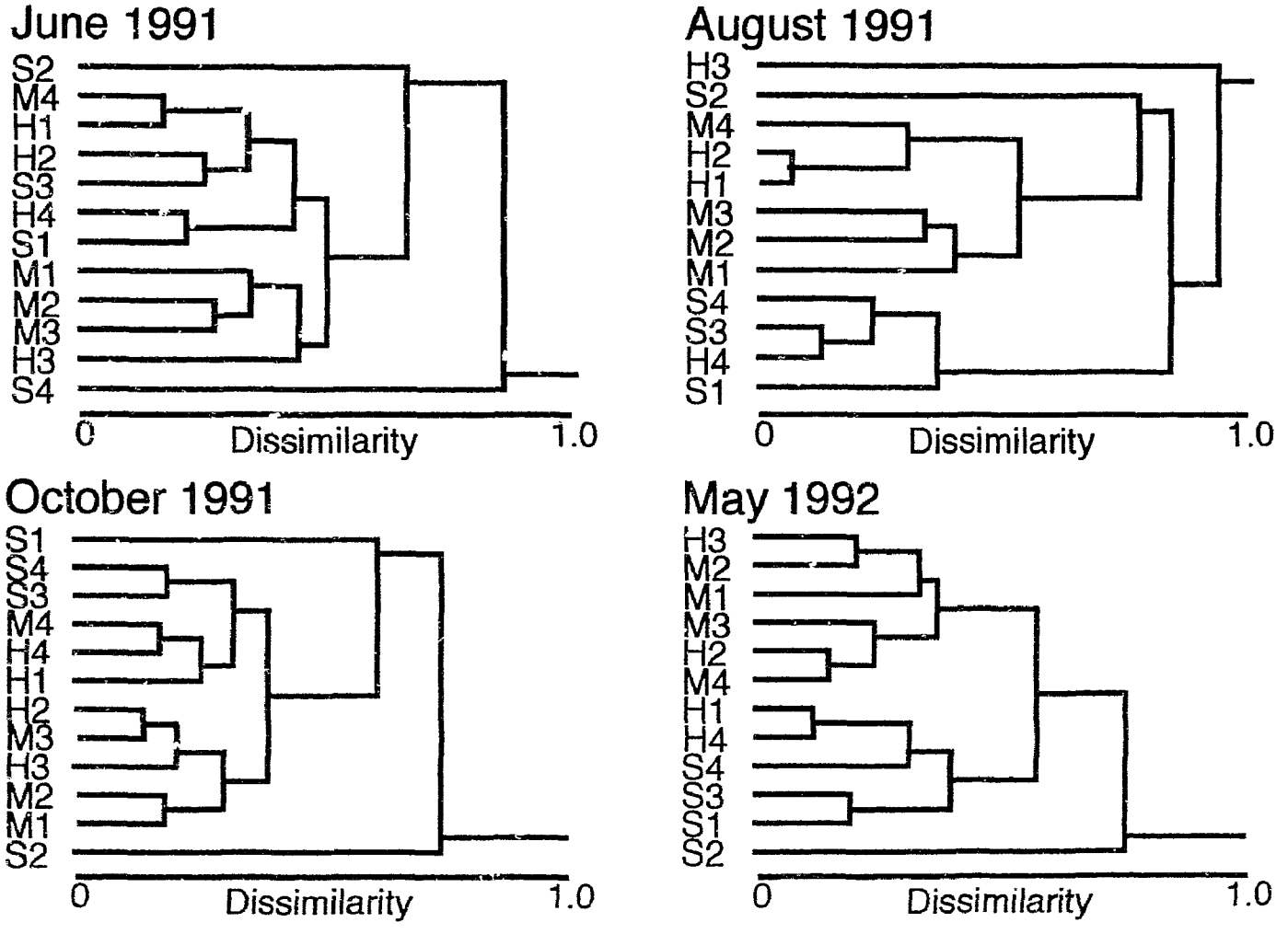
June 1991
S2
M4
H1
H2
S3
H4
S1
M1
M2
M3
H3
S4
0
Dissimilarity
1.0
August 1991
H3
S2
M4
H2
H1
M3
M2
M1
S4
S3
H4
S1
0
Dissimilarity
1.0
October 1991
S1
S4
S3
M4
H4
H1
H2
M3
H3
M2
M1
S2
0
Dissimilarity
1.0
May 1992
H3
M2
M1
M3
H2
M4
H1
H4
S4
S3
S1
S2
0
Dissimilarity
1.0

Figure 2.11

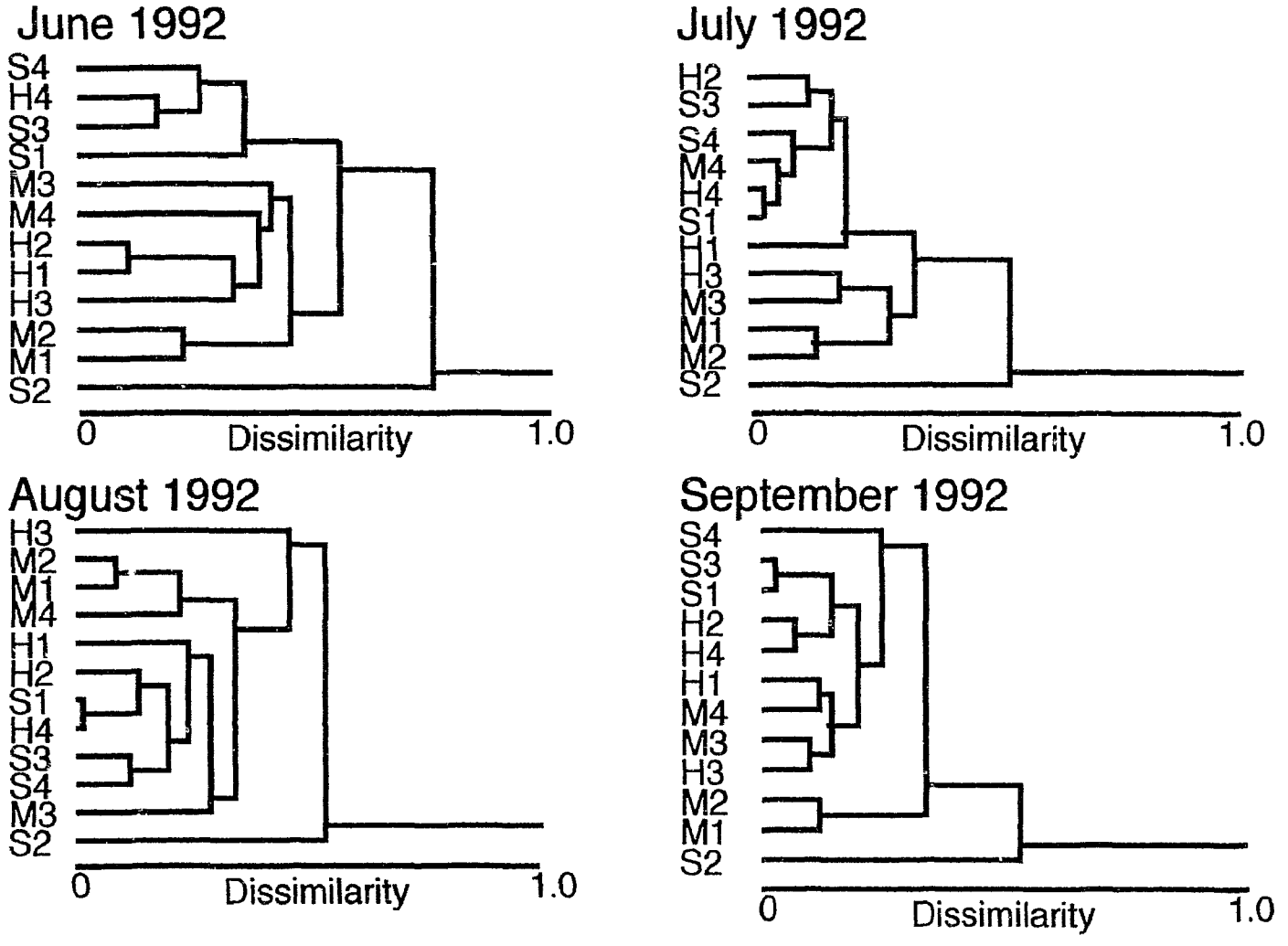

Figure 2.11 (continued)

DISCUSSION

Temporal and spatial patterns of abundance

Seasonal patterns of abundance of sheets and some filamentous and coarsely branched forms of macroalgae in this study contrasted with the patterns observed in 2 previous studies of tidepools in Maine (Femino & Mathieson 1980) and Rhode Island (Wolfe & Harlin 1988a). I found that sheets, such as *Enteromorpha intestinalis*, *Petalonia fascia*, *Scytosiphon lomentaria* and *Ulva lactuca*, were present mostly in early summer, whereas Femino & Mathieson (1980) and Wolfe & Harlin (1988a) recorded the occurrence of *U. lactuca* and *S. lomentaria* throughout the year. I found some filamentous forms, such as *Cladophora* sp. and *Spongomorpha* sp. in the pools throughout the year, whereas Femino & Mathieson (1980) recorded these forms only in late spring and early summer. In contrast, I found other filamentous forms, such as *Ceramium rubrum* and *Chaetomorpha melagonium*, mainly in late spring and summer, whereas Femino & Mathieson (1980) and Wolfe & Harlin (1988a) found that they were present throughout most of the year. I found coarsely branched forms, such as *Chordaria flagelliformis*, only in late summer, whereas Femino & Mathieson (1980) found that they were present from early spring to late fall. Some of these regional differences in macroalgal seasonality may be due to harsher conditions in the spring in Nova Scotia compared to the northeastern U.S.A. The pools in this study freeze in the winter which may preclude the occurrence, at least in a macroscopic form, of sheets, some filamentous algae and the coarsely branched algae during this period. Differences in physical characteristics, such as intertidal height or degree of exposure, between the pools in this study and those in the two previous studies also may account for some of the inconsistencies. Percentage cover of thick leathery and crustose forms did not vary seasonally in my study and in those by Femino & Mathieson (1980) and Wolfe & Harlin (1988a).

Intertidal zonation in tidepools was observed for some macroalgal genera and functional form groups, but not for others, and these observations were not always consistent with previous studies. Percentage cover of thick leathery forms, such as *Fucus vesiculosus*, and crustose macroalgal forms, such as *Phymatolithon* sp., was greater in mid pools than in high and splash pools. Similar zonation patterns were observed in studies by Fraser (1936) in Isle of Man, U.K., Green (1971) in British Columbia, Canada, Daniel & Boyden (1975) at St. Bride's Haven, U.K., and Femino & Mathieson (1980) in Maine. In contrast, Wolfe & Harlin (1988a) found thick leathery (*Fucus vesiculosus* and *Ascophyllum nodosum*) and crustose forms in pools throughout the intertidal gradient, but the pools in their study were lower than the ones I used. In my study, there was no clear zonation of sheets, or coarsely branched macroalgal forms, and among the filamentous forms, only *Cladophora* sp. showed significant differences in abundance among zones. In contrast, other studies have found that some sheets and filamentous forms, such as the green algal genus *Spongomorpha* and the brown algal genus *Scytosiphon*, were more abundant in lower pools, whereas others, such as the green algal genera *Chaetomorpha*, *Cladophora* and *Enteromorpha*, were more abundant in higher pools (Fraser 1936, Femino & Mathieson 1980, Sze 1982, Wolfe & Harlin 1988a).

Steneck & Dethier (in press) examined the distribution of macroalgal functional forms, similar to those in my study, in relation to a gradient of decreasing productivity potential with increasing intertidal height on a rocky shore in Maine, U.S.A. Productivity potential was determined by extrinsic factors (e.g. light, nutrient levels, dessication and freezing) that set the maximum limit of net primary productivity for that environment. Their model suggested that with decreasing productivity potential, leathery and crustose macrophytes should be replaced by macrophytes with lower canopy heights, such as filamentous groups, and eventually crustose algae as the dominant forms. Although the

distribution of the leathery and crustose forms in my study generally agrees with that predicted by their model, the lack of zonation of the sheets and filamentous algae does not.

Littler & Littler (1980, 1984) have characterized thick leathery and crustose macroalgal forms as late successional forms that are poor colonizers. They have more complex structures, higher maintenance costs, and lower productivity than the other groups. Sheets, filamentous and coarsely branched forms are more opportunistic and better colonizers. They allocate most of their energy to reproduction and have higher productivity. The greater abundance of thick leathery and crustose forms in mid pools, compared to those higher on the shore, may be attributable to the more benign and predictable environment in mid pools due to regular inundation by the tides (for review see Chapter 1). In high and splash pools, larger fluctuations in temperature and salinity due to evaporation and freezing create a harsher environment which many of these forms may not tolerate. According to the Littlers' classification, the more opportunistic, highly productive forms, such as sheets and filamentous algae, can quickly colonize and establish populations when space becomes available. In my study, gaps which occurred in mid pools in the spring, and in high and splash pools throughout the year, were readily colonized by these forms.

Percentage cover of all macroalgal functional form groups varied markedly among pools within each zone. Some groups, such as some filamentous and coarsely branched forms, appeared sporadically in mid pools in the spring and summer, respectively. Other groups, such as sheets, filamentous, thick leathery, jointed calcareous, and crustose forms, were present in great abundances in some pools but were completely absent from others. The amount of bare substratum was most variable among high and splash pools in late summer and fall, a period during which heavy wave action due to storms dislodged most of the macroalgal canopy (personal observations). The large horizontal variability in percentage macroalgal cover that I observed among pools with similar periods of tidal

isolation may reflect, in part, the vagaries of recruitment. Furthermore, many of the factors or processes influencing recruitment and survival of macroalgae may vary greatly among individual tidepools and cannot be generalized to intertidal zones.

There was less variability among intertidal zones in macrofaunal abundance than in macroalgal cover. Abundance of mussels, littorines and whelks peaked in summer due to recruitment (Minchinton 1989, Pedersen 1991). Mussels were much more abundant in mid pools than in high and splash pools. I did not record mussels > 2 cm in higher pools, suggesting that their survivorship there was low, presumably due to the harsher conditions. Clarke & Griffiths (1990) suggested that mussels living in tidepools have a larger metabolic cost than those on the emergent substratum because mussels can shut down their metabolism completely when emerged. Whelks were rare in high and splash pools indicating low recruitment, immigration and/or survival there. Littorinid snails were found in pools of all zones (with the exception of 1 pool in the splash zone where they were never found) but were most abundant in high pools. The zonation of macrofauna that I observed is consistent with previous studies of tidepools on rocky shores (Fraser 1936, Ganning 1971, Daniel & Boyden 1975, Goss-Custard *et al.* 1979, Femino & Mathieson 1980). As for the macroalgae, large variability among pools within zones was detected for each of the 3 major groups of macrofauna. Mussel abundance varied significantly among high and splash pools. Littorinid and whelk abundance varied among pools in all zones, mostly in summer. This variability may reflect differential recruitment among pools or differential mortality due to environmental conditions which are specific to individual pools.

Correlates of macroalgal abundance

Multiple linear regressions showed that the relationship between macroalgal percentage cover and snail and mussel abundance, the nutrient regime, and the physical characteristics of tidepools varied among macroalgal functional form groups. For all

groups, a smaller proportion of the variance in percentage cover was explained when the regressions were done for the entire sampling period than for each sampling date, suggesting that the factors affecting cover may change throughout the year. The number of significant regressions was smaller for the more opportunistic, highly productive forms, such as sheets and filamentous forms, than for the late successional, less productive, thick leathery and crustose forms. This is consistent with the view that more opportunistic forms should be capable of rapid growth under a range of environmental conditions, whereas the later successional forms should tend to be physiologically adapted to a more predictable environment (Littler 1980, Littler & Littler 1980, 1984).

None of the macroalgal forms showed a strong, consistent relationship with the dominant grazers in the pools. This may be because the more opportunistic forms can escape losses due to grazing by rapid growth, and later successional forms have reduced palatability (Littler & Littler 1980). However, these observations are inconsistent with previous experimental studies which have manipulated grazers in tidepools in the northwest Atlantic. Lubchenco (1982) showed that the cover of some sheets, filamentous, and thick leathery macroalgae increased when grazer density was decreased in mid pools in a protected and a semi-exposed site, in Maine and Massachusetts, respectively. Chapman (1990) working in high pools at an exposed site ~5 km east of mine showed that grazer removals resulted in an increase in sheets but a decrease in thick leathery forms. Parker *et al.* (1993) working in high pools at my site, found a significant decrease in cover of most functional forms in the presence of littorinid grazers in early successional stage communities, but Parker & Chapman (in press) detected no effects of littorinids on canopy macroalgal groups in established communities in high pools at Sandy Cove, Nova Scotia, Canada. The inconsistency of results among different studies support my suggestion that the importance of grazing may vary among tidepools, and it may not be easily generalizable across intertidal zones, sites or regions (e.g. northwest Atlantic).

All macroalgal functional forms showed a significant relationship with mussel abundance. This may be because they use them as a substrate (e.g. coarsely branched and some filamentous forms, personal observations) or compete with them for space. Although, to my knowledge, no studies have examined competitive processes in tidepools that involve mussels, competition among mussels and macroalgae has been demonstrated on emergent substrata of the rocky shores of the northwest Atlantic (e.g. Lubchenco & Menge 1978, but see McCook & Chapman 1991).

The percentage cover of all macroalgal forms tended to vary with the nutrient regime in summer and fall, periods of low ambient nutrient concentration. The cover of all macroalgal forms also varied significantly with some physical characteristic of the pools, thick leathery and crustose forms more so than sheets or filamentous macroalgae. This suggests that the physical setting of the pool may be of primary importance in determining macroalgal abundance. The physical environment is determined by a combination of factors such as intertidal height, topography, depth, volume and wave exposure that is unique to each pool (see Chapter 1 for review).

Patterns of species diversity and community similarity

Macroalgal species diversity was greater in mid pools than in high and splash pools probably because fewer species can tolerate the harsher conditions in the higher pools. As previously mentioned, high and splash pools were dominated by opportunistic, macroalgal forms, whereas all functional forms were found in the mid pools. Macroalgal species diversity tended to be lowest in summer and fall, especially in mid pools, when intensive grazing by littorinids probably reduced the abundance of the newly-recruited sheet, filamentous and coarsely branched forms. Macrofaunal species diversity also was greater in mid than in high and splash pools in summer and fall, periods of maximal fluctuations in the physical conditions of these higher pools (unpublished data). Previous studies also

have shown a decrease in the number of algal and macroinvertebrate species in pools with increasing intertidal height (Femino & Mathieson 1980, Huggett & Griffiths 1986, Wolfe & Harlin 1988b, Kooistra *et al.* 1989).

Because of the large variability among pools in macroalgal and macrofaunal abundance, pools did not cluster strongly with intertidal height. Opportunistic macroalgal forms appeared only in some mid pools in the spring resulting in low similarity until summer when most of these newly-recruited algae had disappeared. A high pool (Pool 3) and a splash pool (Pool 1) formed a tight cluster in late summer in both years when both had lost all ephemeral macroalgal cover and were covered only with the prostrate form *Hildenbrandia rubra* or were completely bare. The remaining high and splash pools did not form distinct clusters, suggesting that differences in tidal input between these zones are not sufficiently pronounced to have a marked effect on the macroalgal communities. Similarity among tidal zones was even less pronounced for the macrofaunal communities. There was large variability among high and splash pools, with certain pools frequently being dissimilar to all others. In general, mid pools were more similar to high pools than splash pools, suggesting that macrofaunal communities probably are influenced to some degree by regular tidal input regardless of its frequency.

In summary, although significant variability among intertidal zones in percentage cover of macroalgae in tidepools was detected for some functional forms, large and consistent variability in percentage cover of all groups occurred among pools within zones. Therefore, horizontal spatial variability in macroalgal abundance appears to be as great as variability along the intertidal gradient. This suggests that differences in the physical characteristics of individual pools are as important as the period of tidal isolation of the pool in determining macroalgal community composition.

CHAPTER 3: Spatial and temporal variability of tidepool hyperbenthos on a rocky shore in Nova Scotia, Canada

INTRODUCTION

Among the motile benthos of the emergent substrata of intertidal rocky shores are meio- and macrofauna, such as harpacticoid copepods, amphipods and polychaetes, which swim during submergence but attach to the substratum or to macroalgae during emergence (Hawkins & Hartnoll 1983, Hicks & Coull 1983, Dean & Connell 1987a, b, Johnson & Scheibling 1987, Gibbons 1988, 1989, Janke 1990). In tidepools, these animals are continuously submerged and can actively swim and feed during their entire cycle. Tidepools also are microhabitats for zooplankton such as calanoid copepods or cladocerans, which feed only in the water-column, spend most of their time swimming and are not found on the emergent rocks (Fraser 1936, Naylor & Slinn 1958, Ganning 1971, Goss-Custard *et al.* 1979, Preston & Moore 1988, Chapter 1). Some groups, such as amphipods, may be present in constant abundance in pools throughout the year (Femino & Mathieson 1980, but see Ganning 1971), while others, such as harpacticoid copepods, show large seasonal variations in abundance (Goss-Custard *et al.* 1979). The abundance of motile fauna also may vary with increasing intertidal height of the tidepools (Chapter 1). For example, harpacticoid copepods are generally more abundant in tidepools located high on the shore (Fraser 1936, Dethier 1980), whereas calanoid copepods and amphipods are more abundant in tidepools located lower on the shore (Fraser 1936, Ganning 1971, Femino & Mathieson 1980, but see Naylor & Slinn 1958). However, most studies have not measured abundance quantitatively or have shown high variability in abundance among pools within the same intertidal zone, which can mask height effects (e.g. see Naylor & Slinn 1958, Chapter 1).

In this chapter, I examine spatial and temporal patterns of the horizontal and vertical distribution and abundance of the motile fauna or "hyperbenthos" (sensu Beyer 1958, as cited in Sibert 1981) of tidepools in each of 3 intertidal zones (mid, high, splash) on a rocky shore in Nova Scotia, Canada. I compare the variability in abundance, over a 15 mo period, among tidepools within the same zone to the variability among zones and at the sea-surface. These patterns of variation are discussed in relation to differences in tidal input and physical conditions among zones and provide a basis for further studies of the mechanisms regulating the structure and dynamics of this poorly-known faunal assemblage of tidepools.

MATERIALS AND METHODS

Four tidepools, at each of 3 zones (mid, high and splash) along the intertidal gradient were sampled at approximately monthly intervals between March and November 1991, and between April and June 1992, at Cranberry Cove, Nova Scotia, Canada (44°28'N, 63°56'W). (For a detailed description of the pools and study site, see Chapter 2).

In each tidepool, 2 samples of hyperbenthic fauna were collected by hand-pumping 5 L of seawater from 10 to 20 cm above the bottom of the tidepool (sediment/water interface, approximately the mid depth of the pools) through a 60-μm net. The net was then rinsed into a container and the sample fixed with 4% buffered formaldehyde. Two other samples were collected similarly at the sea-surface at each of 2 locations along the shore separated by approximately 250 m. The fauna were identified to the lowest taxonomic level possible (see Table 3.1) according to Smith (1964), Brinkhurst *et al.* (1976), Barnes (1980) and Gardner & Szabo (1982) and enumerated using a Leitz Labovert inverted microscope.

The fauna were assigned to the following taxonomic groups: amphipods, barnacle nauplii, calanoid copepods, cladocerans, cyclopoid copepods, foraminiferans, harpacticoid copepods, isopods, mites, nematodes, ostracods, polychaetes, and rotifers. Taxonomic groups with abundances >25% of the total abundance of the hyperbenthic fauna in any 1 pool, during at least 2 out of the 12 sampling dates, were selected for statistical analyses. For each sampling date, differences in abundance of each selected taxonomic group were examined among intertidal zones and among pools within zones using 2-factor nested analyses of variance. The effect of the nested factor (Pool) was further examined within each Zone (mid, high and splash).

The Shannon Diversity Index (H') was calculated for each tidepool, for each sampling date as $H' = - \sum_{i=1}^{n} P_i \ln P_i$, where P_i is the proportion of the ith taxonomic group in each tidepool. The lowest possible identification levels that were used as taxonomic groups to calculate H' varied among groups: harpacticoid copepods were assigned to planktonic (e.g. *Microsetella rosea*) and benthic (all others) groups; calanoid and cyclopoid copepods, rotifers and cladocerans were identified to genus; isopods and amphipods were identified to species; and nematodes, foraminiferans, mites, polychaetes, ostracods and pycnogonids were not identified to any lower taxonomic level. Since the level of identification was consistent across all pools in all zones, the calculated index is used primarily as a comparative measure. H' was calculated for each pool using the average abundance of each taxonomic group for the 2 samples. Differences in the diversity index among intertidal zones were examined using a 2-factor (Zone and Time) analysis of variance.

For all statistical analyses, the data were ln (x+1)-transformed where heterogeneity of variance was detected using Cochran's test. *A posteriori* multiple comparisons of treatment means were done using Student-Newman-Keuls (SNK) tests. All statistical analyses were carried out using SYSTAT v. 5.1 (Wilkinson 1989) on a Macintosh SE 30 computer.

RESULTS

The abundance of 6 taxonomic groups was >25% of total abundance in any 1 tidepool on any 2 sampling dates: harpacticoid copepodites and nauplii (Families Harpacticidae, Tisbidae, Thalestridae, Diosaccidae); calanoid copepodites and nauplii (the genera *Acartia*, *Calanus*, *Paracalanus*, *Pseudocalanus* and *Temora* at the sea-surface and in the mid pools, and *Eurytemora affinis* in the splash pools); marine cladocerans (*Podon polyphemoides* and *Evadne nordmanii*); foraminiferans; marine rotifers (the genera *Brachionus* and *Synchaeta*); and nematodes (Table 3.1). Generally, the abundance of total hyperbenthos in the tidepools was low (< 10^3 individuals . m^{-3}) in early spring 1991 (March to May), increased in summer (up to 10^7 individuals . m^{-3} in the splash pools), decreased after October 1991, remained low through spring 1992, and increased again in summer 1992 (Fig. 3.1). The temporal trend in abundance in tidepools was similar to that observed at the sea-surface. Temporal changes in the abundance of harpacticoid copepods and nematodes were similar to those observed for total hyperbenthos, both at the sea surface and in the pools (Figs. 3.2 & 3.3). The abundance of calanoid copepods was low at the sea-surface and in the mid and high pools (< 10^3 individuals . m^{-3}), and no pronounced temporal fluctuations were observed (Fig. 3.4). The abundance of this group was highest (10^4-10^5 individuals . m^{-3}) in the splash pools where it peaked in summer 1991 and 1992. Similarly, rotifers were present in low abundance (< 1,000 individuals . m^{-3}) at the sea-surface and in the mid pools in July and August 1992, but were abundant in the high and splash pools in summer 1991 and 1992 (up to 10^6 individuals . m^{-3}) (Fig. 3.5). Cladocerans and foraminiferans were rare to absent at the sea-surface and in tidepools for most of the year and no distinct temporal changes were observed. Pulses in abundance of these 2 groups were observed in some high and splash pools in late summer and late fall 1991 or early spring 1992,

and at those times one or the other group made up >25% of the hyperbenthic fauna in the pool (Figs. 3.6 & 3.7).

The abundance of the different taxonomic groups of the hyperbenthos varied among intertidal zones only on 4 out of 12 sampling dates (Table 3.2). The abundance of total hyperbenthos was significantly different among zones in June 1991, July 1991, September 1991 and May 1992. Total hyperbenthos was significantly more abundant in splash pools than in mid pools in June 1991, in splash pools than in mid and high pools in July 1991, in splash pools than in high pools but not mid pools in September 1991, and in high pools than in mid pools but not splash pools in May 1992 (SNK tests, $p < 0.05$). Harpacticoid and calanoid copepods were significantly more abundant in high pools than in mid and splash pools in May 1992 (SNK tests, $p < 0.05$). Nematodes were significantly more abundant in splash pools than in mid pools in July 1991 (SNK test, $p < 0.05$). Rotifers were significantly more abundant in splash pools than in mid pools in August 1991, and significantly more abundant in splash and high pools than in mid pools in September 1991 (SNK tests, $p < 0.05$).

The abundance of most taxonomic groups of the hyperbenthos varied significantly among tidepools within intertidal zones (Table 3.2). The abundance of total hyperbenthos varied significantly among splash pools from May to October 1991, and in June 1992, among high pools in June 1991 and 1992, and among mid pools in June and September 1991. The abundance of harpacticoid copepods varied significantly among tidepools in the high zone in June, July, and October 1991. Harpacticoid copepods also showed a significant Pool effect in the high zone in September 1991, although the combined Pool effect for all zones was not significant. The abundance of nematodes varied significantly among pools in all zones in June 1991. Nematode abundance also varied significantly among mid pools in September 1991 and among splash pools in July

1992, although the combined Pool effect for all zones was not significant at these times. The abundance of calanoid copepods varied significantly among splash pools from June to September 1991 and in June 1992, among high pools in July 1991 and June 1992, and among mid pools in September 1991. The abundance of rotifers varied significantly among splash pools from May to July and in September 1991, among high pools in June, July and September 1991 and in June 1992, and among mid pools in June 1991. The abundance of marine cladocerans varied significantly among splash pools in May 1992. Cladoceran abundance also differed significantly among high pools in October 1991 although the combined Pool effect for all zones was not significant. The abundance of foraminiferans was significantly different among mid pools in June 1991 and, although the combined Pool effect was not significant, the abundance of this group varied significantly among high pools in May 1992.

The Shannon Diversity Index (H') varied significantly among zones ($F_{2, 108} = 12.028$, $p < 0.001$) and over time ($F_{11, 108} = 2.841$, $p < 0.01$) (Fig. 3.8A), and there was no significant interaction between Zone and Time effects on H' ($F_{22, 108} = 0.962$, $p > 0.05$). H' was significantly smaller in splash pools than in mid and high pools (SNK test, $p < 0.05$). There were no consistent temporal trends in H' in the tidepools (Fig. 3.8B). At the sea-surface, diversity increased between March and October 1991, decreased after October and started increasing again after April 1992.

Table 3.1: List of taxonomic groups of hyperbenthos identified in this study and present at the sea-surface and in the tidepools on any sampling date between March 1991 and June 1992.

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
ACARINA	✔	✔	✔	✔		✔	✔	✔	✔	✔	✔		✔
AMPHIPODS													
Amphithoe rubricata (Montagu)	✔	✔						✔			✔		
Casco bigelowi (Blake)					✔								
Corophium volutator (Pallas)	✔				✔	✔	✔					✔	
Gammarus oceanicus Segerstråle	✔	✔	✔							✔	✔		
Gammarus tigrinus Sexton	✔			✔	✔		✔			✔	✔		
Marinogammarus finmarchicus Dahl	✔		✔		✔						✔		
Pontogeneia inermis (Kröyer)	✔	✔											
CALANOID COPEPODS													
Acartia sp.	✔	✔	✔	✔	✔	✔		✔	✔	✔			
Calanus sp.	✔	✔	✔	✔		✔		✔				✔	
Eurytemora affinis (Poppe)	✔		✔	✔	✔	✔	✔	✔	✔	✔	✔		✔
Paracalanus sp.	✔	✔	✔	✔	✔								
Pseudocalanus sp.	✔	✔	✔	✔	✔	✔	✔	✔					
Temora longicornis (Müller)	✔		✔	✔	✔		✔			✔			
T. stylifera (Dana)		✔											
Calanoid nauplii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
CIRRIPEDIA													
Semibalanus balanoides (L.) nauplii										✔		✔	
CLADOCERANS													
Evadne nordmanii Loven	✔	✔	✔	✔	✔	✔	✔		✔	✔	✔	✔	✔
Podon polyphemoides Leuckart	✔	✔	✔	✔	✔	✔	✔		✔	✔	✔	✔	✔

Table 3.1 (Continued)

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
CYCLOPOIDS													
Oithona similis Claus	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔		✔	✔
FORAMINIFERANS	✔	✔	✔		✔	✔	✔		✔	✔	✔	✔	✔
HARPACTICOID COPEPODS													
Microsetella rosea (Dana)	✔	✔	✔	✔	✔		✔	✔	✔			✔	
Other harpacticoid copepods	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Harpacticoid nauplii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
ISOPODS													
Idotea balthica (Pallas)	✔	✔											✔
Idotea phosphorea Harger	✔						✔						✔
Jaera marina (Fabricius)	✔	✔	✔			✔	✔		✔		✔	✔	✔
NEMATODES	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
OSTRACODS	✔	✔	✔	✔	✔	✔	✔		✔	✔	✔	✔	✔
POLYCHAETES	✔	✔	✔		✔				✔		✔		✔
PYCNOGONIDS	✔	✔		✔	✔	✔		✔	✔		✔	✔	
ROTIFERS													
Brachionus spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔		✔	✔
Synchaeta spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔

Table 3.2: Analyses of variance of the abundance of different groups of hyperbenthos (individuals . m^{-3}) for 12 sampling periods between March 1991 and June 1992. Factors are Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)} = 9, 12$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 21$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

VARIABLE	FACTOR	17-3-91		13-4-91		13-5-91		7-6-91	
		MS	F, p	MS	F, p	MS	F, p	MS	F, p
HARPACTICOIDS	P(Z):	$5.9x10^5$	0.90, NS	5.55	2.64, NS	2.23	2.61, NS	2.73	3.68, *
	Z:	$5.7x10^5$	1.49, NS	14.68	2.11, NS	5.81	0.78, NS	10.07	0.61, NS
NEMATODES	P(Z):	8.46	1.39, NS	6.94	1.04, NS	8.61	1.13, NS	0.35	8.60,***
	Z:	6.09	0.71, NS	7.04	0.98, NS	9.09	0.74, NS	3.05	4.14, NS
CALANOIDS	P(Z):	3.52	2.08, NS	3.58	2.69, NS	6.54	2.77, NS	4.56	6.56, **
	Z:	7.31	1.36, NS	9.62	0.85, NS	18.11	0.88, NS	29.90	1.43, NS
ROTIFERS	P(Z):	IN ONE POOL		ABSENT		5000	38.6,***	4.08	8.06,***
	Z:	HIGH ZONE		ABSENT		$1.9x10^5$	1.15, NS	32.83	0.48, NS
CLADOCERANS	P(Z):	ABSENT		ABSENT		ABSENT		ABSENT	
	Z:	ABSENT		ABSENT		ABSENT		ABSENT	
FORAMINIFERANS	P(Z):	ABSENT		ABSENT		ABSENT		2.69	2.97, *
	Z:	ABSENT		ABSENT		ABSENT		7.99	0.17, NS
TOTAL	P(Z):	$5.9x10^5$	0.75, NS	4.38	1.90, NS	0.90	3.30, *	0.16	22.5,***
	Z:	$5.3x10^5$	1.98, NS	8.30	0.25, NS	2.95	0.57, NS	3.60	5.87, *

Table 3.2 (continued)

VARIABLE	FACTOR	12-7-91		22-8-91		21-9-91		9-10-91	
		MS	F, p	MS	F, p	MS	F, p	MS	F, p
HARPACTICOIDS	P(Z):	3.38	3.88, *	4.04	1.79, NS	7.05	2.23, NS	1.48	2.95, *
	Z:	13.10	1.91, NS	7.21	0.56, NS	15.75	0.87, NS	4.37	1.41, NS
NEMATODES	P(Z):	$3.0x10^6$	0.76, NS	$1.2x10^5$	0.38, NS	4.78	2.51, NS	5.01	1.72, NS
	Z:	$2.7x10^6$	3.63, *	$8.7x10^4$	2.15, NS	12.01	0.24, NS	8.61	1.03, NS
CALANOIDS	P(Z):	6.15	4.49 **	8.55	3.84, *	6.21	7.12,***	11.37	1.38, NS
	Z:	27.59	1.91, NS	32.84	0.09, NS	44.20	0.49, NS	13.23	0.83, NS
ROTIFERS	P(Z):	4.51	11.3,***	1.79	1.52, NS	6.41	3.19, *	2.99	1.00, NS
	Z:	50.78	0.79, NS	2.73	50.0,***	20.42	4.84, *	2.99	0.50, NS
CLADOCERANS	P(Z):	ABSENT		IN ONE POOL		ABSENT		5.81	1.99, NS
	Z:	ABSENT		MID ZONE		ABSENT		11.57	0.03, NS
FORAMINIFERANS	P(Z):	6.24	1.73, NS	9.44	1.15, NS	7.89	0.54, NS	IN ONE POOL	
	Z:	10.78	2.70, NS	10.06	0.13, NS	6.51	1.34, NS	HIGH ZONE	
TOTAL	P(Z):	0.62	6.28, **	0.53	7.02,***	1.05	5.51, **	0.77	3.55, *
	Z:	3.89	7.49, *	3.73	2.53, NS	5.77	5.15,	2.72	0.05, NS

Table 3.2 (continued)

VARIABLE	FACTOR	17-11-91		8-4-92		6-5-92		26-6-92	
		MS	F, p	MS	F, p	MS	F, p	MS	F, p
HARPACTICOIDS	P(Z):	7.47	1.78, NS	8.09	0.88, NS	$7.5x10^6$	0.45, NS	4.08	1.06, NS
	Z:	13.32	0.77, NS	7.67	2.43, NS	$5.7x10^6$	4.55, *	4.18	0.09, NS
NEMATODES	P(Z):	5.22	1.45, NS	5000	0.78, NS	4.64	1.63, NS	4.96	2.35, NS
	Z:	6.23	0.46, NS	4524	1.11, NS	7.57	3.49, NS	11.58	0.71, NS
CALANOIDS	P(Z):	8.85	0.59, NS	7.66	2.35, NS	$9.5x10^4$	0.39, NS	2.46	13.6,***
	Z:	7.29	0.50, NS	18.01	0.62, NS	$7.0x10^4$	9.04, **	33.50	1.66, NS
ROTIFERS	P(Z):	ABSENT		ABSENT		IN ONE POOL		5.65	4.05, *
	Z:	ABSENT		ABSENT		SPLASH ZONE		22.87	3.21, NS
CLADOCERANS	P(Z):	IN ONE POOL		3.44	0.68, NS	3.47	3.23, *	ABSENT	
	Z:	MID ZONE		2.97	2.26, NS	11.20	1.69, NS	ABSENT	
FORAMINIFERANS	P(Z):	3.03	1.00, NS	ABSENT		1.71	2.64, NS	3.52	1.00, NS
	Z:	3.03	0.51, NS	ABSENT		4.51	2.67, NS	3.52	0.00, NS
TOTAL	P(Z):	$1.1x10^6$	1.19, NS	6.86	1.57, NS	$1.2x10^8$	0.81, NS	1.31	4.73, **
	Z:	$1.2x10^6$	1.79, NS	10.78	0.97, NS	$1.1x10^7$	3.55, *	6.20	1.80, NS

Figure 3.1: Abundance of total hyperbenthos at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

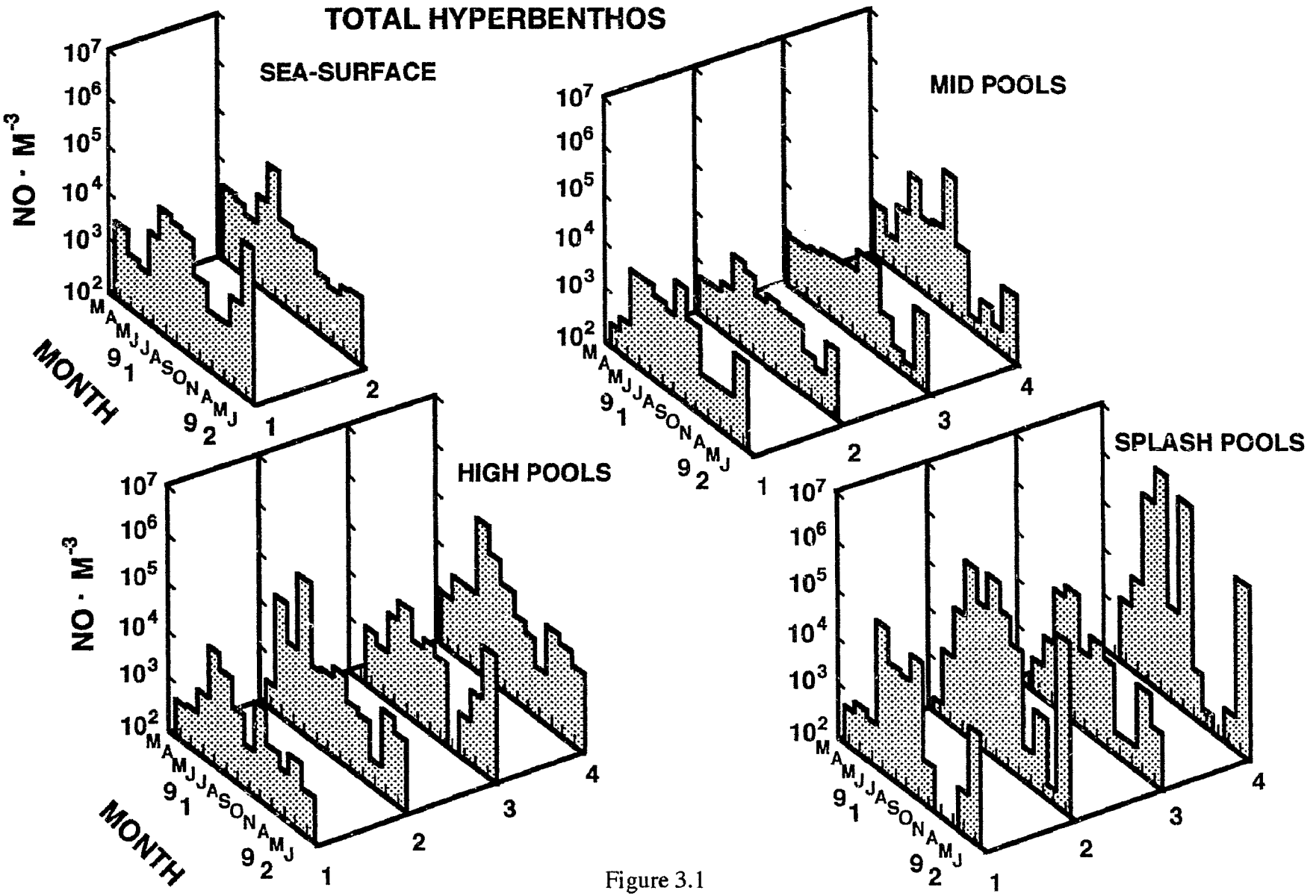
TOTAL HYPERBENTHOS
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
NO · M-3
MONTH
M A M J J A S O N A M J
9 1
9 2
1
2
3
4
10^7
10^6
10^5
10^4
10^3
10^2

Figure 3.1

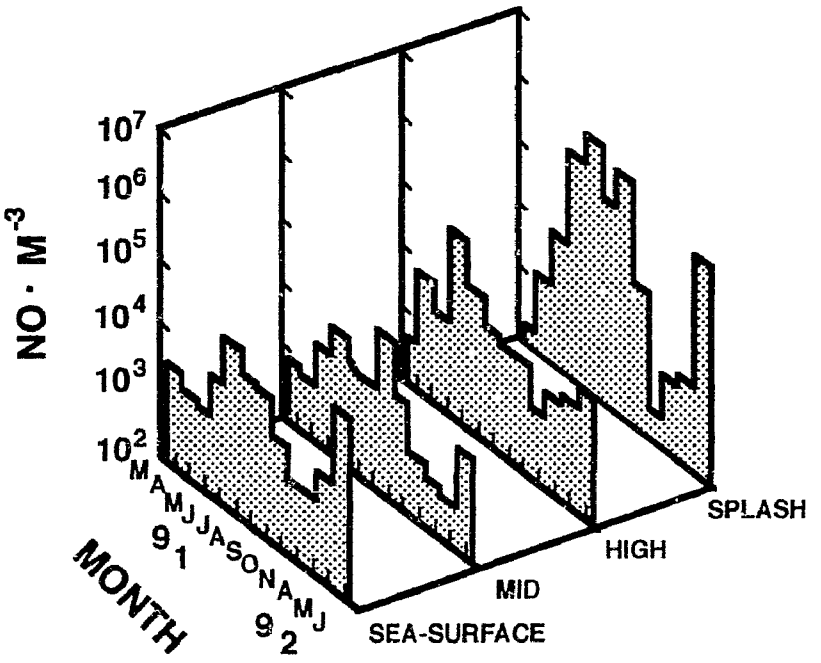

Figure 3.1 (continued)

Figure 3.2: Abundance of harpacticoid copepods at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

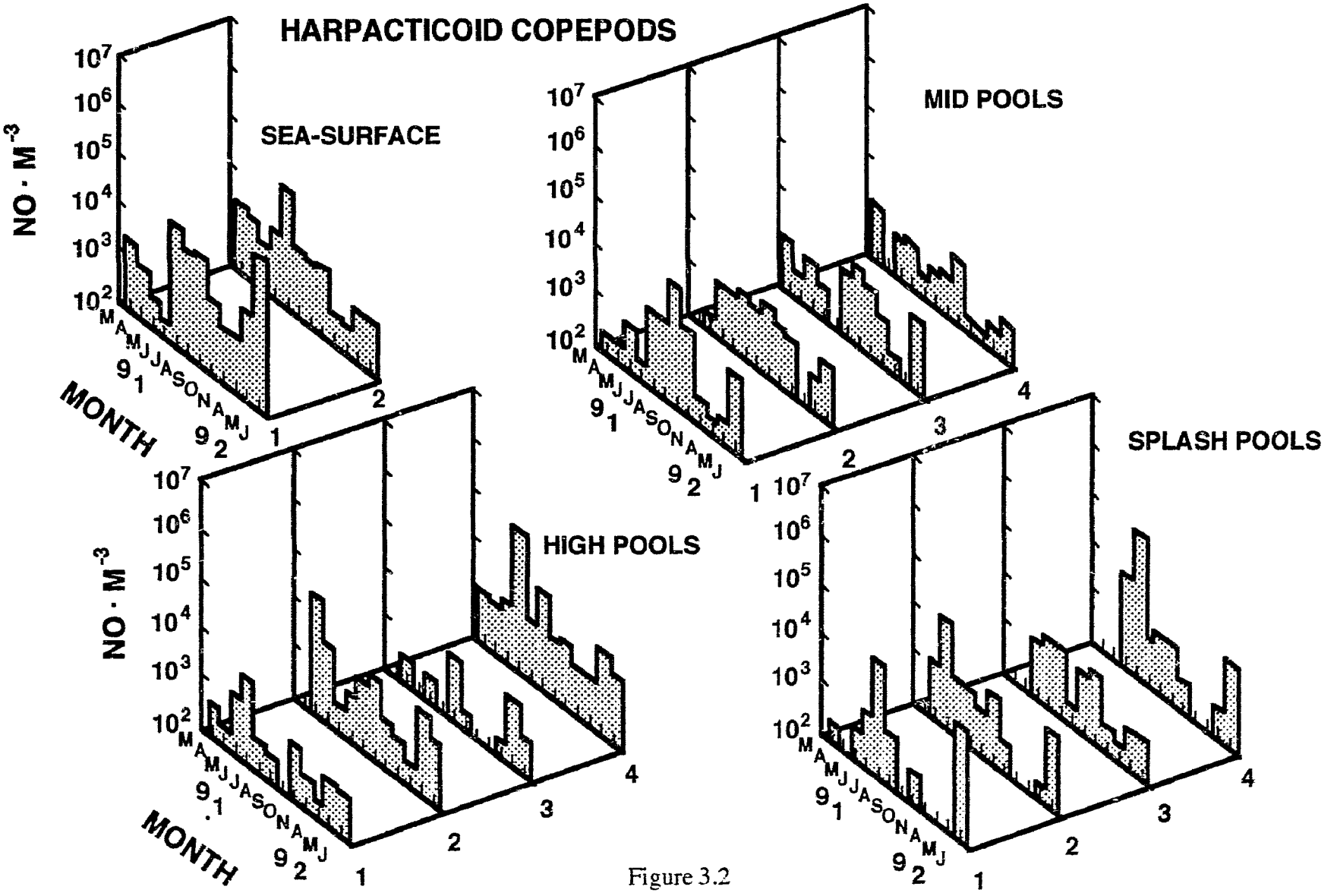
HARPACTICOID COPEPODS
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
NO · M-3
MONTH
10^7
10^6
10^5
10^4
10^3
10^2
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.2

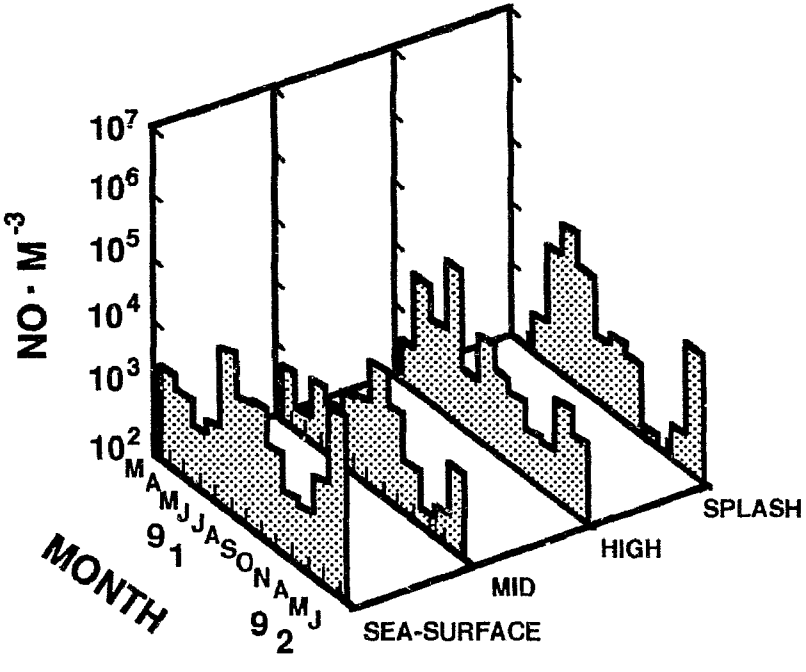

Figure 3.2 (continued)

Figure 3.3: Abundance of nematodes at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

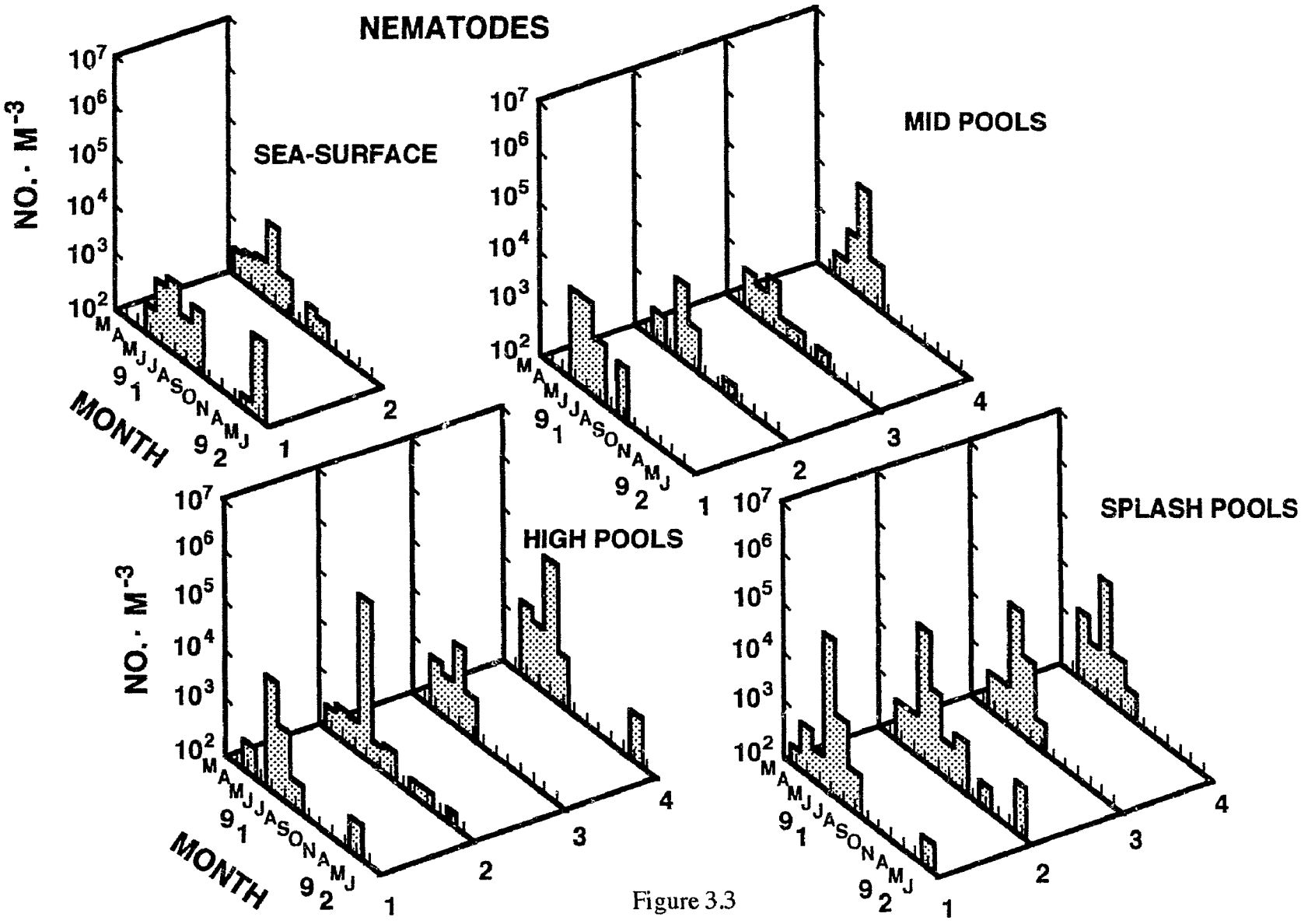
NEMATODES
NO. · M-3
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
MONTH
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.3

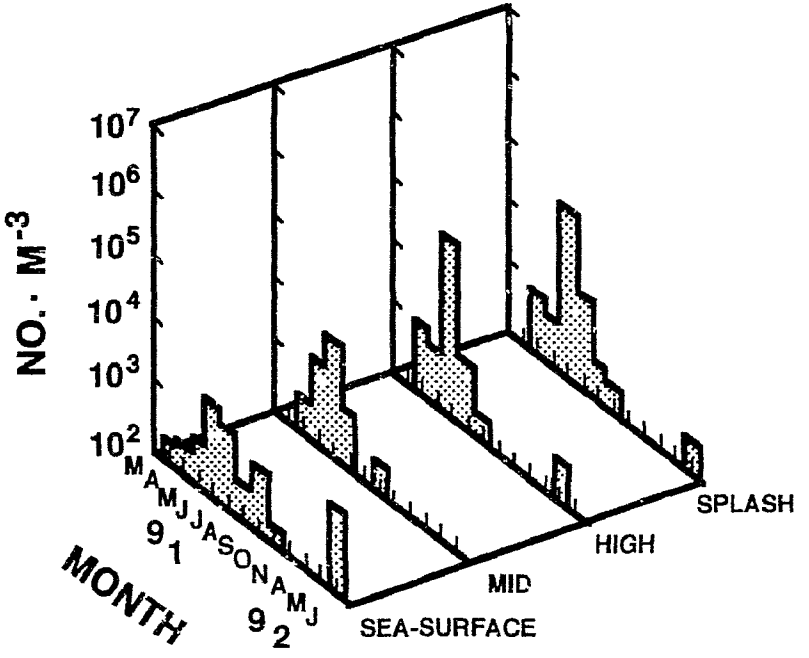

Figure 3.3 (continued)

Figure 3.4: Abundance of calanoid copepods at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

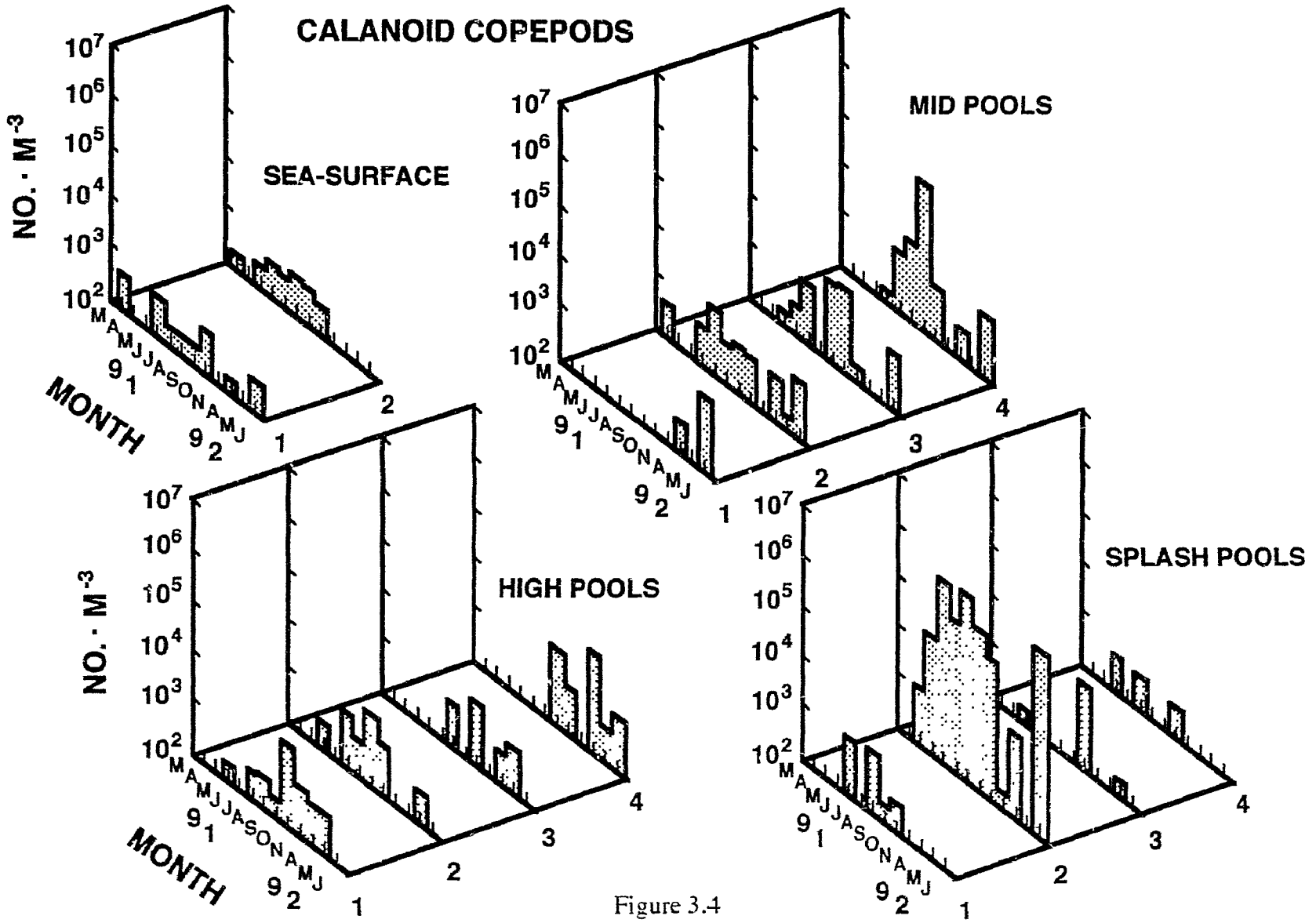
CALANOID COPEPODS
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
NO. · M-3
MONTH
10^7
10^6
10^5
10^4
10^3
10^2
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.4

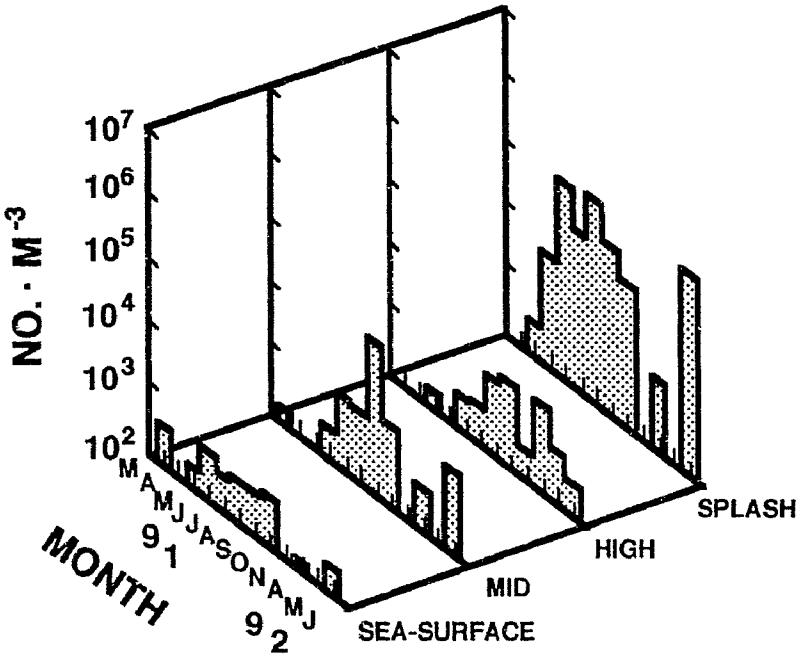

Figure 3.4 (continued)

Figure 3.5: Abundance of rotifers at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

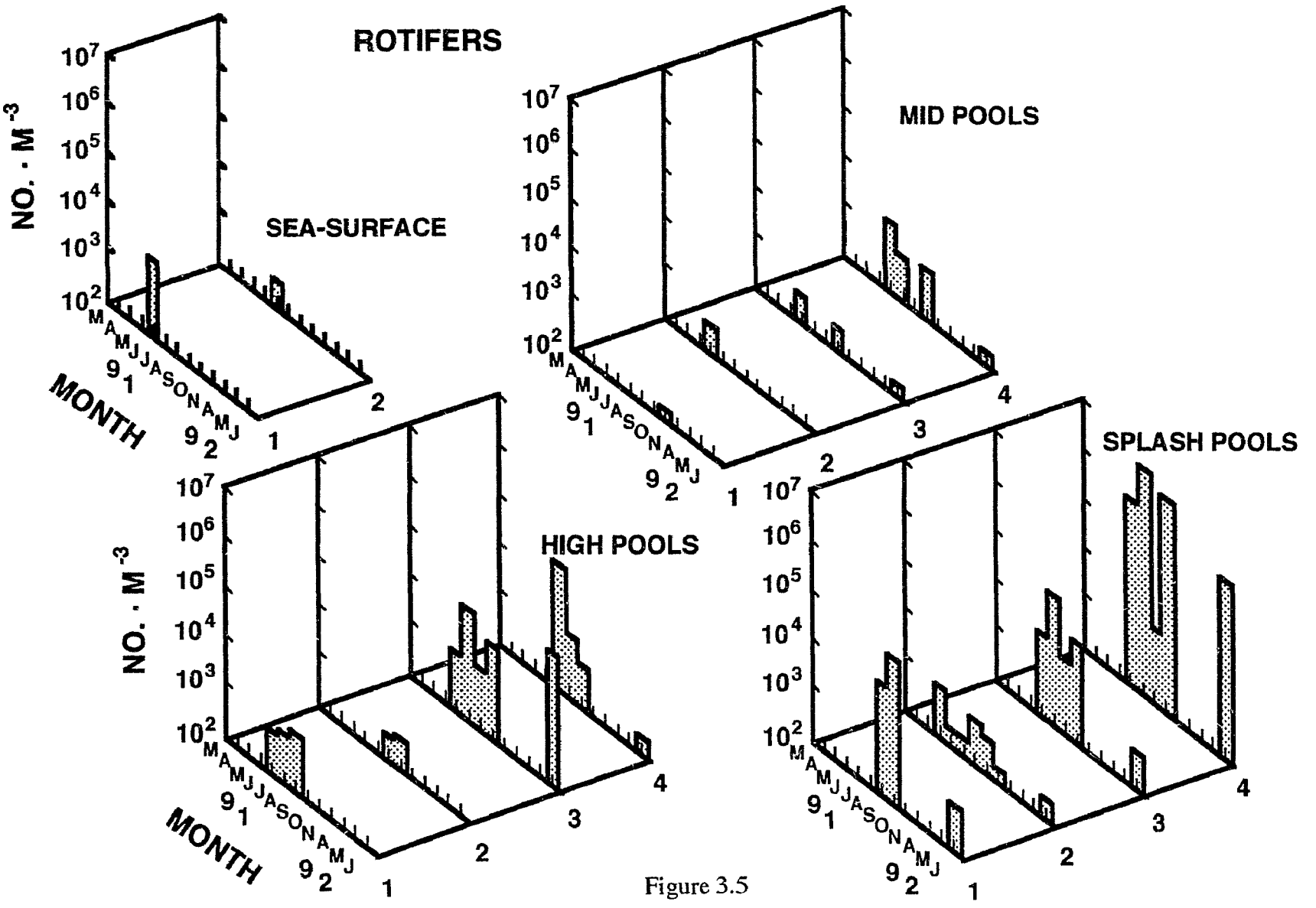
ROTIFERS
NO. · M-3
10^7
10^6
10^5
10^4
10^3
10^2
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
MONTH
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.5

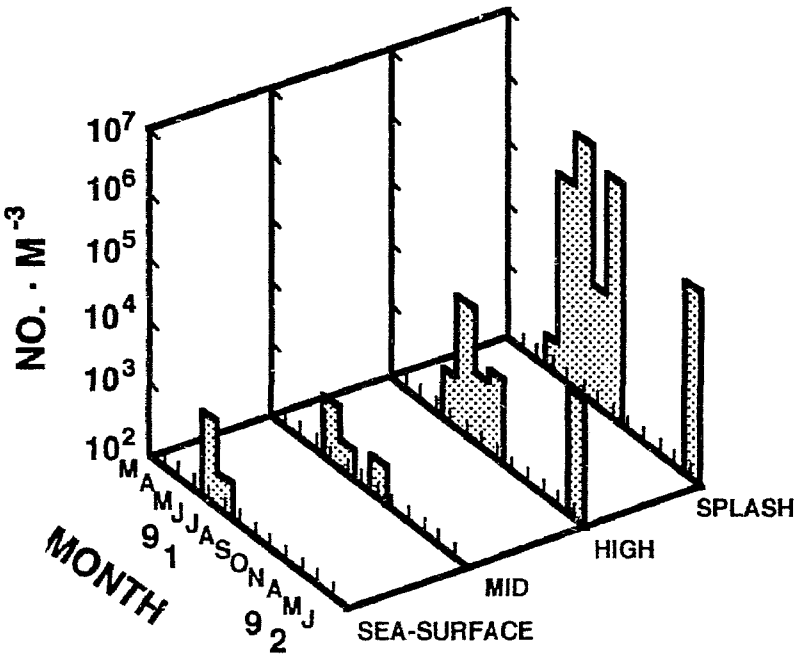

Figure 3.5 (continued)

Figure 3.6: Abundance of cladocerans at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

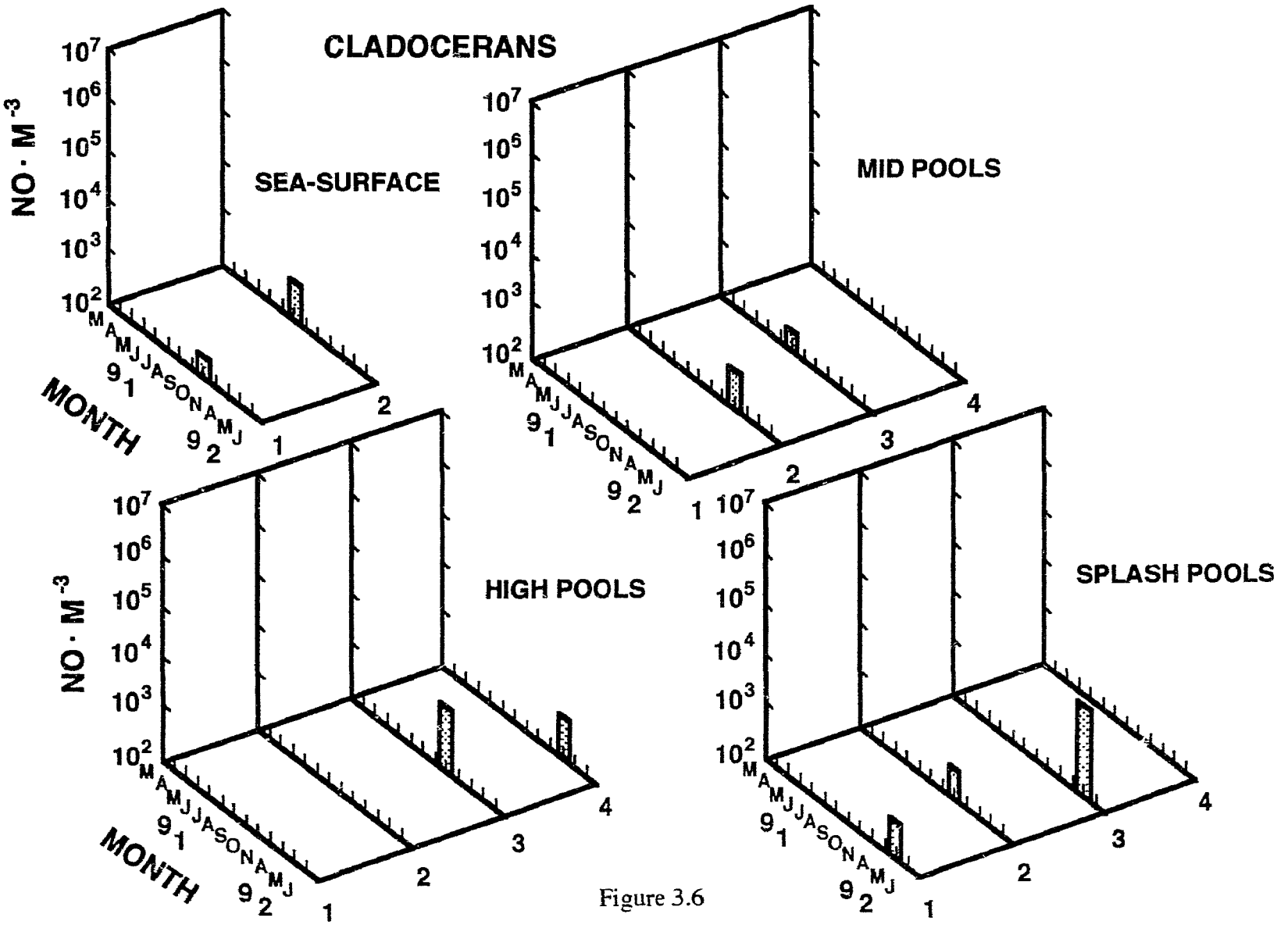
CLADOCERANS
NO · M-3
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
MONTH
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.6

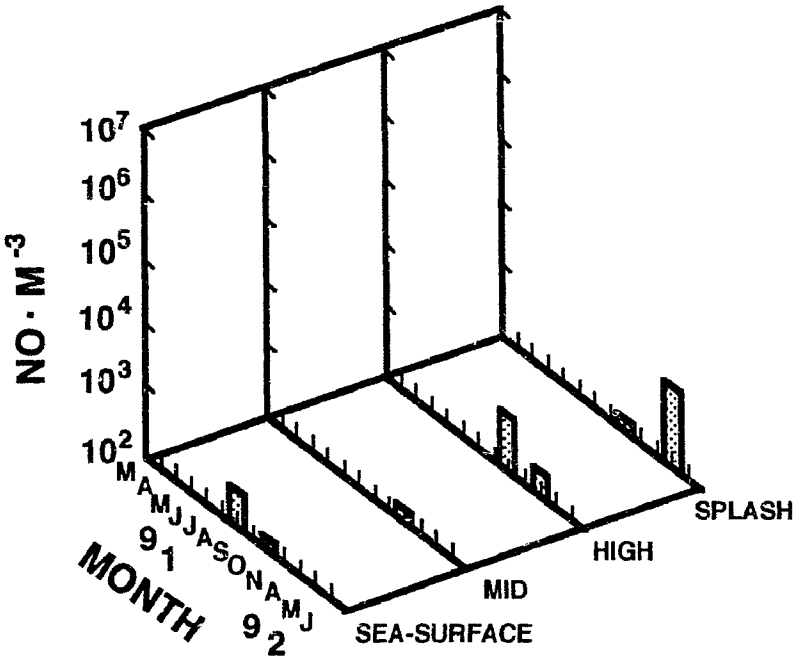

Figure 3.6 (continued)

Figure 3.7: Abundance of foraminiferans at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. The top 4 panels show abundance at each sea-surface location and in each tidepool, at each zone. The bottom panel shows mean abundance at the sea-surface (2 locations) and in each intertidal zone (4 tidepools).

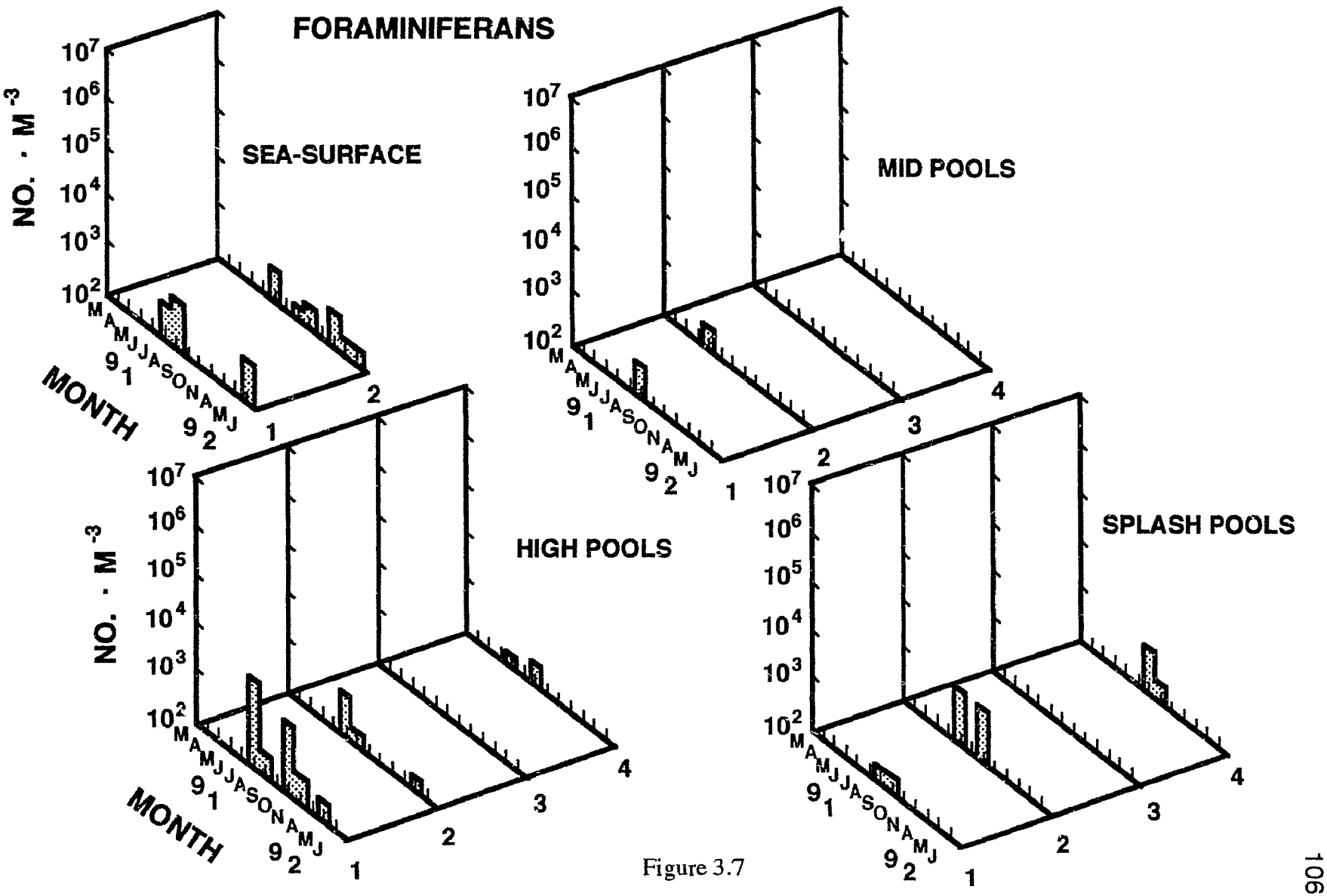
FORAMINIFERANS
SEA-SURFACE
MID POOLS
HIGH POOLS
SPLASH POOLS
NO. · M-3
MONTH
10^7
10^6
10^5
10^4
10^3
10^2
M A M J J A S O N A M J
9 1
9 2
1
2
3
4

Figure 3.7

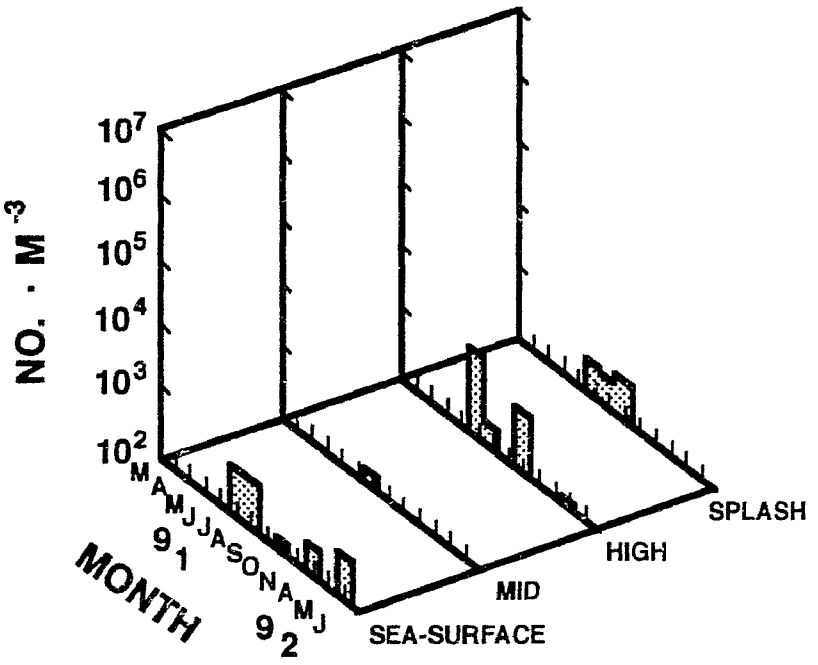

Figure 3.7 (continued)

Figure 3.8: (A) Changes in the Shannon Diversity Indices of faunal hyperbenthic communities at the sea-surface and in tidepools in 3 intertidal zones (mid, high and splash), at Cranberry Cove, Nova Scotia, sampled at monthly intervals between March and November 1991 and April and June 1992. Error bars are standard deviations (n = 2 at the sea-surface and n = 4 in the mid, high and splash zones). (B) Student-Newman-Keuls test for changes in the diversity indices over the 12 sampling dates. Bars connect dates among which diversity indices were not significantly different at the 0.05 level of significance.

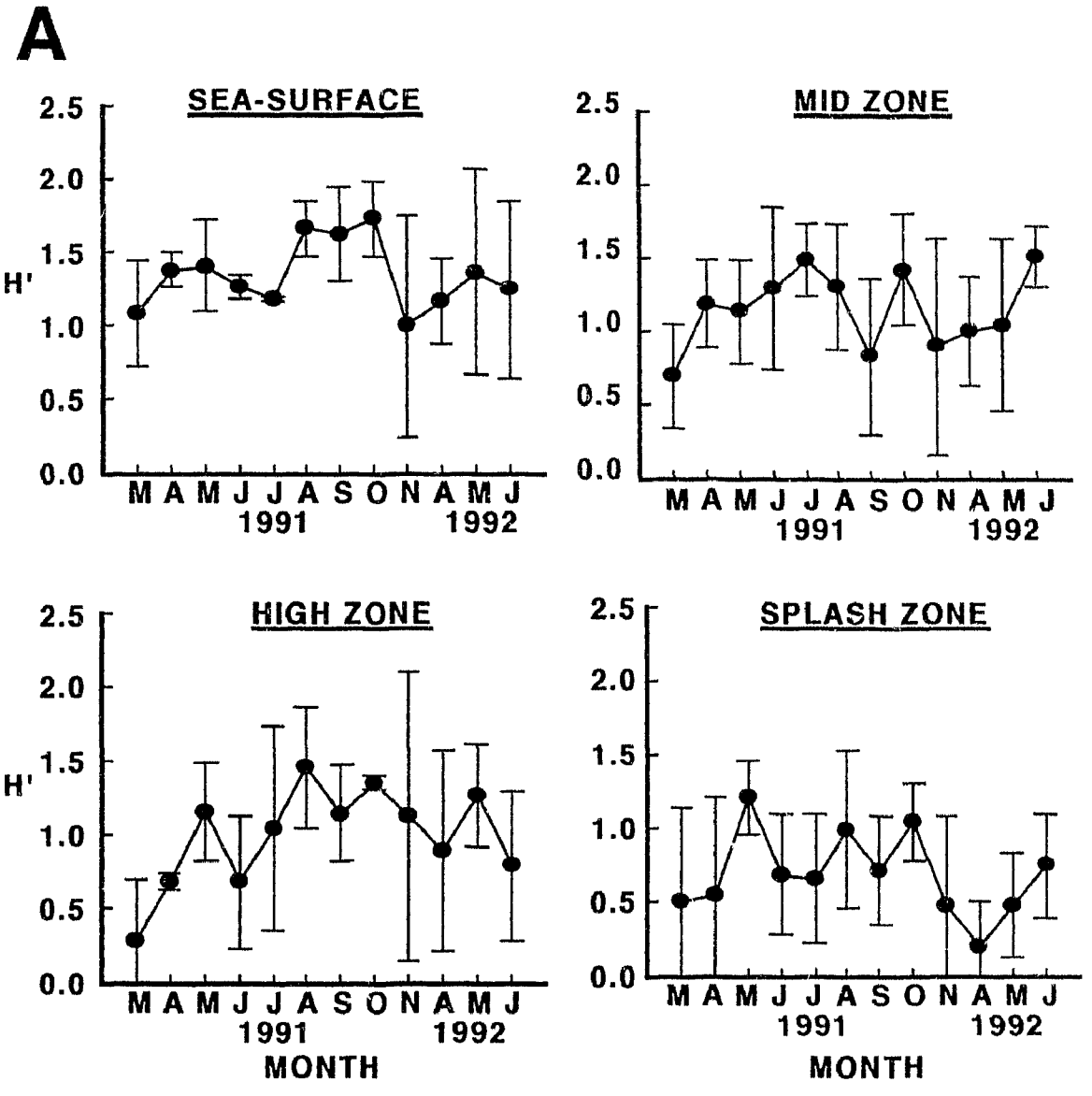
A
SEA-SURFACE
MID ZONE
HIGH ZONE
SPLASH ZONE
H'
2.5
2.0
1.5
1.0
0.5
0.0
M A M J J A S O N A M J
1991
1992
MONTH
B
MAR91
APR91
JUN91
MAY92
JUL91
AUG91
APR92
NOV91
SEP91
JUN92
MAY91
OCT91

Figure 3.8

DISCUSSION

The major components of the hyperbenthos in this study represented different functional groups. Calanoid copepods and cladocerans filter feed in the water-column and spend most of their time swimming. Rotifers become attached to hard surfaces but filter feed in the water-column. Harpacticoid copepods, nematodes and foraminiferans feed on hard surfaces and spend less time swimming than calanoid copepods and cladocerans. Most of these groups generally showed temporal patterns of abundance that suggest seasonality, increasing between late spring and late summer of both years with increasing water temperature, and decreasing in the late fall and over the winter 1991, both at the sea-surface and in the tidepools. The diversity also tended to increase from early spring to mid summer of both years as the different taxa became progressively more abundant, and was less in the late fall and early winter with decreasing faunal abundance.

The hyperbenthos of tidepools can be assigned to 3 categories based on temporal patterns in their abundance in tidepools relative to the sea-surface. Harpacticoid copepods and nematodes showed temporal changes in abundance that were similar at the sea-surface and in the pools, suggesting that their abundance in tidepools was determined either by tidal input or by the same factors as in the surrounding sea-water. Calanoid copepods and rotifers were present in low abundance and showed no temporal fluctuations at the sea-surface or in the mid and high pools, but were abundant in summer of both years and early fall 1991 in the splash pools. The abundance of these 2 groups in splash pools, therefore, was not set by daily tidal input and may have been determined by founder effects or competitive exclusion. Cladocerans and foraminiferans showed pulses in abundance in the tidepools in the late summer and early fall 1991. In late summer, these pulses

corresponded to pulses at the sea-surface, suggesting that they reflected tidal input. In late fall, however, the pulses in the tidepools were not associated with changes in abundance of these groups at the sea-surface and, therefore, were independent of tidal input.

The number of taxonomic groups of hyperbenthos decreased with a decrease in the isolation period of the pools. For example, 5 genera of calanoid copepods (*Acartia*, *Calanus*, *Pseudocalanus*, *Paracalanus*, *Temora*) were found in mid and high pools, whereas *Eurytemora affinis* was the only species of calanoid copepod found in splash pools. Other studies also have shown that macroalgal and macroinvertebrate species diversity decreases in tidepools with increasing intertidal height (Gustavsson 1972, Femino & Mathieson 1980, Huggett & Griffiths 1986, Lawrence & McClintock 1987, Wolfe & Harlin 1988b, Kooistra *et al.* 1989). Decreased diversity in pools that are located high on the shore may be due to increased physiological stress during extended periods of isolation from tidal input. This can result in low food abundance, high temperature and increased salinity due to evaporation in summer, and freezing and increased salinity in winter. Such adverse conditions can constrain a number of organisms to pools that are located lower on the shore, and receive regular tidal input that resets the physical environment. The fauna of pools in the high intertidal and splash zones, therefore, may be restricted to those taxonomic groups that can withstand the extreme variations in physical conditions.

The abundance of the total hyperbenthos differed significantly among intertidal zones only on 4 sampling dates. On 3 of those dates, abundance was greatest in splash pools and on the other, abundance was greatest in the high pools (although they were not statistically different from splash pools). In particular, the abundance of calanoid and harpacticoid copepods, nematodes and rotifers was greater in high and/or splash

pools on 1 or 2 sampling dates. These results are in partial agreement with previous studies. Fraser (1936), Ganning (1971) and Dethier (1980) showed that the abundance of harpacticoid copepods increases in tidepools of increasing intertidal height. However, Fraser (1936) found that the abundance of calanoid copepods decreased in the higher intertidal zones in pools on the Isle of Man, U.K. This was not the case in my study mainly because a large population of *Eurytemora affinis* occupied 1 of the splash pools and was particularly abundant in summer of both years. To my knowledge, the only record of rotifers in tidepools was provided by Ganning (1971) who found these organisms in one of the lower pools in his study (probably similar to my mid pools) and in a higher pool in mid summer.

The small number of significant zone effects on the abundance of hyperbenthos can be explained by the large variability among tidepools within each zone. I detected significant pool effects for most groups on most sampling dates, particularly among high or splash pools. For example, the abundance of harpacticoid copepods in 2 of the high pools was consistently less than in the other 2. The calanoid copepod *Eurytemora affinis* and rotifers each reached abundances in the order of 10^6 individuals . m^{-3} in 1 splash pool but were virtually absent in all 3 other pools. A pulse in the abundance of cladocerans occurred only in 1 pool (but on different dates) in both the high intertidal and the splash zones. Similarly, different pulses in the abundance of foraminiferans occurred only in 1 pool both in the mid and high intertidal zones.

Despite harsh physical conditions, splash pools harbour populations of certain tolerant groups of organisms with densities of up to 3 orders of magnitude higher than at the sea-surface. The dominant species vary among splash pools but the populations are persistent in the particular pools between years. The populations that inhabit splash pools are probably endemic and do not depend upon tidal input to become re-

established every year. Furthermore, the low flushing frequency in the high and splash pools may enable the persistence of these populations which may become diluted or replaced in tidepools lower on the shore. Although the abundance of hyperbenthos in tidepools does not show a consistent zonation along the intertidal gradient, variability in abundance increases among pools with increasing intertidal height. The variability in the dominant taxa among splash pools may be the result of a founder effect early in the establishment of tidepool communities. Alternatively, it may reflect variability in local environmental conditions which favour different competitively dominant taxa in different tidepools.

CHAPTER 4: Changes in phytoplankton abundance in tidepools over the period of tidal isolation

INTRODUCTION

The importance of examining ecological processes at various spatial and temporal scales has been emphasized recently in studies of phytoplankton dynamics (see review by Harris 1980). For example, Owen (1989) attributed patchiness in plankton density in coastal waters off California to physical factors such as water-column stability and wind-stress. Carpenter & Kitchell (1987) showed that the strength of the relationship of limnetic primary production with nutrient loading varied over different temporal scales. Tont (1987) showed that variability in marine diatom populations was explained by different physical factors (e.g. air and sea-surface temperature, sea-level) operating at different temporal scales (days to years).

Tidepools, because of their defined boundaries, can be particularly useful as mesocosms to examine plankton dynamics at varying scales. Little is known about planktonic communities of tidepools, however, and most previous studies have simply recorded or provided qualitative descriptions of phytoplankton and zooplankton in a small number of pools (e.g. Pyefinch 1943, Droop 1953, Naylor & Slinn 1958, Ganning 1971, Goss-Custard *et al.* 1979, Dethier 1980, Coull & Wells 1983, Metaxas & Lewis 1992).

Microalgae are introduced into tidepools with the incoming tide and are subsequently isolated from the surrounding seawater for variable periods depending upon the height of the pool on the shore. During the period of isolation, the abundance of phytoplankton in a pool may be altered in a number of ways. Benthic filter-feeders, such as mussels, or planktonic filter-feeders, such as calanoid copepods, may remove

phytoplankton from the water-column, and benthic grazers, such as nematodes and harpacticoid copepods, may consume microalgae that sink to the bottom of the pool (e.g. Stenton-Dozey & Brown 1992). The physical conditions of the pool can vary markedly and may even reach lethal limits for microalgae during the period of tidal isolation (e.g. Ganning 1971, Daniel & Boyden 1975, Morris & Taylor 1983, Huggett & Griffiths 1986). Alternatively, nutrient enrichment due to excretion by tidepool fauna can promote rapid growth of phytoplankton. Changes that occur in the phytoplankton assemblages over the period of tidal isolation may persist, or these assemblages may be completely replaced by the incoming tide, depending upon the extent to which the tidepools are flushed.

To examine processes that determine the structure and dynamics of phytoplankton assemblages in tidepools, I measured phytoplankton abundance in tidepools in 3 intertidal zones (mid, high and splash) during the period of tidal isolation, both at a time of low phytoplankton abundance in summer and during the autumn phytoplankton bloom in the surrounding seawater. I compared changes in phytoplankton abundance during the period of tidal isolation to changes in density of planktonic and benthic micrograzers, the nutrient regime, and the physical environment. I also examined changes in phytoplankton abundance over a 50 d period to determine how consistent the composition of these phytoplankton assemblages is over a longer period.

MATERIALS AND METHODS

Four tidepools, at each of 3 zones along the intertidal gradient (mid, high and splash), were sampled on 22 August and 9 October 1991, at Cranberry Cove, Nova Scotia, Canada (44°28'N, 63°56'W). (For a detailed description of the pools and study site see Chapter 2).

The tidepools were sampled immediately after the tide receded and immediately before the following period of submergence, with the exception of high pools in October which were sampled after 7.5 h (due to the shorter daylength available for sampling). In August, the period during which pools were isolated between samples was 2-4.75 h for mid pools, 7.75-12 h for high pools, and 7.25-12 h for splash pools. In October, the splash pools were not sampled and the isolation periods between samples was 2-4 h for mid pools and 7.5 h for high pools. At each sampling period, 2 60-mL samples of phytoplankton were collected with a polypropylene syringe at each of 2 strata within each pool (at the surface and < 1cm above the bottom) and from the surrounding seawater at each of 4 locations along the shore, immediately below the mid pools. The phytoplankton samples were placed in a container and the syringe was rinsed into the same container using 20 mL of distilled water. The samples were preserved in Lugol's solution and stored in the dark for subsequent enumeration. Before counting, the phytoplankton samples were inverted 50 times, and subsamples were allowed to settle overnight in 25 mL settling chambers (Lund *et al.* 1958). Two samples of micrograzers were collected by hand-pumping 5 L of seawater through a 60-μm net. The net was then rinsed into a container and the sample fixed with 4% buffered formaldehyde. Phytoplankton and micrograzers were enumerated using a Leitz Labovert inverted microscope. Phytoplankton were identified according to Cupp

(1943), Hendey (1964), Sournia (1986), Ricard (1987) and Chrétiennot-Dinet (1990). Micrograzers were identified as in Chapter 3.

At each sampling period, the temperature of each pool was measured using a hand-held thermometer, salinity was measured with an Endeco type 102 refractometer, and pH was measured with a Cole Palmer pH Wand (Model 05830-00) (pH was not measured in August because of equipment malfunctioning). Two 60-mL samples of pool water were collected and stored for nutrient analysis as in Chapter 2. Nitrate+nitrite, silicate and phosphate concentrations were measured in these samples using a Technicon AA2 autoanalyzer and ammonia concentration was determined spectrophotometrically according to Parsons *et al.* (1984).

For the statistical analyses, phytoplankton were assigned to 5 taxonomic groups: centric diatoms, pennate diatoms, flagellates, dinoflagellates and nanoflagellates (Table 4.1). Micrograzers were grouped as benthic and planktonic according to their feeding environment. For each sampling date, change in abundance within the period of tidal isolation of each group of phytoplankton and micrograzers, as well as the totals for all groups of phytoplankton and micrograzers, were analyzed using repeated measures analyses of variance. Temperature, salinity, pH, nutrient concentration and nutrient ratios (DIN:P and Si:P) were similarly analyzed. For phytoplankton in the tidepools, I used a 3-factor (Intertidal Zone: mid, high and splash; Stratum: surface and bottom of the pool; and Time: beginning and end of the period of isolation) analysis with repeated measures on 2 factors (Stratum and Time) because pools were nested within zones (Table 4.2). For all other variables, I used a 2-factor analysis (Intertidal Zone and Time) with repeated measures on 1 factor (Time) (Table 4.2). I also examined the change in phytoplankton abundance in tidepools between

sampling dates by averaging the abundance for the sampling periods at each date and using 1- or 3-factor repeated measures analysis as above. I used 1-factor (Time) repeated measures analyses of variance to determine changes in phytoplankton abundance in the surrounding seawater over the period of isolation of the tidepools. There were no significant differences in the abundance of total phytoplankton or any of the phytoplankton groups in the surrounding seawater over the 12 h period of isolation of the pools on either sampling date (August: $F_{3,9} < 5.08$, $p > 0.05$, October: $F_{2,6} < 7.26$, $p > 0.05$). Therefore, I averaged the abundances for all sampling periods at each sampling date for comparisons between dates.

In the cases where heterogeneity of variance was detected using Cochran's test, the data were ln (x+1)-transformed successfully. When significant interactions were obtained in the factorial analyses, simpler analyses of variance were done within levels of a factor. *A posteriori* multiple comparisons of treatment means were done using Student-Newman-Keuls (SNK) tests after the analyses of variance. All statistical analyses were based on models given in Winer (1971) and carried out using SYSTAT v. 5.1 (Wilkinson 1989).

RESULTS

Phytoplankton abundance varied between intertidal zones and between strata within pools for different taxonomic groups in both August and October 1991 (Figs. 4.1 & 4.2, Table 4.3). In August, the most abundant groups in the pools were flagellates (*Cryptomonas* sp.) and nanoflagellates (*Dunaliella tertiolecta*) (Fig. 4.1). Because of significant 3-way interactions, 2-factor (Zone and Stratum) analyses were done for flagellates within each level of the factor Time (at the beginning of and after the period of tidal isolation). This group was most abundant in the high pools and least abundant in the mid pools when the tide first receded ($F_{2,18} = 5.03$, $p < 0.05$, SNK test, $p < 0.05$), but this effect was not detected at the end of the period of tidal isolation ($F_{2,18} = 2.49$, $p > 0.05$). Flagellates also were more abundant near the bottom than at the surface when the tide first receded ($F_{1,18} = 12.74$, $p < 0.01$). Nanoflagellates did not vary significantly among zones but were significantly more abundant near the bottom than at the surface of the pools both at the beginning of and after the period of tidal isolation. Centric diatoms, mainly *Chaetoceros* spp. and *Skeletonema costatum,* were significantly more abundant in mid and splash pools than in high pools, and their abundance did not vary with pool stratum (SNK test, $p < 0.05$). No significant effects of Zone or Stratum were detected for pennate diatoms or dinoflagellates. Total phytoplankton did not vary significantly among zones but was significantly more abundant near the bottom of the pools both in the beginning and the end of the period of isolation.

In October, centric diatoms (*Chaetoceros* spp., *Rhizosolenia fragilissima* and *Skeletonema costatum*) were the most abundant group, particularly in the bottom stratum (Fig. 4.2). Flagellates were the only group that showed a significant Zone

effect (Table 4.3). Two-factor (Stratum and Zone) analyses at each sampling time showed that flagellates were more abundant in high than in mid pools ($F_{1,12} = 5.40$, 9.79; $p < 0.05$, $p < 0.01$ for the beginning of and after the period of tidal isolation, respectively). There were no significant differences in abundance between pool strata for any group in October. Total phytoplankton did not vary significantly between zones or pool strata.

The effect of the period of tidal isolation also varied among phytoplankton groups on both sampling dates (Table 4.3). In August, nanoflagellates were the only group which increased significantly in abundance during the period of tidal isolation (from 14,000 to 26,000 cells . L^{-1}). In October, centric diatoms decreased significantly during the period of tidal isolation (from 140,000 to 34,000 cells . L^{-1}) resulting in a significant decrease in total phytoplankton (from 200,000 to 80,000 cells . L^{-1}). A significant 2-way interaction (Stratum by Time) was detected for dinoflagellates and 1-factor ANOVA (Time at each Stratum) showed a statistically significant decrease in abundance only in the bottom stratum over the period of tidal isolation ($F_{1,7} = 10.53$, $p < 0.05$), but the change was small (from 70 to 5 cells . L^{-1}).

Although total phytoplankton abundance in pools was similar between sampling dates (Figs. 4.1 and 4.2, Table 4.4), the abundance of each phytoplankton group, except dinoflagellates, changed significantly, with pennate diatoms and flagellates decreasing significantly and nanoflagellates increasing significantly over the 50 d interval (Table 4.4). There was a significant Time by Zone interaction for centric diatoms, and 1-factor ANOVA (Zone at each sampling date) indicated that this group was significantly more abundant in mid than in high pools in August ($F_{1,14} = 96.54$, $p < 0.001$), but did not differ significantly between zones in October. However, the

abundance of centric diatoms increased significantly over the interval between sampling dates (1-factor ANOVA, Time at each Zone) in both the mid and high pools ($F_{1,7}$ = 24.2, 246 ; $p < 0.01$, $p < 0.001$, respectively). Pennate diatoms also were significantly more abundant in the pools in the mid zone than in the high zone (Table 4.4). Nanoflagellates and total phytoplankton were more abundant near the bottom than at the surface of the pools but no Stratum effects were detected for any other group (Table 4.4).

Total phytoplankton increased in the surrounding seawater between August and October 1991 (Fig. 4.3, $F_{1,3} = 315.2$, $p < 0.001$) due to an autumn bloom. The bloom consisted of centric diatoms, mainly *Chaetoceros* spp., which increased significantly in abundance between the 2 sampling dates ($F_{1,3} = 1040$, $p < 0.001$). The abundance of pennate diatoms, dinoflagellates and flagellates did not vary significantly between sampling dates (in all cases, $F_{1,3} < 17.4$, $p > 0.05$). Nanoflagellates were absent in the seawater samples in October.

In August, the most common planktonic micrograzers of phytoplankton were calanoid copepod nauplii and adults (*Acartia* spp., *Pseudocalanus* spp.) in the mid pools, and marine rotifers (*Brachionus* spp., *Synchaeta* spp.) in the high and splash pools. The most common benthic micrograzers in pools of all zones were harpacticoid copepod nauplii and adults (Families Harpacticidae, Tisbidae, Thalestridae, Diosaccidae), nematodes and isopods (*Idotea balthica, Jaera marina*). The high average density of planktonic grazers in the splash pools (mean $\pm$ SD: 193,000 $\pm$ 367,000 individuals . m^{-3}, n = 4) (Fig. 4.4) was due to large numbers of the calanoid copepod *Eurytemora affinis* in 1 pool (290,000 adults and 300,000 nauplii . m^{-3}). In October, the most abundant planktonic micrograzers were calanoid copepods (*Acartia*

spp., *Pseudocalanus* spp.) in the mid pools and marine cladocerans (Genera *Podon* and *Evadne*) in the high pools (Fig. 4.5). Harpacticoid copepods were the most abundant benthic micrograzers in pools of both zones. Neither total nor planktonic micrograzer density varied significantly within the period of tidal isolation, however, benthic micrograzers decreased significantly from ≈ 4,000 to ≈ 2,200 individuals . m^{-3} over the period of tidal isolation in August (Table 4.5).

Nutrient concentrations did not vary significantly among zones and over the period of tidal isolation on either sampling date (Figs. 4.6 & 4.7, Table 4.6). There was a significant Time by Zone interaction for NO_3+NO_2 concentration in August. Single-factor ANOVA (Zone at each sampling Time) showed no significant Zone effect ($F_{1,10}$ = 1.47, 0.001; $p > 0.05$, for the beginning of and after the period of tidal isolation, respectively) but the concentration of these nutrients decreased significantly in the high pools, from 4.6 to 3.3 μM, during the period of tidal isolation ($F_{1,3}$ = 17.7, $p < 0.05$).

Temperature was the most variable physical factor measured in tidepools on both sampling dates (Tables 4.7 & 4.8). In August, no significant interactions were detected and temperature was significantly warmer in high and splash pools than in mid pools (SNK test, $p < 0.05$). Temperature also increased significantly during the period of tidal isolation (Tables 4.7 & 4.8). In October, a significant Time by Zone interaction was detected and 1-factor ANOVA (Zone at each Time) showed that the mid pools were significantly warmer than high pools immediately after the tide receded ($F_{1,6}$ = 62.6, $p < 0.001$), but there was no significant difference after the period of tidal isolation ($F_{1,6}$ = 0.17, $p > 0.05$). Single-factor ANOVA (Time at each Zone) detected a significant increase in temperature in the high pools after the period of

isolation ($F_{1,3} = 150$, $p = 0.001$). This warming of the high pools explains the lack of a significant Zone effect after the period of tidal isolation.

Salinity in tidepools did not vary significantly with intertidal zone or over the period of tidal isolation in August (Tables 4.7 & 4.8). In October, a significant Time by Zone interaction was detected and 1-factor ANOVA (Time at each Zone) showed that salinity increased significantly in high pools during the period of tidal isolation ($F_{1,3} = 39.8$, $p < 0.01$) (Tables 4.7 & 4.8). No significant Zone effects on salinity were detected when examined within each sampling Time.

In October, a significant Time by Zone interaction was detected for pH (Tables 4.7 & 4.8). Single-factor ANOVA (Zone at each sampling Time) showed that pH was significantly greater in mid pools (8.62) than in high pools (7.51) when the tide receded ($F_{1,6} = 20.1$, $p < 0.01$), but there were no significant differences in pH among pools at different zones at the end of the period of tidal isolation. Single-factor ANOVA (Time at each Zone) showed that pH increased significantly from 8.63 to 9.06 in the mid pools ($F_{1,3} = 26.1$, $p = 0.015$) and from 7.51 to 8.70 in the high pools ($F_{1,3} = 33.5$, $p = 0.01$). This increase in pH explains the lack of significant differences in pH after the period of tidal isolation.

Table 4.1: List of phytoplankton and micrograzer taxonomic groups identified in this Chapter and present at the sea-surface and in the tidepools in August or October 1991.

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
PHYTOPLANKTON													
CENTRIC DIATOMS													
Chaetoceros spp.	✔	✔	✔		✔			✔		✔			✔
Rhizosolenia alata Brightwell	✔	✔	✔	✔	✔					✔		✔	
R. delicatula Cleve	✔		✔						✔				
R. fragilissima Bergon	✔	✔	✔	✔	✔	✔	✔	✔	✔				✔
R. setigera Brightwell	✔	✔	✔	✔	✔	✔	✔	✔	✔				
R. styliformis Brightwell	✔	✔	✔										
Skeletonema costatum (Greville) Cleve	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
PENNATE DIATOMS													
Amphiprora spp.	✔		✔	✔	✔			✔		✔		✔	✔
Amphora spp.				✔							✔		
Cylindrotheca closterium (Ehr.) Reimann *et* Lewin	✔	✔	✔	✔	✔	✔	✔	✔	✔				
Fragilaria crotonensis Kitton	✔	✔	✔	✔							✔	✔	
Grammatophora angulosa Ehrenberg	✔	✔		✔	✔	✔			✔				
Gyrosigma sp.			✔		✔					✔			
Licmophora gracilis (Ehrenberg) Grunow	✔			✔	✔	✔						✔	
L. juergensii Agardh	✔	✔	✔	✔	✔	✔	✔	✔	✔			✔	✔
Navicula spp.	✔	✔	✔	✔	✔	✔	✔						
Nitzschia delicatissima Cleve								✔					
N. longissima (Brébisson) Ralfs	✔		✔	✔		✔		✔		✔			
N. seriata Cleve	✔	✔	✔	✔	✔		✔	✔	✔	✔			
Nitzschia spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Striatella unipunctata (Lyngbye) Agardh			✔										
Surirella spp.					✔	✔	✔		✔	✔			
Thalassionema nitzschioides Grunow	✔												
Thalassiothrix frauenfeldii Grunow	✔	✔	✔	✔	✔	✔	✔			✔	✔	✔	

Table 4.1 (continued)

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
Unidentified pennates	✔	✔	✔	✔	✔	✔	✔		✔	✔	✔	✔	
DINO-FLAGELLATES													
Amphisolenia sp.	✔	✔											
Ceratium spp.	✔		✔					✔	✔				
Dictyocha sp.	✔		✔		✔								
Dinophysis sp.	✔												
Gonyaulax sp.	✔												
Gymnodinium sp.		✔											
Peridinium sp.	✔	✔	✔	✔	✔		✔	✔	✔	✔			✔
Protoperidinium sp.		✔	✔										
FLAGELLATES													
Cryptomonas spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
NANO-FLAGELLATES													
Dunaliella tertiolecta Butcher	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
PLANKTONIC MICROGRAZERS													
CALANOID COPEPODS													
Acartia sp.	✔				✔	✔		✔	✔	✔			
Calanus sp.	✔	✔	✔	✔				✔					
Eurytemora affinis (Poppe)	✔		✔		✔			✔	✔	✔	✔		
Pseudocalanus sp.	✔	✔	✔	✔	✔			✔					
Temora longicornis (Müller)	✔		✔	✔	✔								
Calanoid nauplii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
CLADOCERANS													
Evadne nordmanii Loven	✔	✔	✔	✔	✔	✔	✔						✔
Podon polyphemoides Leuckart	✔	✔	✔	✔	✔	✔	✔						✔
CYCLOPOIDS													
Oithona similis Claus	✔	✔	✔	✔	✔	✔		✔	✔	✔			✔

Table 4.1 (continued)

TAXONOMIC GROUP	SEA		IID POOLS			HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
HARPACTICOID COPEPODS													
Microsetella rosea (Dana)	✔		✔	✔	✔		✔	✔					
ROTIFERS													
Brachionus spp.	✔	✔		✔				✔		✔			✔
Synchaeta spp.	✔			✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
BENTHIC MICROGRAZERS													
AMPHIPODS													
Amphithoe rubricata (Montagu)	✔	✔						✔					
Corophium volutator (Pallas)	✔				✔	✔							
Gammarus oceanicus Segerstråle	✔	✔									✔		
Gammarus tigrinus Sexton	✔												
Marinogammarus finmarchicus Dahl	✔												
Pontogeneia inermis (Kröyer)	✔												
FORAMINIFERANS	✔	✔	✔		✔	✔	✔		✔	✔	✔		✔
HARPACTICOID COPEPODS													
Diosaccidae	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Harpacticidae	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Thalestridae	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Tisbidae	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Harpacticoid nauplii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
ISOPODS													
Idotea balthica (Pallas)	✔												✔
Jaera marina (Fabricius)	✔	✔							✔			✔	✔
NEMATODES	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
OSTRACODS	✔	✔				✔					✔		✔
POLYCHAETES	✔	✔	✔						✔		✔		✔
PYCNOGONIDS	✔	✔			✔	✔						✔	

Table 4.2: Summary of the models of analyses of variance used in Chapter 4. For phytoplankton there are 3 fixed factors, Intertidal Zone (Z) with p levels, Stratum(S) with q levels and Time (T) with r levels, with repeated measures on the last 2 factors. For all other variables (micrograzers, nutrients, temperature, salinity, pH) there are 2 fixed factors, Intertidal Zone (Z) and Time (T), with repeated measures on the last factor. Subjects are pools, with n levels, which are nested within zones. In October 1991, splash pools were not sampled.

SOURCE OF VARIATION	DEGREES OF FREEDOM	22-8-91	9-10-91
Phytoplankton			
Between Pools	(np-1)	11	7
Z	(p-1)	2	1
Pool w. Zone [Error(Z)]	p(n-1)	9	6
Within Pools	np(qr-1)	36	24
S	q-1	1	1
SxZ	(p-1)(q-1)	2	1
S x Pool w. Zone [Error(S)]	p(n-1)(q-1)	9	6
T	r-1	1	1
TxZ	(p-1)(r-1)	2	1
T x Pool w. Zone [Error(T)]	p(n-1)(r-1)	9	6
SxT	(q-1)(r-1)	1	1
SxTxZ	(p-1)(q-1)(r-1)	2	1
SxT x Pool w. Zone [Error(SxT)]	p(n-1)(q-1)(r-1)	9	6
Other variables			
Between Pools	np-1	11	7
Z	p-1	2	1
Pools w. Zones	p(n-1)	9	6
Within Pools	np(r-1)	12	8
T	r-1	1	1
TxZ	(p-1)(r-1)	2	1
T x Pools w. Zones [Error(TxZ)]	p(n-1)(r-1)	9	6

Table 4.3: Analyses of variance of phytoplankton abundance during the period of tidal isolation. There are 3 fixed factors, Intertidal Zone (Z), Stratum (S) and Time (T), with repeated measures on the last 2 factors. The degrees of freedom are for 22-8-91: F_{SxTxZ}, F_{TxZ}, F_{SxZ}, F_Z = 2,9, F_{SxT}, F_S, F_T = 1,9; for 9-10-91: F_{SxTxZ}, F_{SxT}, F_{TxZ}, F_{SxZ}, F_S, F_T, F_Z = 1,6; *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$; MS = Mean Square (Mean Squares in exponential notation are for untransformed data).

FACTOR	CENTRICS MS	F	p	PENNATES MS	F	p	FLAGELLATES MS	F	p
22-8-91									
Between Pools									
Z	163.4	8.48	0.009**	21.56	2.71	NS	$0.30x10^{12}$	3.53	NS
Error(Z)	19.27			7.94			$0.85x10^{11}$		
Within Pools									
S	21.08	1.75	NS	18.13	4.00	NS	$0.47x10^{12}$	8.66	*
SxZ	3.78	0.31	NS	1.12	0.25	NS	$0.10x10^{12}$	1.93	NS
Error(S)	12.04			4.54			$0.54x10^{11}$		
T	12.30	0.98	NS	13.60	1.28	NS	$0.50x10^{10}$	0.18	NS
TxZ	2.04	0.16	NS	2.51	0.24	NS	$0.23x10^{11}$	0.83	NS
Error(T)	12.53			10.67			$0.28x10^{11}$		
SxT	6.19	1.34	NS	0.46	0.12	NS	$0.1?x10^{12}$	12.7	**
SxTXZ	0.59	0.13	NS	2.79	0.74	NS	$.10^{11}$	4.52	*
Error(SxT)	4.61			3.78			$0.97x10^{10}$		
9-10-91									
Between Pools									
Z	$0.18x10^{10}$	0.12	NS	26.26	4.95	NS	198.9	5.89	NS
Error(Z)	$0.15x10^{11}$			5.31			33.75		
Within Pools									
S	$0.47x10^{10}$	1.33	NS	38.51	2.65	NS	0.27	0.06	NS
SxZ	$2.7x10^{6}$	0.001	NS	15.62	1.07	NS	11.11	2.35	NS
Error(S)	$0.36x10^{10}$			14.54			4.73		
T	$0.92x10^{11}$	8.69	*	9.89	0.81	NS	20.89	1.78	NS
TxZ	$0.73x10^{9}$	0.07	NS	1.33	0.11	NS	4.06	0.34	NS
Error(T)	$0.11x10^{11}$			12.18			11.90		
SxT	$0.96x10^{8}$	0.02	NS	0.19	0.04	NS	1.88	0.59	NS
SxTxZ	$0.23x10^{10}$	0.42	NS	2.42	0.52	NS	20.16	6.31	*
Error(SxT)	$0.56x10^{10}$			4.70			3.19		

Table 4.3 (continued)

FACTOR	DINO FLAGELLATES			NANO FLAGELLATES			TOTAL		
	MS	F	p	MS	F	p	MS	F	p
22-8-91									
Between Pools									
Z	19.52	1.42	NS	34.98	4.22	NS	15.45	1.88	NS
Error(Z)	13.73			8.28			8.22		
Within Pools									
S	23.10	3.39	NS	5.04	6.94	*	19.1	9.90	*
SxZ	3.74	0.55	NS	0.05	0.06	NS	2.00	1.04	NS
Error(S)	6.81			0.73			1.93		
T	5.54	1.70	NS	4.06	6.70	*	0.33	0.43	NS
TxZ	5.18	1.59	NS	0.67	1.11	NS	0.83	1.08	NS
Error(T)	3.26			0.61			0.77		
SxT	11.27	1.94	NS	0.02	0.03	NS	0.36	1.16	NS
SxTXZ	3.20	0.55	NS	0.08	0.14	NS	0.04	0.12	NS
Error(SxT)	5.81			0.58			0.37		
9-10-91									
Between Pools									
Z	0.37	0.01	NS	$0.19x10^{10}$	2.50	NS	$0.36x10^{10}$	0.21	NS
Error(Z)	26.18			$0.76x10^{9}$			$0.17x10^{11}$		
Within Pools									
S	1.02	0.17	NS	$0.19x10^{10}$	3.32	NS	$0.24x10^{11}$	3.23	NS
SxZ	0.45	0.08	NS	$0.43x10^{9}$	0.76	NS	$0.13x10^{9}$	0.02	NS
Error(S)	5.86			$0.56x10^{9}$			$0.73x10^{10}$		
T	28.13	7.07	*	$0.34x10^{9}$	1.89	NS	$0.11x10^{12}$	7.96	*
TxZ	2.43	0.61	NS	$0.17x10^{9}$	0.94	NS	$0.69x10^{9}$	0.05	NS
Error(T)	3.98			$0.18x10^{9}$			$0.14x10^{11}$		
SxT	6.31	7.76	*	$0.23x10^{9}$	1.29	NS	$0.99x10^{9}$	0.10	NS
SxTxZ	4.72	5.80	NS	$0.11x10^{9}$	0.59	NS	$0.73x10^{10}$	0.77	NS
Error(SxT)	0.81			$0.18x10^{9}$			$0.96x10^{10}$		

Table 4.4: Analyses of variance of phytoplankton abundance between August and October 1991. Factors are Intertidal Zone (Z), Stratum (S) and Time (T), with repeated measures on the last 2 factors; degrees of freedom: F_{ZxTxS}, F_{ZxT}, F_{SxZ}, F_Z = 2,9; F_{TxS}, F_S, F_T = 1,9. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$; MS= Mean Square.

FACTOR	CENTRICS			PENNATES			FLAGELLATES		
	MS	F	p	MS	F	p	MS	F	p
Between Pools									
Z	86.54	40.8	**	32.03	7.18	*	132.9	5.25	NS
Error(Z)	2.12			4.46			25.32		
Within Pools									
S	6.70	2.73	NS	20.02	3.83	NS	5.72	2.00	NS
SxZ	1.54	0.63	NS	5.62	1.07	NS	9.43	3.31	NS
Error(S)	2.46			5.23			2.85		
T	282.6	104.5	***	8.81	7.70	*	107.4	45.5	**
TxZ	72.33	26.8	**	0.29	0.25	NS	6.64	2.81	NS
Error(T)	2.70			1.15			2.36		
SxT	0.04	0.09	NS	3.00	0.69	NS	3.52	3.47	NS
SxTxZ	0.02	0.05	NS	2.50	0.58	NS	0.07	0.07	NS
Error(SxT)	0.47			4.32			1.01		

Table 4.4 (continued)

FACTOR	DINOFLAGELLATES			NANOFLAGELLATES			TOTAL		
	MS	F	p	MS	F	p	MS	F	p
Between Pools									
Z	1.40	0.24	NS	7.42	2.41	NS	4.68	1.38	NS
Error(Z)	5.93			3.08			3.39		
Within Pools									
S	25.11	4.56	NS	3.28	11.8	*	7.26	12.7	*
SxZ	1.43	0.26	NS	0.28	0.99	NS	1.24	2.17	NS
Error(S)	5.51			0.28			0.57		
T	12.12	1.05	NS	4.51	6.95	*	2.47	3.09	NS
TxZ	2.05	0.18	NS	0.78	1.20	NS	1.89	2.40	NS
Error(T)	11.50			0.65			0.79		
SxT	0.32	0.13	NS	0.02	0.03	NS	1.29	1.93	NS
SxTxZ	1.92	0.76	NS	0.08	0.16	NS	0.69	1.03	NS
Error(SxT)	2.54			0.48			0.67		

Table 4.5: Analyses of variance of micrograzer abundance during the period of tidal isolation. There are 2 fixed factors, Intertidal Zone (Z) and Time (T), with repeated measures on the last factor. The degrees of freedom are for 22-8-91: F_{ZxT}, F_Z = 2,9, F_T = 1,9; for 9-10-91: F_{ZxT}, F_T, F_Z = 1,6. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$; MS = Mean Square (Mean Squares in exponential notation are for untransformed data).

FACTOR	PLANKTONIC			BENTHIC			TOTAL		
	MS	F	p	MS	F	p	MS	F	p
22-8-91									
Between Pools									
Z	20.24	2.77	NS	0.11	0.06	NS	5.75	1.23	NS
Error(Z)	7.32			1.87			4.67		
Within Pools									
T	0.98	0.87	NS	2.10	8.43	*	0.40	2.20	NS
TxZ	0.01	0.01	NS	0.14	0.58	NS	0.39	2.18	NS
Error(TxZ)	1.13			0.25			0.18		
9-10-91									
Between Pools									
Z	$0.43x10^6$	0.07	NS	$0.83x10^7$	1.18	NS	$0.50x10^7$	0.37	NS
Error(Z)	$0.64x10^7$			$0.70x10^7$			$0.13x10^8$		
Within Pools									
T	$0.43x10^6$	0.21	NS	$0.11x10^6$	0.05	NS	$0.11x10^6$	0.02	NS
TxZ	$0.49x10^6$	0.25	NS	$0.12x10^7$	0.54	NS	$0.33x10^7$	0.61	NS
Error(TxZ)	$0.20x10^8$			$0.23x10^7$			$0.55x10^7$		

Table 4.6: Analyses of variance of nutrient concentrations and nutrient ratios during the period of tidal isolation. There are 2 fixed factors, Intertidal Zone (Z) and Time (T), with repeated measures on the last factor. The degrees of freedom are for 22-8-91: F_{ZxT}, F_Z = 2,9, F_T = 1,9; for 9-10-91: F_{ZxT}, F_T, F_Z = 1,6. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$; MS = Mean Square.

FACTOR	SiO_4			NO_3+NO_2			NH_4		
	MS	F	p	MS	F	p	MS	F	p
22-8-91									
Between Pools									
Z	0.27	0.14	NS	1.16	1.44	NS	8.92	3.47	NS
Error(Z)	1.95			0.81			2.57		
Within Pools									
T	0.20	1.12	NS	0.14	3.21	NS	7.03	3.28	NS
TxZ	0.22	1.22	NS	0.23	5.37	*	6.33	2.95	NS
Error(TxZ)	0.18			0.04			2.15		
9-10-91									
Between Pools									
Z	0.05	0.20	NS	0.00	0.00	NS	0.26	1.41	NS
Error(Z)	0.27			0.11			0.18		
Within Pools									
T	0.11	0.94	NS	0.03	0.25	NS	0.30	1.20	NS
TxZ	0.02	0.15	NS	0.35	3.10	NS	0.21	0.85	NS
Error(TxZ)	0.11			0.11			0.25		

Table 4.6 (continued)

FACTOR	PO_4			DIN:P			Si:P		
	MS	F	p	MS	F	p	MS	F	p
22-8-91									
Between Pools									
Z	0.01	0.05	NS	0.03	0.90	NS	0.82	1.83	NS
Error(Z)	0.23			0.03			0.45		
Within Pools									
T	0.00	0.02	NS	0.02	1.17	NS	0.38	0.88	NS
TxZ	0.02	0.42	NS	0.01	0.92	NS	0.35	0.80	NS
Error(TxZ)	0.06			0.02			0.44		
9-10-91									
Between Pools									
Z	0.07	0.63	NS	0.06	0.01	NS	7.26	0.72	NS
Error(Z)	0.12			4.41			10.11		
Within Pools									
T	0.00	0.63	NS	0.08	0.04	NS	0.34	0.14	NS
TxZ	0.03	5.78	NS	3.14	1.73	NS	1.32	0.54	NS
Error(TxZ)	0.01			1.82			2.45		

Table 4.7: Temperature, salinity and pH in tidepools in 3 intertidal zones, in August and October 1991, immediately after the tide receded and immediately before the incoming tide. Data are mean ± standard deviation for 4 replicate pools at each intertidal zone. - = not measured.

INTERTIDAL ZONE	DATE	TIME	TEMPERATURE (°C)	SALINITY	pH
MID	22-8-91	1	13.2 ± 1.17	30.3 ± 1.39	-
		2	17.9 ± 1.70	27.6 ± 3.77	-
	9-10-91	1	14.6 ± 1.23	30.1 ± 0.731	8.62 ± 0.224
		2	15.6 ± 1.11	29.8 ± 0.846	9.06 ± 0.306
HIGH	22-8-91	1	17.2 ± 2.11	24.7 ± 5.53	-
		2	22.7 ± 1.78	26.3 ± 3.15	-
	9-10-91	1	8.50 ± 0.913	24.4 ± 9.15	7.51 ± 0.441
		2	16.0 ± 1.47	26.0 ± 8.94	8.70 ± 0.322
SPLASH	22-8-91	1	18.0 ± 1.08	16.5 ± 8.78	-
		2	20.9 ± 2.35	17.5 ± 9.51	-

Table 4.8: Analyses of variance of physical factors during the period of tidal isolation. There are 2 fixed factors, Intertidal Zone (Z) and Time (T), with repeated measures on the last factor. The degrees of freedom are for 22-8-91: F_{ZxT}, F_Z = 2,9, F_T = 1,9; for 9-10-91: F_{ZxT}, F_T, F_Z = 1,6. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$; MS = Mean Square.

FACTOR	TEMPERATURE			SALINITY			pH		
	MS	F	p	MS	F	p	MS	F	p
22-8-91									
Between Pools									
Z	46.99	16.2	**	1.05	2.02	NS			
Error(Z)	2.91			0.52					
Within Pools									
T	112.9	34.6	***	0.00	0.06	NS			
TxZ	3.49	1.1	NS	0.02	1.19	NS			
Error(TxZ)	3.27			0.01					
9-10-91									
Between Pools									
Z	32.35	14.8	**	90.73	1.11	NS	2.17	12.6	*
Error(Z)	2.18			82.00			0.17		
Within Pools									
T	73.32	106.0	***	1.56	3.83	NS	2.62	53.5	***
TxZ	41.44	59.9	***	3.61	8.84	*	0.56	11.4	*
Error(TxZ)	0.69			0.41			0.05		

Figure 4.1: Abundance of 6 phytoplankton groups (total phytoplankton, centric diatoms, pennate diatoms, dinoflagellates, flagellates and nanoflagellates) in tidepools in each of 3 intertidal zones, mid (M), high (H) and splash (S), at Cranberry Cove, Nova Scotia. The pools were sampled at the surface (SUR) and near the bottom (BOT), immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in August 1991. Error bars represent standard deviations (n = 4 pools).

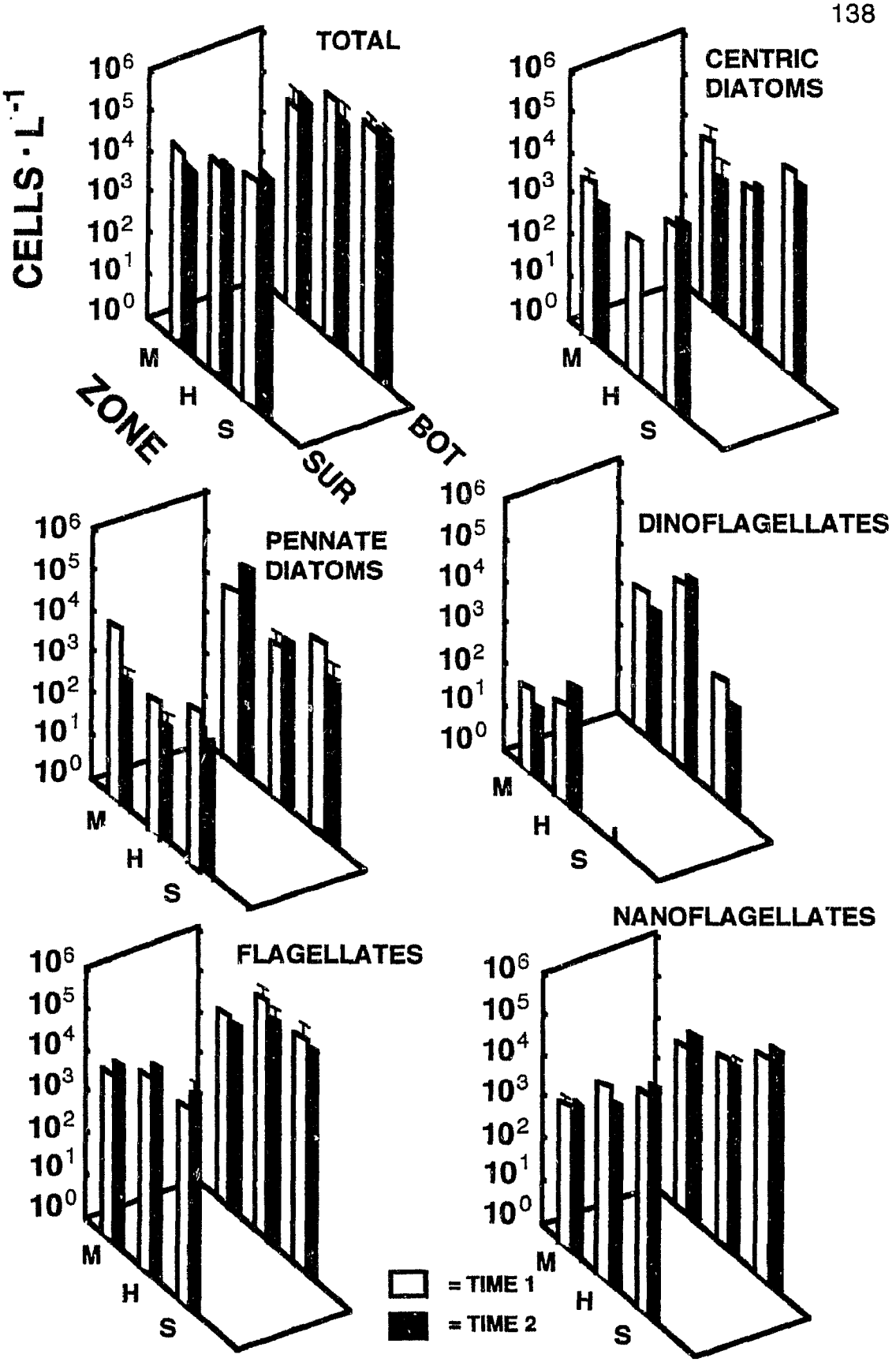
TOTAL
CENTRIC DIATOMS
PENNATE DIATOMS
DINOFLAGELLATES
FLAGELLATES
NANOFLAGELLATES
CELLS · L-1
10^6
10^5
10^4
10^3
10^2
10^1
10^0
M
H
S
ZONE
SUR
BOT
= TIME 1
= TIME 2

Figure 4.1

Figure 4.2: Abundance of 6 phytoplankton groups (total phytoplankton, centric diatoms, pennate diatoms, dinoflagellates, flagellates and nanoflagellates) in tidepools in each of 2 intertidal zones, mid (M) and high (H), at Cranberry Cove, Nova Scotia. The pools were sampled at the surface (SUR) and near the bottom (BOT), immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in October 1991. Error bars represent standard deviations (n = 4 pools).

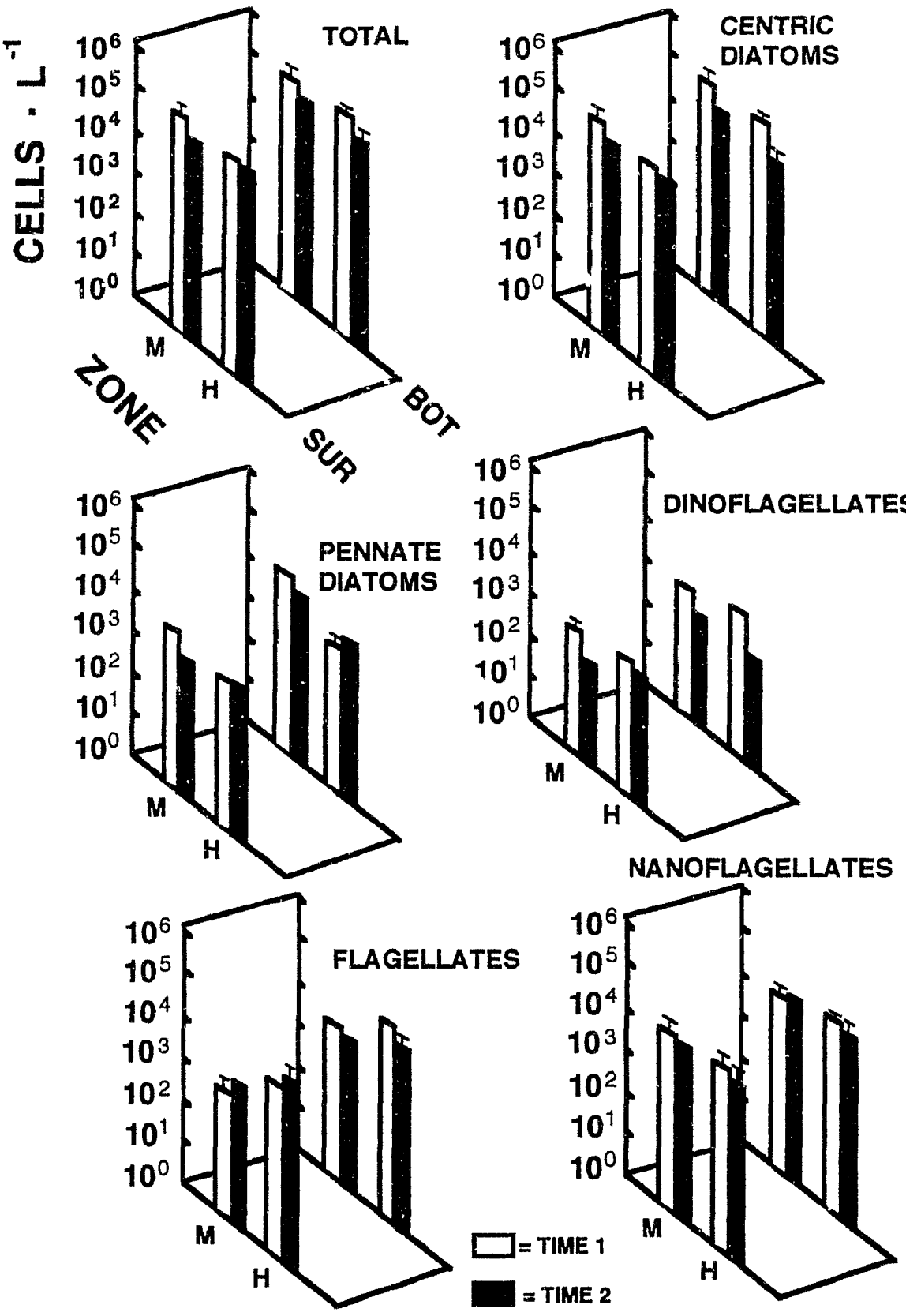
CELLS · L⁻¹
TOTAL
CENTRIC DIATOMS
PENNATE DIATOMS
DINOFLAGELLATES
FLAGELLATES
NANOFLAGELLATES
10⁶
10⁵
10⁴
10³
10²
10¹
10⁰
M
H
ZONE
SUR
BOT
= TIME 1
= TIME 2

Figure 4.2

Figure 4.3: Abundance of 6 phytoplankton groups (total phytoplankton, centric diatoms, pennate diatoms, dinoflagellates, flagellates and nanoflagellates) in the surrounding seawater at Cranberry Cove, Nova Scotia, in August and October 1991. Error bars represent standard deviations ($n = 4$ sampling locations).

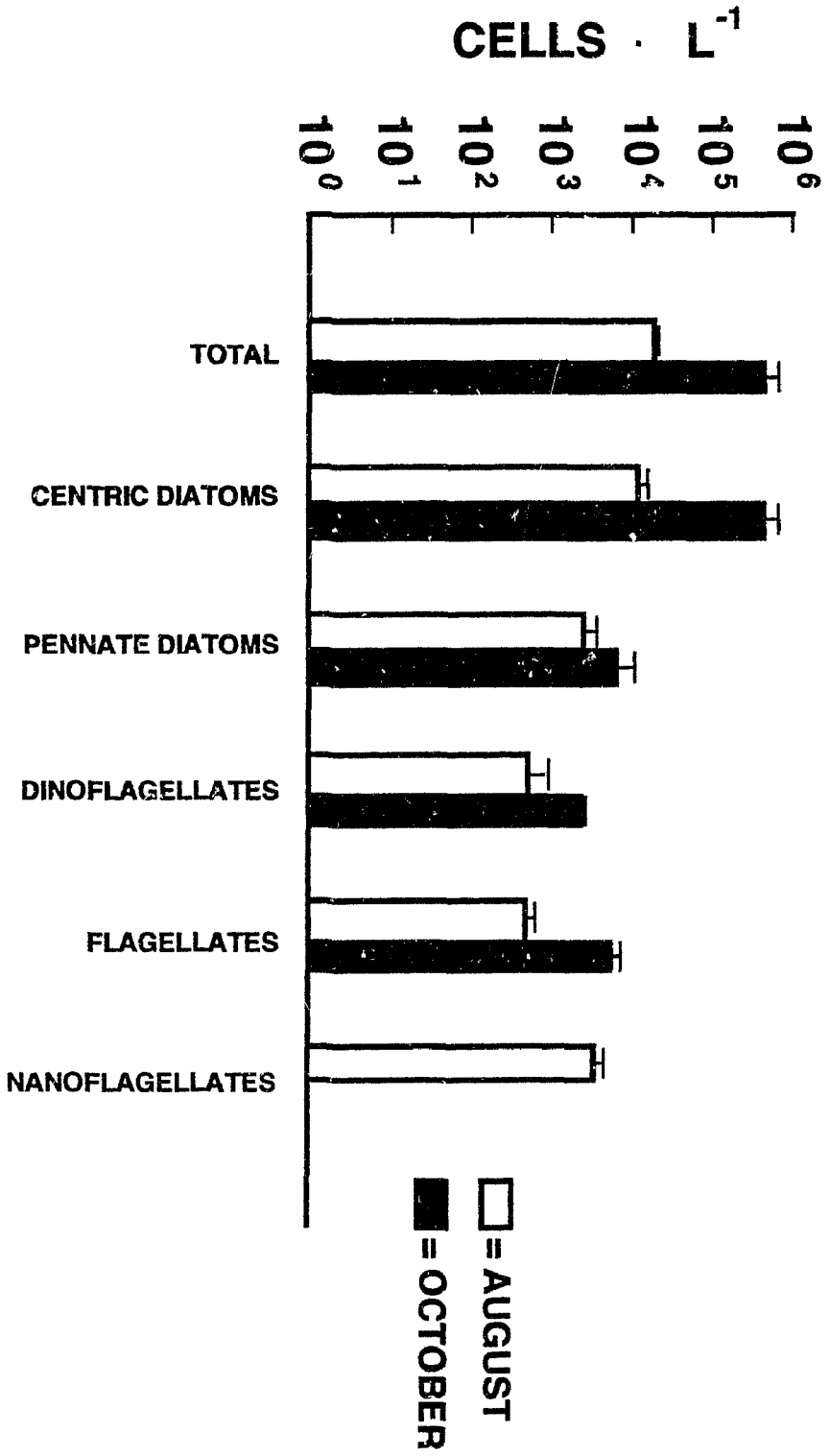
CELLS · L-1
10 0
10 1
10 2
10 3
10 4
10 5
10 6
TOTAL
CENTRIC DIATOMS
PENNATE DIATOMS
DINOFLAGELLATES
FLAGELLATES
NANOFLAGELLATES
= AUGUST
= OCTOBER

Figure 4.3

Figure 4.4: Density of planktonic, benthic and total micrograzers in tidepools in each of 3 intertidal zones, mid (M), high (H) and splash (S), at Cranberry Cove, Nova Scotia. The pools were sampled immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in August 1991. Error bars represent standard deviations (n = 4 pools).

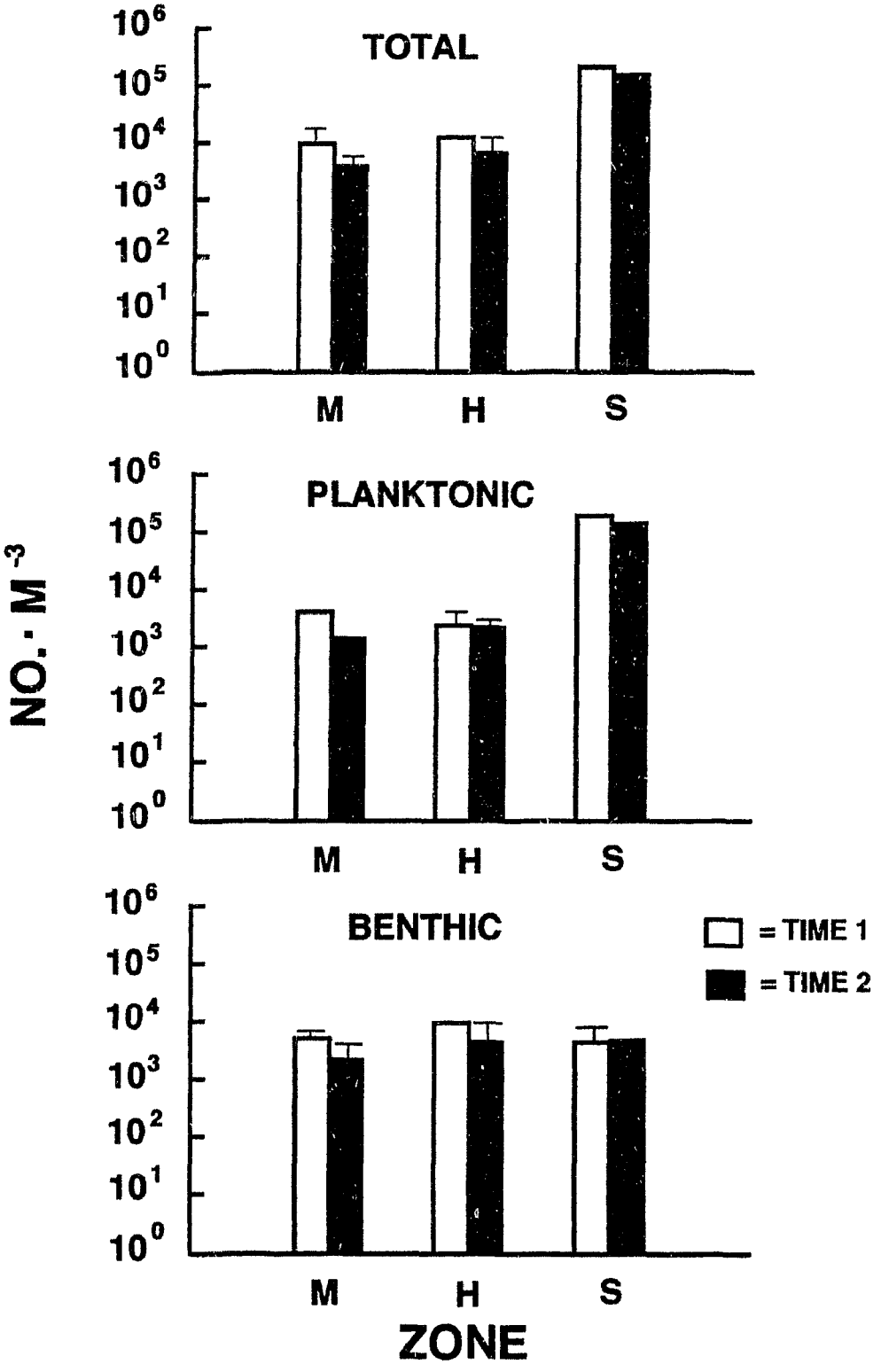
TOTAL
PLANKTONIC
BENTHIC
NO. · M⁻³
10⁶
10⁵
10⁴
10³
10²
10¹
10⁰
M
H
S
ZONE
= TIME 1
= TIME 2

Figure 4.4

Figure 4.5: Density of planktonic, benthic and total micrograzers in tidepools in each of 2 intertidal zones, mid (M) and high (H), at Cranberry Cove, Nova Scotia. The pools were sampled immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in October 1991. Error bars represent standard deviations (n = 4 pools).

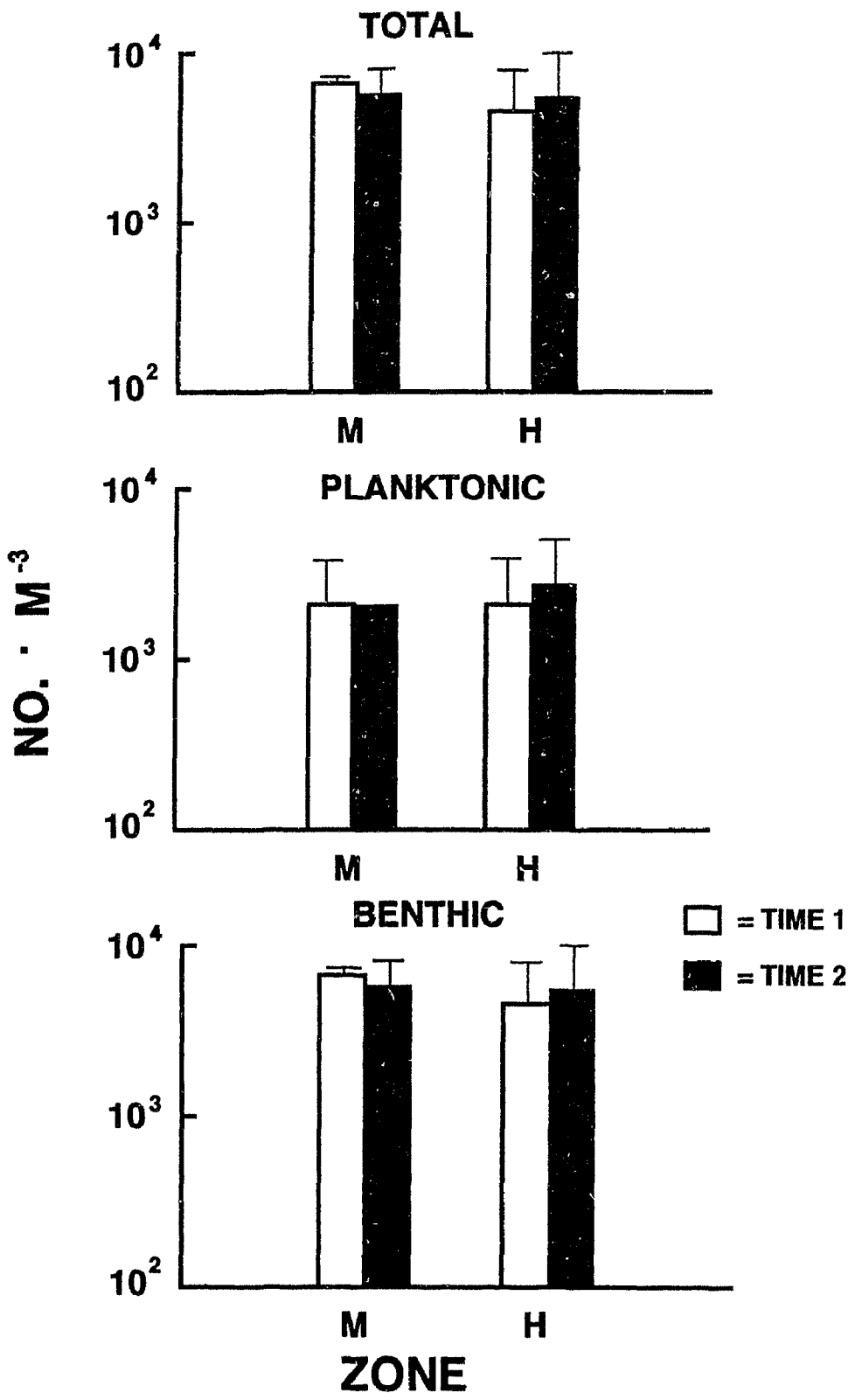
TOTAL
PLANKTONIC
BENTHIC
NO. · M-3
10^4
10^3
10^2
M
H
= TIME 1
= TIME 2
ZONE

Figure 4.5

Figure 4.6: Nutrient concentrations and ratios in tidepools in each of 3 intertidal zones, mid (M), high (H) and splash (S), at Cranberry Cove, Nova Scotia. The pools were sampled immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in August 1991. Error bars represent standard deviations (n = 4 pools).

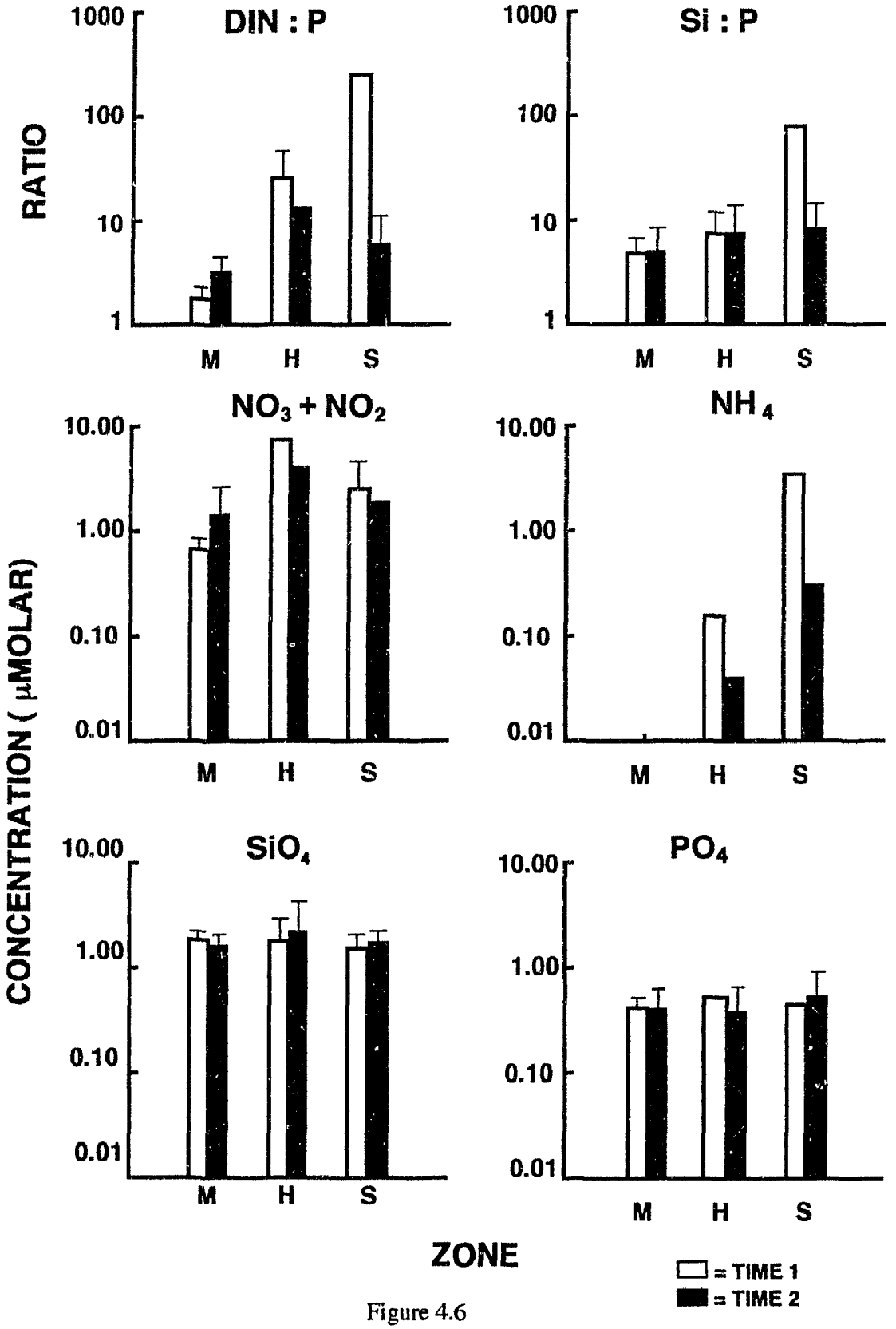
DIN : P
Si : P
$NO_3 + NO_2$
NH_4
SiO_4
PO_4
RATIO
CONCENTRATION (µMOLAR)
1000
100
10
1
10.00
1.00
0.10
0.01
M
H
S
ZONE
= TIME 1
= TIME 2

Figure 4.6

Figure 4.7: Nutrient concentrations and ratios in tidepools in each of 2 intertidal zones, mid (M) and high (H), at Cranberry Cove, Nova Scotia. The pools were sampled immediately after the tide receded (TIME 1) and immediately before receiving new tidal input (TIME 2), in October 1991. Error bars represent standard deviations (n = 4 pools).

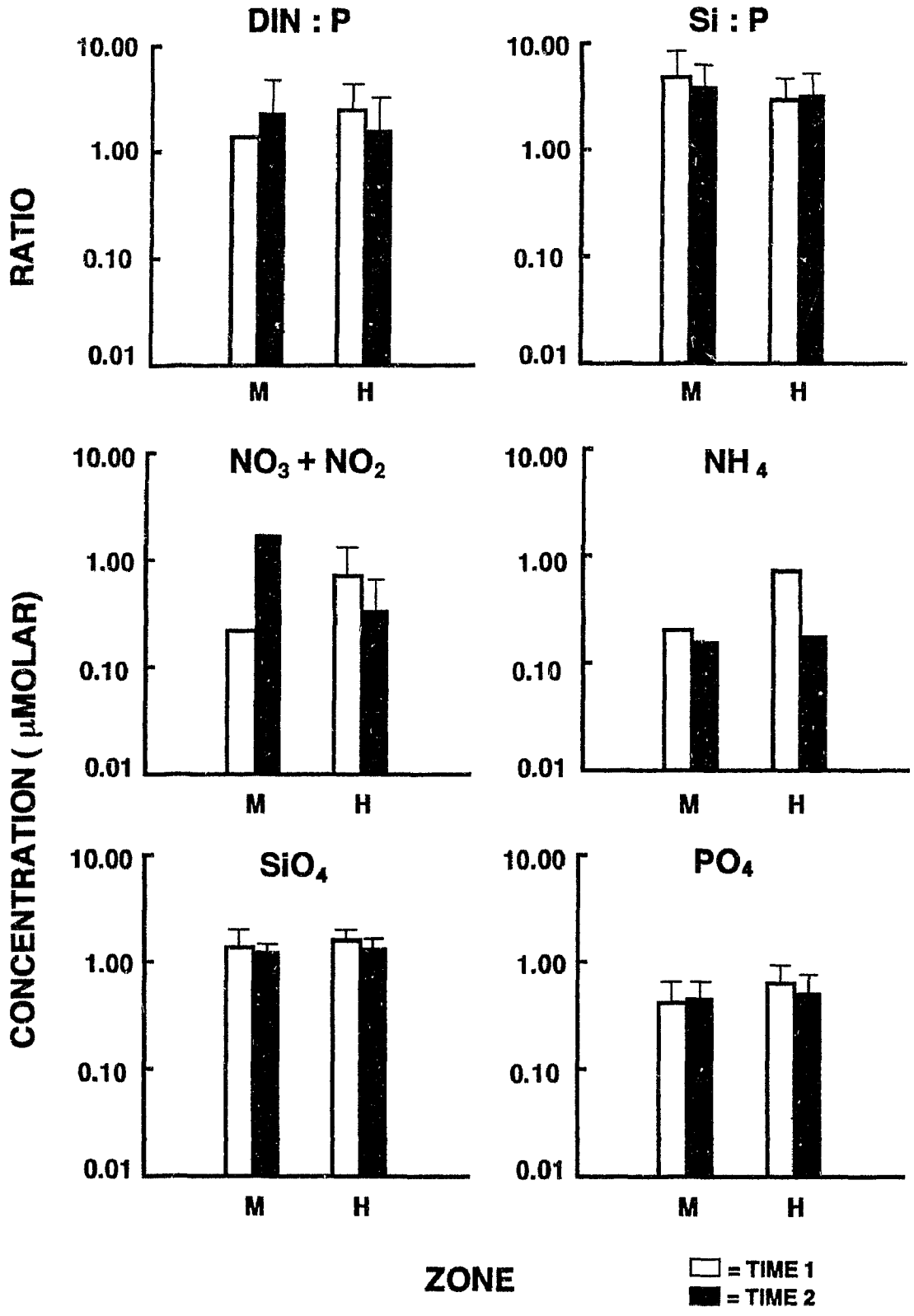
DIN : P
Si : P
NO3 + NO2
NH4
SiO4
PO4
RATIO
CONCENTRATION (µMOLAR)
10.00
1.00
0.10
0.01
M
H
ZONE
= TIME 1
= TIME 2

Figure 4.7

DISCUSSION

Changes in abundance of phytoplankton during the period of tidal isolation of tidepools varied among taxonomic groups and dates. Nanoflagellates were the only group that increased significantly during the period of isolation of the pools, and this occurred only in August. This increase probably reflects population growth since the abundance of nanoflagellates nearly doubled during the period of isolation in August, which approximated their generation time (Brand 1984). Most other phytoplankton groups have generation times which exceed the period of isolation (Harrison *et al.* 1980, Brand 1984).

The abundance of centric diatoms (and consequently total phytoplankton) decreased significantly over the period of tidal isolation in October. A possible explanation for this is that these diatoms sank to the bottom. However, if these were losses due to sinking, I should have detected a significant Time by Stratum interaction, i.e. abundance should have increased near the bottom and decreased in the water-column of the pools during the period of tidal isolation. Since this was not observed for centric diatoms (or any other phytoplankton group), I disregard sinking as a factor. Another possibility is that physical / chemical changes in the pools during isolation had lethal effects on diatoms. However, the magnitude of fluctuations in the physical parameters was small: the greatest increases in temperature, salinity and pH occurred in the high zone, and by the end of the period of tidal isolation the values were similar to those of the mid pools. The decrease in the abundance of centric diatoms also cannot be explained by a change in nutrient availability, since nutrient concentration did not change significantly over the period of tidal isolation of the pools. Therefore, the decrease in centric diatoms was probably due to grazing, either by planktonic and benthic micrograzers, which were abundant in tidepools in all zones, and/or by sessile filter-feeders such as mussels. Mussels (*Mytilus edulis* L. and *M. trossulus* Gould) were

abundant in the mid pools (but virtually absent from the high and splash pools) and could have contributed to the reduction in the abundance of centric diatoms over the period of tidal isolation (see also Frechette *et al.* 1989, Stenton-Dozey & Brown 1992). However, if mussels were mainly responsible for the decrease in centric diatoms, I should have detected a significant Time by Zone interaction which I did not.

Significant changes in the abundance of most phytoplankton groups (except dinoflagellates) in the tidepools were observed over a period of ≈ 50 d. Flagellates and pennate diatoms decreased and centric diatoms and nanoflagellates increased in abundance, while the abundance of total phytoplankton did not change. In the surrounding seawater, the abundance of flagellates, pennate diatoms and dinoflagellates did not change over the same period, whereas the abundance of centric diatoms and total phytoplankton increased, and the abundance of nanoflagellates decreased. The abundance of flagellates in August, and the abundance of nanoflagellates on both dates, were 2 to 4 orders of magnitude higher in the tidepools than the surrounding seawater. These results suggest that the changes in phytoplankton abundance in the tidepools do not simply reflect those in the surrounding seawater at the time of pool flooding. Since the percentage volume of water that is turned over during one tidal inundation is larger in lower pools, their phytoplankton assemblages can be completely replaced and should reflect those of the surrounding seawater more than higher pools. Phytoplankton assemblages in higher pools, because of prolonged isolation and reduced oceanic input, may develop differently over time from the assemblages of the surrounding seawater. If this is the case I would expect the changes in abundance in pools to vary with zone and significant Time by Zone interactions to arise. For example, the abundance of centric diatoms increased in both the mid and the high zones over the 50 d period, but the increase was more pronounced in the high zone. My results suggest that although phytoplankton abundance in tidepools changes within the period of tidal isolation,

processes that occur over longer temporal scales may be primarily responsible for the composition of phytoplankton assemblages in the pools.

CHAPTER 5: Spatial heterogeneity of phytoplankton assemblages in tidepools: effects of abiotic and biotic factors

INTRODUCTION

The importance of spatial variability in ecological processes and community organization has been emphasized in recent studies (Addicott *et al.* 1987, Wiegert 1988, Wiens 1989). In any ecological system, different patterns of species abundance and community organization emerge at different spatial scales of investigation and the relative importance of small-scale phenomema versus broader-scale processes indicates the "openness" of the system (Wiens 1989). Levin (1992) recommended that patterns of variability in community organization within and across systems must be described if prediction of community dynamics is to be successful. Both the small-scale phenomena and the broad-scale processes that affect an ecological system have to be defined before their relative importance can be assessed. The importance of sampling procedures in examining variability at different spatial scales has been emphasized (see Andrew & Mapstone 1987, for review) and statistical and numerical models have been developed that examine the different sources of spatial variability (e.g. Morris 1987, Perry 1988, Downes *et al.* 1993).

Community structure and organization has been studied extensively on rocky intertidal shores (e.g. Stephenson & Stephenson 1950, 1952, 1954a, b, Dayton 1971, Connell 1972, Menge 1976, Underwood 1981a). Research on this system has provided useful concepts, empirical evidence and models that are applicable to many other communities (e.g. Paine 1966, Connell 1983, Sousa 1984a, b). Studies of

community structure of rocky intertidal shores have been focussed largely on the ubiquitous vertical zonation of organisms along the intertidal gradient (e.g. Connell 1961, Dayton 1971, Paine 1974, Lubchenco & Menge 1978, Schonbeck & Norton 1978, Denley & Underwood 1979). Recent studies, however, have attempted to identify and describe potential sources of natural variability at different spatial scales (from meters to kilometres) (e.g. Underwood & Denley 1984, Caffey 1985, Jernakoff & Fairweather 1985, McGuinness 1987a, b, Foster 1990, Lively *et al.* 1993). These studies have shown that spatial variability on rocky intertidal shores does not change monotonically with scale, i.e. variability does not always increase or decrease on larger spatial scales. The extent to which small-scale variability can affect the outcome of large-scale processes has not been established as yet.

Tidepools are a conspicuous component of the rocky intertidal habitat that are less studied than the emergent substrata. However, because of their well-defined boundaries and manageable size, tidepools provide a useful system for examining sources of variability at different spatial scales. The biological zonation which characterizes the emergent substrata is not as apparent in tidepools (see Chapters 1 to 4). Spatial variability in community structure is probably larger among pools than among locations on the emergent substrata at the same spatial scale, since the physical characteristics of tidepools (e.g. pool depth, volume, orientation, and flushing rate) make individual pools unique (Chapter 1). In Chapter 2, I showed that horizontal spatial variability among pools within intertidal zones may mask the vertical zonation observed on emergent substrata, at least for some functional groups of macrobenthos.

Microalgae, particularly pennate diatoms, are among the first colonizers of bare rocky intertidal shores (Sousa 1979a, MacLulich 1986) and may exhibit vertical zonation on emergent substrata. Earlier studies have shown that some benthic

diatoms, such as the pennate diatom *Acnanthes*, are more abundant higher on the shore while others, such as the centric diatom *Melosira*, are more abundant lower on the shore (Aleem 1950, Castenholz 1963, Hopkins 1964). Recently, however, Hill & Hawkins (1991) found large horizontal spatial variability in the abundance of epilithic diatoms on a rocky shore in the Isle of Man, U.K.

Very few studies have examined the distribution and abundance of microalgae in tidepools on rocky shores (see Chapter 1). Droop (1953) provided a classification of pools on the basis of their phytoplankton assemblages which varied along the intertidal gradient. Metaxas & Lewis (1992) found that the abundance of centric diatoms decreased in pools higher on the shore while that of pennate diatoms tended to increase. Neither of these studies, however, used replicate pools within zones to determine whether the observed pattern would persist across space. Dethier (1984) used a large number of tidepools and found that diatoms were more abundant in lower pools in protected shores. However, she did not quantify horizontal spatial variability and only examined the diatom community of the benthos and not the water-column of the pools.

It is well established that phytoplankton community structure in large aquatic systems such as lakes and the open ocean, can be directly affected by nutrients and/or herbivory. Spring and fall phytoplankton blooms are triggered by increased nutrient concentrations in the euphotic zone after vertical mixing; blooms collapse because of nutrient depletion, cell sinking or increased grazing (e.g. see Reynolds *et al.* 1982, Harrison *et al.* 1983, Reid *et al.* 1990, Sommer 1991, Wassman 1991 for reviews). The growth of different groups of phytoplankton is limited in different nutrient regimes and species can coexist when limited by different resources (Tilman 1977, but see Hobson 1988/1989). Conversely, nutrient uptake rates and efficiency vary among

different groups of phytoplankton, and the nutrient levels in the environment can determine patterns of dominance and succession (Parsons *et al.* 1978, Vanni & Temte 1990, Gervais 1991, Pomeroy 1991, Sommer 1991). Selective grazing also may result in shifts in phytoplankton dominance (Vanni & Temte 1990, Gervais 1991, Sommer 1991).

In tidepool systems, microalgae are introduced through input from the surrounding sea-water, by the ascending tide and through spray. The microalgal assemblages subsequently become isolated from external input for extended periods of time, depending upon the period of isolation of the pool. During this period, the assemblage may change due to a number of factors (Chapter 4). Phytoplankton may remain suspended because of buoyancy or motility (e.g. centric diatoms, flagellates, nanoflagellates) or may sink to the bottom (e.g. benthic centric and pennate diatoms). Phytoplankon may be consumed by macrobenthic filter-feeders such as mussels, or planktonic filter-feeders such as calanoid copepods and rotifers. Benthic micrograzers such as harpacticoid copepods, may consume microalgae that have sunk to the bottom of the pool. The nutrient regime can change either through uptake by micro- and macroalgae or through excretion by the fauna. The physical conditions of the pools can change and may even reach lethal limits for certain groups of microalgae. The magnitude of changes affecting the phytoplankton assemblage will depend on the length of the period of tidal isolation of the pool. Predictable zonation patterns may arise if the magnitudes of change are similar among pools with similar periods of isolation (within the same intertidal zone). However, horizontal spatial variability among pools within zones may mask the broad-scale phenomenon of zonation.

In this chapter, I examine the sources of vertical and horizontal spatial variability of phytoplankton assemblages in tidepools, located in 3 intertidal zones over

a period of 17 mo. Specifically, I wanted to determine whether the broad-scale phenomenon of intertidal zonation is evident in these assemblages, or whether the horizontal spatial variability in the abundance of phytoplankton among tidepools within intertidal zones overrides any pattern of zonation. I also measured the sources of spatial variability in the nutrient regime, the grazer field, and in a number of abiotic characteristics of the tidepools to determine whether variability in abiotic and biotic factors could explain the observed patterns of phytoplankton abundance at these spatial scales.

MATERIALS AND METHODS

Four tidepools at each of 3 intertidal zones (mid, high and splash) were sampled at Cranberry Cove, an exposed rocky shore near Halifax, Nova Scotia, Canada (44°28'N, 63°56'W) at approximately monthly intervals between March 1991 and June 1992. (For a detailed description of the pools and study site see Chapter 2).

At each sampling period, 2 60-mL samples of phytoplankton were collected at each of 2 strata within each pool (at the surface and < 1cm above the bottom) and from the surrounding seawater at 2 locations along the shore, immediately below the 2 farthest pools. The phytoplankton samples were collected, processed and enumerated as described in Chapter 4. Two samples of micrograzers were collected from 0.1-0.2 m above the bottom of each tidepool, at approximately the mid depth of the pools. Two other samples were collected similarly from the surrounding seawater at the same locations as the phytoplankton samples. The micrograzer samples were collected, processed and enumerated as in Chapter 3. Mussel density (*Mytilus edulis* and/or *M. trossulus*) was measured in 5 0.2 x 0.2 m quadrats which were randomly located in each tidepool at each sampling date. Two 60-mL water samples were collected from each pool and at the 2 sea-surface locations for analysis of nitrate+nitrite, ammonium, silicate and phosphate concentrations. The nutrient samples were collected and processed as described in Chapter 2 (my unpublished data suggest that freezing over periods of 7 mo. had no effect on the concentration of ammonium). Temperature of each pool and the surrounding sea-water was measured using a hand-held thermometer, salinity was measured with an Endeco type 102 refractometer, and pH was measured with a Cole Palmer pH Wand (Model 05830-00).

For statistical analysis, phytoplankton were assigned to 4 taxonomic groups: centric diatoms, pennate diatoms, flagellates, and nanoflagellates (Table 5.1) This is a

conventional grouping based on successional patterns (e.g. see Vanni & Temte 1990, Venrick 1990, Haigh *et al.* 1992, Weeks *et al.* 1993). Micrograzers were grouped as benthic and planktonic according to their functional morphology and mode of feeding. Mussels were grouped to 3 size-classes, small (< 1 cm), medium (1 - 2 cm) and large (> 2 cm) because filtering rate, and therefore effect on phytoplankton abundance, varies largely with mussel size (e.g. Winter 1973, Kemp *et al.* 1990). For each sampling date, differences in abundance of each taxonomic group of phytoplankton, as well as differences in the abundance of total phytoplankton, were compared among Intertidal Zones (mid, high and splash), among Pools nested within Zones (4 per Zone), and among Strata (surface and bottom of the pools) using 3-factor nested ANOVA. The model used in the ANOVA was:

$$X_{ijkl} = \mu + Stratum_i + Zone_j + Stratum*Zone_{ij} + Pool(Zone)_{k(j)} + Stratum * Pool(Zone)_{ik(j)} + e_{l(ijk)}$$

The effect of the interaction term Stratum*Pool(Zone) was examined against the residual error, and the effect of the terms Stratum and Stratum*Zone were examined against the interaction term Stratum*Pool(Zone). In cases where the interaction term Stratum*Pool(Zone) was significant, the effect of the factor Stratum was examined within each Zone. The effect of the factor Zone was examined against the factor Pool(Zone); if Pool(Zone) was not significant at $p > 0.250$, I pooled the term Pool(Zone) with the residual error and tested the effect of the factor Zone against the pooled error term. The magnitude of the experimental effect of each factor (ω^2) was calculated for each sampling date, based on models in Howell (1987), using mean square estimates that were defined according to Underwood (1981b).

Differences in densities of micrograzers and mussels, and nutrient concentrations were examined among Intertidal Zones and among Pools nested within Zones using 2-factor nested ANOVA, since Stratum was not applicable. Differences in temperature, salinity and pH were examined among Zones using 1-factor ANOVA. The analyses of variance were based on models given in Winer (1971) and Underwood (1981b). A posteriori multiple comparisons of treatment means were done using Student-Newman-Keuls (SNK) tests. The null hypothesis was rejected at $p < 0.05$ in all statistical tests (ANOVA and SNK).

Forward stepwise multiple regressions (Sokal and Rohlf 1981, Kleinbaum *et al.* 1988) were done to examine relationships between the abundance of each phytoplankton group at the surface and at the bottom of the pools with the abundance of planktonic and benthic micrograzers and mussels, the concentration of nutrients (nitrate+nitrite, ammonium, phosphate, and silicate), the physical and chemical characteristics of the pools (temperature, salinity, pH, height above chart datum, surface area, volume and flushing rate) and the macroalgal cover in the pools as given in Chapter 2. Regressions were carried out for the entire sampling period. The α-to-add value was 0.150.

For all statistical analyses, variables were ln (x+1)-transformed to successfully remove heterogeneity of variance when detected using Cochran's test, or non-normality when detected in residual plots. All analyses were carried out using SYSTAT v. 5.1 and v. 5.2 (Wilkinson 1989) on a Macintosh SE 30 computer.

RESULTS

Spatial patterns of physical and chemical characteristics

The physical characteristics of the tidepools are given in Chapter 2. Since phytoplankton can be introduced into the pools through any amount of input of the surrounding seawater (including spray), I assigned replicate pools to intertidal zones according to the period of isolation from tidal input.

Mean temperature at the sea-surface and in the tidepools increased from a low around March to a peak in July 1991 (Fig. 5.1). It remained high throughout the summer and early autumn but decreased by November 1991. The increase between March and June 1992 was similar to that of the previous year. Mid pools were significantly (SNK test) colder than high and splash pools in May 1991 ($F_{2,9} = 5.07$, $p < 0.05$), and in April ($F_{2,9} = 6.80$, $p < 0.05$) and June 1992 ($F_{2,9} = 11.65$, $p < 0.01$). Mid pools were significantly colder than high pools in August 1991 ($F_{2,9} = 6.19$, $p < 0.05$). Splash pools were significantly colder than mid and high pools in October 1991 ($F_{2,9} = 28.77$, $p < 0.001$). Mean salinity remained relatively constant at the sea-surface and in the mid pools over the 17 mo study, but was reduced significantly due to rain in splash pools in October ($F_{2,9} = 4.60$, $p < 0.05$) and November 1991 ($F_{2,9} = 22.19$, $p < 0.001$), and in May 1992 ($F_{2,9} = 5.34$, $p < 0.05$) (Fig. 5.1). However, salinity was significantly greater in splash pools than in mid and high pools in March 1992 ($F_{2,9} = 6.05$, $p < 0.05$). Mean pH at the sea-surface did not fluctuate over the 17 months, but was greater and more variable in the pools (Fig. 5.1). pH was greatest in mid pools and smallest in splash pools in October 1991 ($F_{2,9} = 8.41$, $p < 0.01$) and was greater in splash pools than in mid pools in May 1992 ($F_{2,9} = 4.50$, $p < 0.05$).

Spatial patterns of phytoplankton abundance

The abundance of total phytoplankton was greatest in the surrounding seawater in March 1991 and May 1992 due to spring blooms, and in October 1991 due to an autumn bloom (Fig. 5.2). Similar patterns of abundance were observed for centric diatoms, the dominant phytoplankton group during the blooms (Fig. 5.3). The abundance of pennate diatoms was greatest after the spring bloom in 1991 and around the bloom in 1992 (Fig. 5.4). Flagellates and nanoflagellates were less abundant than diatoms: their mean abundance never exceeded 10^4 cells. L^{-1} at the sea-surface (Figs. 5.5 & 5.6).

In tidepools, the abundance of total phytoplankton and of individual taxonomic groups varied significantly between strata on a number of sampling dates. Total phytoplankton was more abundant at the bottom than at the surface of pools in spring (all pools: 17 March, April, May 1991, April and June 1992; mid pools: 27 March 1991; splash pools: May 1992), and in autumn (all pools: October, November 1991) (Fig. 5.2, Table 5.2). Centric diatoms were more abundant at the bottom than at the surface of all pools on 3 out of the 11 dates (August, October 1991, May 1992), but they were more abundant at the surface than at the bottom in all pools on 1 date (September 1991), and in the splash pools only on another date (March 1992) (Fig. 5.3, Table 5.3). Pennate diatoms were more abundant at the bottom than at the surface of pools in spring (all pools: 17 March, April 1991, April, May, June 1992; mid pools: May 1991), although they were more abundant at the surface than at the bottom of all pools on 1 date (27 March 1991) (Fig. 5.4, Table 5.4). Flagellates were more abundant at the bottom than at the surface of pools on 3 dates (all pools: April, November 1991; high pools: April 1992), but they were more abundant at the surface than at the bottom of all pools on 1 date (27 March 1991) (Fig. 5.5, Table 5.5).

Nanoflagellates were more abundant at the bottom than at the surface of all pools on 4 out of the 7 sampling dates (October, November 1991, April, June 1992) (Fig. 5.6, Table 5.6).

The abundance of total phytoplankton varied significantly (SNK test) among intertidal zones on 1 sampling date (November 1991) when it was greatest in the splash pools (Fig. 5.2, Table 5.2). Among the individual taxonomic groups, centric and pennate diatoms were significantly more abundant in mid (M) than in high (H) and/or splash (S) pools on several dates (centric diatoms: August 1991: M, S > H; April 1992: M > H, S; pennate diatoms: 27 March 1991: M > S; June 1991: M > H; July 1991: M, H > S; September 1991: M > H, S) (Figs. 5.3 & 5.4, Tables 5.3 & 5.4). Flagellates were significantly more abundant in splash pools than mid and high pools on 1 sampling date (November 1991, Fig. 5.5, Table 5.5). Nanoflagellates were significantly more abundant in splash pools than in mid pools on one date (August 1991), but this difference was reversed on another date (May 1992) (Fig. 5.6, Table 5.6).

The abundance of total phytoplankton and all taxonomic groups was highly variable among pools within zones throughout the study. The abundance of total phytoplankton varied significantly among pools within zones on all sampling dates (mid pools: all dates except May, July to September 1991, May 1992; high pools: all dates except August and November 1991; splash pools: all dates except May 1992) (Fig. 5.2, Table 5.2). The abundance of centric diatoms varied significantly among pools within zones on 9 out of 11 dates (mid pools: 17 March, 27 March, September 1991, April 1992; high pools: 17 March, 27 March, October 1991, May, June 1992; splash pools: 17 March, 27 March, May, August, October 1991, March 1992) (Fig. 5.3, Table 5.3). The abundance of pennate diatoms varied significantly among pools

on 11 out of 14 dates (mid pools: 17 March, 27 March, November 1991, March to May 1992; high pools: 17 March, May, June, July, October 1991, April, May 1992; splash pools: 17 March to May, October, November 1991, March to May 1992) (Fig. 5.4, Table 5.4). The abundance of flagellates varied significantly among pools on 13 out of 14 dates (mid pools: 17 March to June, August, October, November 1991, May and June 1992; high pools: 17 March to September, November 1991, April to June 1992; splash pools: on all dates except March 1992) (Fig. 5.5, Table 5.5). The abundance of nanoflagellates varied significantly among pools within zones on all dates (mid pools: August, October, November 1991, March to May 1992; high pools: August, October 1991, March to June 1992; splash pools: August, September, November 1991, March, April, June 1992) (Fig. 5.6, Table 5.6).

The magnitude of the effect that each source of spatial variability had on phytoplankton abundance varied among groups but was relatively consistent among dates for most groups (Fig. 5.7). Variability in abundance of total phytoplankton, flagellates and nanoflagellates was explained largely by variability among pools within zones, whereas variability in abundance of centric and pennate diatoms was explained to similar extents by variability among zones and between strata, as well as among pools within zones. Variability among pools within intertidal zones was 13-96% (on all dates) of total variability for total phytoplankton; for flagellates, it was 6-96% (on all dates); for nanoflagellates, it was 33-86% (on all dates); for centric diatoms, it was 11-69% (on 9 out of 11 dates); and for pennate diatoms, it was 10-42% (on 12 of 14 dates) of total variability. Variability among zones was 1-49% (on 7 of 14 dates) of total variability for total phytoplankton; for flagellates, it was 1-59% (on 7 of 14 dates); for nanoflagellates, it was 3-42% (on 6 of 7 dates); for centric diatoms, it was 8-35% (on 4 of 11 dates); and for pennate diatoms, it was 7-23% (on 9 of 14 dates) of

total variability. Variability between strata was 1-20% (on 11 of 14 dates) of total variability for total phytoplankton; for flagellates, it was 1-9% (on 10 of 14 dates); for nanoflagellates, it was 1-7% (on 5 of 7 dates); for centric diatoms, it was 1-23% (on 9 of 11 dates); and for pennate diatoms, it was 1-42% (on 10 of 14 dates) of total variability. The interaction term Zone * Stratum accounted for <23% and the interaction term Pool (Zone) * Stratum accounted for <28% of the variability in the abundance of all phytoplankton groups on all sampling dates. The amount of residual variability in abundance varied among phytoplankton groups and among sampling dates: for total phytoplankton, residual variability was 4-37% of total variability; for centric diatoms, it was 8-40% except in April and November 1991 when it was 100% and 89%, respectively; for pennate diatoms, it was 9-67% except in August 1991 when it was 85%; for flagellates, it was 3-29% except in March 1992 when it was 72%; and for nanoflagellates, it was 8-43% of total variability.

Spatial patterns of grazer abundance

The major groups of planktonic micrograzers were calanoid copepodites and nauplii (the genera *Acartia*, *Calanus*, *Paracalanus*, *Pseudocalanus* and *Temora* at the sea-surface and in mid pools, and *Eurytemora affinis* in splash pools), marine cladocerans (*Podon polyphemoides* and *Evadne nordmanii*) and marine rotifers (the genera *Brachionus* and *Synchaeta*) (for a more detailed description see Chapter 3). Planktonic micrograzers were significantly (SNK test) more abundant in the splash pools than in the high pools on only 1 date (September 1991), but they varied significantly among pools within zones on 6 of 14 sampling dates (May to September 1991, June 1992) (Fig. 5.8. Table 5.7).

The major groups of benthic micrograzers included harpacticoid copepodites and nauplii (Families Harpacticidae, Tisbidae, Thalestridae and Diosaccidae), foraminiferans and nematodes (see Chapter 3). Although the abundance of benthic micrograzers varied significantly among zones in May 1992, SNK tests did not reveal significant differences among Zone means (Fig. 5.8, Table 5.7). The abundance of benthic grazers varied significantly among pools within zones on 2 of 14 sampling dates (June, July 1991).

Mussels (*Mytilus edulis* and/or *M. trossulus*) were abundant in mid and high pools throughout the sampling season, but small mussels were never found in some high and splash pools (Fig. 5.9, see Chapter 2). The abundance of small mussels was greater in mid than high and splash pools on 1 sampling date (September 1991) but varied significantly (SNK test) among pools within zones on 5 of 14 dates (June to August 1991, May, June 1992) (Table 5.8). The abundance of medium-sized mussels was greater in mid than high and/or splash pools on 4 sampling dates (August, September 1991, May, June 1992), and varied significantly among pools within zones on all sampling dates except August 1991 (Table 5.8). The abundance of large mussels was greater in mid than high and /or splash pools on 3 dates (August 1991, May, June 1992), and varied significantly among pools within zones on all sampling dates except May 1992 (Table 5.8).

Spatial patterns of nutrient concentration

The concentrations of macronutrients varied little among zones but was variable throughout the sampling season among pools within zones (Figs. 5.10 & 5.11). The concentration of nitrate+nitrite and ammonium did not vary significantly among zones

on any sampling date but varied significantly among pools within zones on 6 of 14 and 5 of 9 dates, respectively (nitrate+nitrite: 17 March, 27 March, April, August 1991, May, June 1992; ammonium: May, July, September, October 1991, April 1992) (Table 5.9). The concentration of phosphate was significantly greater in mid pools than high and splash pools on 17 March 1991, and varied significantly among pools within zones on 8 of 14 sampling dates (27 March to May, July, September 1991, March, May, June 1992). The concentration of silicate was significantly greater in mid than high and/or splash pools on 3 dates (17 March, November 1991, April 1992), and varied significantly among pools on all sampling dates except May 1991.

Relationships of phytoplankton abundance with biotic and abiotic factors

The abundance of phytoplankton varied significantly with most of the biotic and some of the abiotic characteristics of individual tidepools. Although the significant independent factors differed among phytoplankton groups, I obtained similar relationships between the abundances of each group at the surface and bottom of the pools for each group, but not for total phytoplankton (Table 5.10). Among the biotic factors, the abundance of total phytoplankton at the bottom, and of each phytoplankton group (except centric diatoms) at both strata varied significantly with the density of small mussels, whereas only the abundance of pennate diatoms at the bottom of the pools varied significantly with the density of medium-sized mussels. Only the abundance of nanoflagellates at the surface of the pools varied significantly with the density of benthic micrograzers. No phytoplankton group showed a significant relationship with the density of planktonic micrograzers or large mussels.

In terms of nutrients, the abundance of total phytoplankton at the surface of the pools varied significantly with the concentration of nitrate+nitrite, and the abundance of centric diatoms at the surface and of nanoflagellates at both strata varied significantly with the concentration of ammonium. Only the abundance of nanoflagellates at the bottom of the pools varied significantly with phosphate. The abundance of total phytoplankton, flagellates and nanoflagellates at both strata, and of pennate diatoms at the bottom of the pools varied significantly with the concentration of silicate.

Fewer significant relationships were detected between abiotic factors and the abundance of phytoplankton over the entire sampling period. The abundance of total phytoplankton at the bottom of the pools and of flagellates at both strata varied significantly with temperature. The abundance of total phytoplankton at the bottom of the pools varied significantly with salinity. The abundance of pennate diatoms and nanoflagellates at both strata varied significantly with percentage cover of macroalgae, and the abundance of flagellates at both strata varied significantly with flushing rate.

Table 5.1: Species list for each of the 4 taxonomic groups of phytoplankton that were identified in this chapter. ✔ indicates species present at the sea-surface or in any of the 4 tidepools (1-4) sampled in each of the 3 zones (mid, high splash) on any of 14 sampling dates between March 1991 and June 1992.

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
CENTRIC DIATOMS													
Chaetoceros spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Coscinodiscus spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔		✔	✔
Detonula confervacea	✔	✔											
Leptocylindrus danicus	✔	✔	✔	✔	✔	✔	✔	✔		✔		✔	✔
Melosira nummuloides	✔	✔	✔	✔		✔							
Odontella aurita	✔										✔		
Rhizosolenia alata	✔	✔	✔	✔	✔					✔		✔	
R. delicatula	✔		✔		✔		✔		✔	✔			✔
R. fragilissima	✔	✔	✔	✔	✔	✔	✔	✔	✔				✔
R. setigera	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔			
R. styliformis	✔	✔	✔										
Skeletonema costatum	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Thalassiosira gravida	✔										✔		
T. hyalina	✔	✔	✔	✔	✔						✔		
T. nordenskioldii	✔	✔	✔	✔	✔		✔	✔	✔	✔	✔	✔	✔
PENNATE DIATOMS													
Amphiprora spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Amphora spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Campylosira cymbelliformis			✔										
Cylindrotheca closterium	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Fragilaria crotonensis	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Grammatophora angulosa	✔	✔	✔	✔	✔	✔		✔	✔		✔		
Gyrosigma sp.		✔	✔		✔					✔			
Licmophora gracilis	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
L. juergensii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Navicula spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Nitzschia delicatissima	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
N. longissima	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
N. seriata	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Nitzschia spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔

Table 5.1 (continued)

TAXONOMIC GROUP	SEA	MID POOLS				HIGH POOLS				SPLASH POOLS			
		1	2	3	4	1	2	3	4	1	2	3	4
Plagiogramma stauroforum	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Striatella unipunctata	✔	✔	✔	✔	✔	✔	✔						
Surirella spp.		✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Thalassionema nitzschioides	✔	✔	✔		✔	✔	✔	✔		✔	✔	✔	✔
Thalassiothrix frauenfeldii	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Unidentified pennates	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
FLAGELLATES													
Cryptomonas spp.	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
Euglena spp.								✔					
NANO-FLAGELLATES													
Dunaliella tertiolecta	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔

Table 5.2: Analyses of variance of the abundance of total phytoplankton (cells . L^{-1}) for 14 sampling periods, between March 1991 and June 1992. Factors are Stratum (S), Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)*S} = 9,24$; $F_{Z*S} = 2,9$ if $p_{P(Z)*S} < 0.250$ and $F_{Z*S} = 2,33$ if $p_{P(Z)*S} > 0.250$; $F_S = 1,9$ if $p_{P(Z)*S} < 0.250$ and $F_S = 1,33$ if $p_{P(Z)*S} > 0.250$; $F_{P(Z)} = 9, 24$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 33$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

DATE	P(Z)*S		Z*S		S		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91	0.57	1.07, NS	0.61	3.45, NS	0.61	17.97, **	0.60	14.84,***	8.85	0.97, NS
27-3-91	$2.2x10^4$	4 92, **	$1.1x10^5$	0.20, NS	$1.1x10^5$	11.68, **	$2.2x10^4$	25.23,***	$5.6x10^5$	0.22, NS
13-4-91	1.06	1.38, NS	1.17	0.98, NS	1.17	11.28, **	1.06	10.06,***	10.67	0.32, NS
13-5-91	$3.3x10^{10}$	1.80, NS	$6.0x10^{10}$	0.90, NS	$6.0x10^{10}$	5.43, *	$3.3x10^{10}$	5.51,***	$1.8x10^{11}$	1.61, NS
7-6-91	0.41	2.57, *	1.04	0.90, NS	1.04	0.04, NS	0.41	61.40,***	24.95	0.42, NS
12-7-91	$8.8x10^{10}$	0.40, NS	$7.3x10^{10}$	0.36, NS	$7.3x10^{10}$	0.20, NS	$8.8x10^{10}$	110, ***	$9.6x10^{12}$	1.04, NS
22-8-91	$1.7x10^{11}$	0.67, NS	$1.5x10^{11}$	0.01, NS	$1.5x10^{11}$	3.20, NS	$1.7x10^{11}$	6.12,***	$1.0x10^{12}$	1.73, NS
21-9-91	4.43	0.35, NS	3.64	0.08, NS	3.64	1.88, NS	4.43	10.78,***	47.75	0.01, NS
9-10-91	0.42	2.08, NS	0.87	2.48, NS	0.87	5.52, *	0.42	7.33,***	3.06	2.86, NS
17-11-91	0.35	0.61, NS	0.31	0.58, NS	0.31	5.99, *	0.35	12.71,***	4.39	6.10, *
15-3-92	28.27	0.63, NS	25.43	4.03, *	25.43	1.67, NS	28.27	29.15,***	824	0.85, NS
8-4-92	0.46	1.00, NS	0.46	0.01, NS	0.46	14.25,***	0.46	11.23,***	5.16	0.94, NS
6-5-92	$5.0x10^{11}$	2.83, *	$1.4x10^{12}$	0.15, NS	$1.4x10^{12}$	5.04, NS	$5.0x10^{11}$	2.68, *	$1.3x10^{12}$	3.71, NS
26-6-92	0.37	0.62, NS	0.33	0.89, NS	0.33	10.55, **	0.37	17.71,***	6.51	1.94, NS

Table 5.3: Analyses of variance of the abundance of centric diatoms (cells . L^{-1}) for 14 sampling periods, between March 1991 and June 1992. Factors are Stratum (S), Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)): degrees of freedom: $F_{P(Z)*S} = 9,24$; $F_{Z*S} = 2,9$ if $p_{P(Z)*S} < 0.250$ and $F_{Z*S} = 2,33$ if $p_{P(Z)*S} > 0.250$; $F_S = 1,9$ if $p_{P(Z)*S} < 0.250$ and $F_S = 1,33$ if $p_{P(Z)*S} > 0.250$; $F_{P(Z)} = 9, 24$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 33$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. - = centric diatoms were absent. MS = denominator mean square used in F-ratios.

DATE	P(Z)*S		Z*S		S		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91	$2.9x10^9$	2.74, *	$7.9x10^9$	0.44, NS	$7.9x10^9$	5.48, *	$2.9x10^9$	21.50,***	$6.2x10^{10}$	0.80, NS
27-3-91	7.12	4.61, **	32.83	0.87, NS	32.83	8.09, *	7.12	37.52,***	267	0.25, NS
13-4-91	20.31	0.45, NS	17.26	0.36, NS	17.26	0.45, NS	20.31	0.92, NS	19.86	0.41, NS
13-5-91	8.74	0.69, NS	8.00	1.83, NS	8.00	2.95, NS	8.74	3.79, **	33.13	1.65, NS
7-6-91		-		-		-		-		-
12-7-91		-		-		-		-		-
22-8-91	9.88	1.22, NS	10.47	0.61, NS	10.47	4.79, *	9.88	2.82, *	27.85	5.57, *
21-9-91	3.22	0.50, NS	2.78	5.06, *	2.78	5.06, *	3.22	3.04, *	9.77	4.11, NS
9-10-91	6.68	1.37, NS	7.35	1.52, NS	7.35	9.16, **	6.68	7.36,***	49.16	0.91, NS
17-11-91	3.91	0.82, NS	3.71	1.74, NS	3.71	1.42, NS	3.91	0.82, NS	3.71	0.39, NS
15-3-92	4.78	2.46, *	11.76	2.97, NS	11.76	0.57, NS	4.78	2.13, NS	10.18	0.64, NS
8-4-92	3.61	2.81, *	10.11	1.45, NS	10.11	1.63, NS	3.61	6.34,***	22.85	5.71, *
6-5-92	9.87	1.10, NS	10.14	6.50, *	10.14	17.50, **	9.87	3.49, **	34.48	0.66, NS
26-6-92		-		-		-		-		-

Table 5.4: Analyses of variance of the abundance of pennate diatoms (cells . L^{-1}) for 14 sampling periods, between March 1991 and June 1992. Factors are Stratum (S), Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)*S} = 9,24$; $F_{Z*S} = 2,9$ if $p_{P(Z)*S} < 0.250$ and $F_{Z*S} = 2,33$ if $p_{P(Z)*S} > 0.250$; $F_S = 1,9$ if $p_{P(Z)*S} < 0.250$ and $F_S = 1,33$ if $p_{P(Z)*S} > 0.250$; $F_{P(Z)} = 9, 24$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 33$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

DATE	P(Z)*S		Z*S		S		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F. p
17-3-91	1.61	0.99, NS	1.61	1.16, NS	1.61	55.44,***	1.61	7.18,***	11.58	0.32, NS
27-3-91	14.86	1.45, NS	21.55	2.26, NS	21.55	26.99, **	14.86	3.84, **	57.16	5.56, *
13-4-91	2.34	4.39, **	1.63	0.47, NS	1.63	41.29,***	2.34	4.18, **	9.76	2.10, NS
13-5-91	1.56	4.03, **	6.30	0.56, NS	6.30	11.64, **	1.56	20.08,***	31.37	2.71, NS
7-6-91	9.25	0.82, NS	8.80	0.84, NS	8.80	1.52, NS	9.25	2.26, *	20.86	7.73, *
12-7-91	11.74	1.05, NS	11.90	0.10, NS	11.90	0.83, NS	11.74	1.80, NS	21.18	8.50, **
22-8-91	13.16	1.03, NS	13.26	0.05, NS	13.26	0.97, NS	13.16	1.66, NS	21.81	0.92, NS
21-9-91	8.99	0.99, NS	8.97	3.96, *	8.97	0.07, NS	8.99	1.01, NS	9.01	15.30, **
9-10-91	11.56	0.30, NS	9.35	2.19, NS	9.35	3.62, NS	11.56	2.65, *	30.67	0.87, NS
17-11-91	7.71	1.72, NS	13.28	1.15, NS	13.28	0.18, NS	7.71	2.43, *	18.70	0.19, NS
15-3-92	8.97	0.11, NS	65.48	0.01, NS	65.48	0.09, NS	8.97	4.40, **	39.49	1.53, NS
8-4-92	0.90	1.98, NS	1.78	1.17, NS	1.78	24.94, **	0.90	5.85,***	5.28	0.18, NS
6-5-92	18.67	3.44, **	64.26	0.73, NS	64.26	19.53, **	18.67	8.54,***	160	3.22, NS
26-6-92	2.02	0.70, NS	1.86	0.85, NS	1.86	9.92, **	2.02	0.72, NS	1.87	3.20, NS

Table 5.5: Analyses of variance of the abundance of flagellates (cells . L^{-1}) for 14 sampling periods, between March 1991 and June 1992. Factors are Stratum (S), Intertidal zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)*S} = 9,24$; $F_{Z*S} = 2,9$ if $p_{P(Z)*S} < 0.250$ and $F_{Z*S} = 2,33$ if $p_{P(Z)*S} > 0.250$; $F_S = 1,9$ if $p_{P(Z)*S} < 0.250$ and $F_S = 1,33$ if $p_{P(Z)*S} > 0.250$; $F_{P(Z)} = 9, 24$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 33$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

DATE	P(Z)*S		Z*S		S		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91	4.43	0.91, NS	4.32	4.76, *	4.32	3.26, NS	4.43	92.49,***	410	0.21, NS
27-3-91	5.80	1.55, NS	8.97	2.26, NS	8.97	18.87, **	5.80	41.97,***	243	0.80, NS
13-4-91	0.91	1.17, NS	0.95	2.51, NS	0.95	5.02, *	0.91	14.28,***	12.98	0.86, NS
13-5-91	8.53	1.44, NS	12.26	0.53, NS	12.26	0.39, NS	8.53	9.09,***	77.57	4.02, NS
7-6-91	0.96	1.06, NS	0.98	0.77, NS	0.98	0.04, NS	0.96	33.47,***	32.27	0.63, NS
12-7-91	$8.5x10^{10}$	0.32, NS	$6.9x10^{10}$	377,***	$6.9x10^{10}$	1.78, NS	$8.5x10^{10}$	114,***	$9.6x10^{12}$	1.08, NS
22-8-91	19.64	2.38, *	46.70	0.71, NS	46.70	4.68, NS	19.64	10.15,***	199	1.65, NS
21-9-91	4.03	0.44, NS	3.42	0.18, NS	3.42	2.65, NS	4.03	11.12,***	44.87	0.03, NS
9-10-91	2311	7.79,***	$1.7x10^{4}$	4.08, NS	$1.7x10^{4}$	1.92, NS	2311	31.70,***	$7.3x10^{4}$	3.95, NS
17-11-91	1.64	0.80, NS	1.55	5.88, **	1.55	6.05, *	1.64	25.11,***	41.20	8.22, **
15-3-92	$3.1x10^{8}$	0.87, NS	$3.0x10^{8}$	0.50, NS	$3.0x10^{8}$	3.90, NS	$3.1x10^{8}$	1.31, NS	$3.4x10^{8}$	1.47, NS
8-4-92	$9.4x10^{8}$	3.07, *	$2.9x10^{9}$	1.34, NS	$2.9x10^{9}$	1.47, NS	$9.4x10^{8}$	27.20,***	$2.5x10^{10}$	1.90, NS
6-5-92	1.04	0.97, NS	1.04	1.45, NS	1.04	4.64, NS	1.04	9.76,***	10.18	0.04, NS
26-6-92	$3.6x10^{10}$	2.90, *	$1.0x10^{11}$	1.22, NS	$1.0x10^{11}$	0.07, NS	$3.6x10^{10}$	50.83,***	$1.8x10^{12}$	0.61, NS

Table 5.6: Analyses of variance of the abundance of nanoflagellates (cells . L^{-1}) for 14 sampling periods, between March 1991 and June 1992. Factors are Stratum (S), Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)*S} = 9,24$; $F_{Z*S} = 2,9$ if $p_{P(Z)*S} < 0.250$ and $F_{Z*S} = 2,33$ if $p_{P(Z)*S} > 0.250$; $F_S = 1,9$ if $p_{P(Z)*S} < 0.250$ and $F_S = 1,33$ if $p_{P(Z)*S} > 0.250$; $F_{P(Z)} = 9, 24$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 33$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. - = nanoflagellates were absent. MS = denominator mean square used in F-ratios.

DATE	P(Z)*S		Z*S		S		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91		-		-		-		-		-
27-3-91		-		-		-		-		-
13-4-91		-		-		-		-		-
13-5-91		-		-		-		-		-
7-6-91		-		-		-		-		-
12-7-91		-		-		-		-		-
22-8-91	0.41	2.66, *	1.10	0.17, NS	1.10	5.15, *	0.41	21.48,***	8.92	4.98, *
21-9-91		-		-		-		-		-
9-10-91	5.72	0.64, NS	3.35	0.33, NS	3.35	5.35, *	5.72	4.98, **	18.52	1.51, NS
17-11-91	2.07	0.73, NS	1.97	0.29, NS	1.97	4.83, *	2.07	15.08,***	31 26	2.08, NS
15-3-92	28.01	0.67, NS	25.50	4.36, *	25 50	1.96, NS	28.01	30.30,***	849	0.83, NS
8-4-92	0.41	0.49, NS	0.35	0.16, NS	0.35	7.84, **	0.41	15.91,***	6.44	1.37, NS
6-5-92	0.18	1.63, NS	0.30	0.29, NS	0.30	0.36, NS	0.18	5.99,***	1.10	4.37, *
26-6-92	0.24	1.34, NS	0.26	0.73, NS	0.26	10.95 **	0.24	26.71,***	6.33	2.65, NS

Table 5.7: Analyses of variance of the abundance of planktonic and benthic micrograzers (individuals . m^{-3}) for 12 sampling periods, between March 1991 and June 1992. Factors are Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)} = 9, 12$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 21$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

DATE	PLANKTONIC GRAZERS				BENTHIC GRAZERS			
	P(Z)		Z		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91	6.18	1.78, NS	11.02	0.29, NS	$5.9x10^5$	1.01, NS	$5.9x10^5$	1.46, NS
13-4-91	6.28	1.65, NS	10.33	1.69, NS	4.35	1.83, NS	7.95	0.32, NS
13-5-91	4.23	4.29, *	18.14	0.42, NS	$2.7x10^7$	1.77, NS	$4.8x10^7$	0.94, NS
7-6-91	4.74	5.07, **	24.05	1.94, NS	0.41	7.04, **	2.88	4.26, *
12-7-91	1.80	18.75, ***	33.78	0.53, NS	$2.7x10^7$	3.93, *	$1.1x10^8$	1.63, NS
22-8-91	0.63	7.85, **	4.92	4.01, NS	0.93	2.39, NS	2.23	0.09, NS
21-9-91	2.44	4.72, **	11.52	4.63, *	6.25	1.13, NS	6.60	1.71, NS
9-10-91	5.61	1.75, NS	9.80	0.09, NS	$5.5x10^6$	1.97, NS	$1.1x10^7$	1.16, NS
17-11-91	9.47	1.18, NS	10 19	0.53, NS	$4.3x10^5$	1.41, NS	$5.0x10^5$	1.44, NS
8-4-92	7.64	2.41, NS	18.40	0.65, NS	7.00	1.04, NS	7.10	2.84, NS
6-5-92	9.27	1.16, NS	9.90	2.60, NS	$9.0x10^6$	0.38, NS	$6.7x10^6$	5.67, *
26-6-92	2.44	9.18, ***	22.43	1.63, NS	4.22	1.08, NS	4.36	0.12, NS

Table 5.8: Analyses of variance of the abundance of 3 size classes of mussels (individuals . m^{-2}) for 7 sampling periods, between March 1991 and June 1992. Factors are Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)} = 9, 48$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 57$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = denominator mean square used in F-ratios.

DATE	SMALL MUSSELS				MEDIUM-SIZED MUSSELS				LARGE MUSSELS			
	P(Z)		Z		P(Z)		Z		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p	MS	F, p
7-6-91	5.34	2.97, **	15.84	3.20, NS	2.43	7.90,***	19.18	2.24, NS	0.65	6.94,***	4.81	2.15, NS
12-7-91	1.15	9.17,***	10.52	6.48, NS	0.99	5.03,***	4.95	2.12, NS	0.66	5.56,***	3.66	3.30, NS
22-8-91	2.51	4.76,***	11.96	3.62, NS	865	1.83, NS	1580	5.34, *	0.31	11.16,***	3.46	4.81, *
21-9-91	2.68	1.94, NS	5.20	9.59, **	1.21	4.92,***	5.93	5.82, *	0.76	8.10,***	6.12	1.96, NS
27-10-91	2.48	1.44, NS	3.58	3.87, NS	1.43	6.87,***	9.85	0.80, NS	0.22	35.25,***	7.90	0.86, NS
6-5-92	3.66	4.97,***	18.17	2.28, NS	1.73	2.70, **	4.67	14.90, **	0.43	0.87, NS	0.43	6.16, *
26-6-92	3.20	5.89,***	18.86	2.36, NS	1.28	9.65,***	12.33	4.35, *	1.10	3.48, **	3.80	4.87, *

Table 5.9: Analyses of variance of nutrient concentrations (μM) for 14 sampling periods, between March 1991 and June 1992. Factors are Intertidal Zone (Z) and Pool (nested within Zone) (P(Z)); degrees of freedom: $F_{P(Z)} = 9, 12$; $F_Z = 2, 9$ if $p_{P(Z)} < 0.250$ and $F_Z = 2, 21$ if $p_{P(Z)} > 0.250$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. - = not measured. MS = denominator mean square used in F-ratios.

DATE	NO_3+NO_2				NH_4			
	P(Z)		Z		P(Z)		Z	
	MS	F, p	MS	F, p	MS	F, p	MS	F, p
17-3-91	0.01	14.05, **	0.13	0.53, NS		-		-
27-3-91	0.06	62.40,***	3.60	0.41, NS		-		-
13-4-91	0.004	26.08,***	0.11	0.83, NS		-		-
13-5-91	1.45	0.80, NS	1.33	0.37, NS	0.008	148,***	1.16	0.81, NS
7-6-91	1.90	0.36, NS	7.21	0.13, NS	0.003	0.83, NS	0.003	0.67, NS
12-7-91	10.19	0.53, NS	8.11	1.38, NS	0.149	86.28,***	12.86	1.32, NS
22-8-91	5.20	5.37, **	27.90	0.60, NS		-		-
21-9-91	1.79	1.02, NS	1.81	0.18, NS	0.027	11.19,***	0.30	0.71, NS
9-10-91	6.40	0.82, NS	5.90	0.61, NS	0.136	3.31, *	0.45	2.63, NS
17-11-91	2.28	0.54, NS	1.83	1.65, NS	0.038	0.95, NS	0.037	0.76, NS
15-3-92	1.84	2.43, NS	4.46	0.04, NS	0.082	2.54, NS	0.21	0.36, NS
8-4-92	0.68	0.89, NS	0.60	0.49, NS	0.112	5.92, **	0.67	1.87, NS
6-5-92	4.48	21.67,***	97.18	0.61, NS		-		-
26-6-92	0.80	9.41,***	7.50	0.65, NS	0.115	1.50, NS	0.17	1.35, NS

Table 5.9 (continued)

DATE	PO4						SiO4			
	P(Z)			Z			P(Z)		Z	
	Ms	F, p	MS	F, p	MS		F, p	F,	p	
17-3-91	0.028	1.74, NS	0.048	4.76, *	0.20		7.33, **	1.44	4.37, *	
27-3-91	0.006	12.28, **	0.076	0.01, NS	0.08		13.71, **	1.14	1.58, NS	
13-4-91	0.006	11.47,***	0.065	0.94, NS	0.02		13.33, **	0.30	0.42, NS	
13-5-91	0.009	4.68, **	0.044	0.06, NS	1.44		2.12, NS	3.05	0.24, NS	
7-6-91	0.044	1.85, NS	0.082	0.11, NS	3.48		3.73, *	12.98	1.84, NS	
12-7-91	0.058	2.99, *	0.173	1.38, NS	3.96		27.52,***	109	1.08, NS	
22-8-91	0.096	1.89, NS	0.182	0.27, NS	0.04		71.74,***	3.11	0.26, NS	
21-9-91	0.066	8.64, **	0.567	0.06, NS	0.02		13.82,***	0.32	0.27, NS	
9-10-91	0.068	1.47, NS	0.080	2.58, NS	0.08		3.59, *	0.28	0.46, NS	
17-11-91	0.064	1.64, NS	0.104	1.47, NS	0.05		3.81, *	0.18	21.99,***	
15-3-92	0.015	2.82, *	0.042	1.18, NS	0.25		4.74, *	1.19	3.02, NS	
8-4-92	0.072	1.68, NS	0.645	0.07, NS	0.01		25.01,***	0.33	8.79, **	
6-5-92	0.087	3.50, *	0.306	0.22, NS	0.01		25.38,***	0.29	0.46, NS	
26-6-92	0.052	4.92, *	0.210	0.85, NS	0.003		63.18,***	0.14	3.29, NS	

Table 5.10: Significant forward stepwise multiple regressions for abundance of 5 phytoplankton groups at the surface and near the bottom of the tidepools against the biotic and abiotic characteristics of the pools for the entire sampling period between June 1991 and September 1992. Independent variables are: PL = density of planktonic grazers; BE = density of benthic grazers; M<1 = density of small mussels; M1-2 = density of medium mussels; M>2 = density of large mussels; NO = nitrate+nitrite concentration; NH = ammonium concentration; PO = phosphate concentration; Si = silicate concentration; T = temperature; S = salinity; pH = pH; AL = macroalgal cover; H = height above chart datum; A = surface area; V = volume; F = flushing rate. Within each multiple regression, independent variables with significant partial F-values are shown in bold.

DEPENDENT VARIABLE	N	MODEL	R^2	F,	p
Total phytoplankton (surface)	168	=**11.52** -1.00(**Si**) +0.61(**NO**) +0.01(T) +0.03(S)	0.054	3.38,	*
Total phytoplankton (bottom)	106	=**6.60** +0.31(**M<1**) +0.54(NO) -1.43(**Si**) +0.07(**T**) -0.08(**S**) +0.82(**pH**) -0.01(F)	0.247	5.92,	***
Centric diatoms (surface)	144	=**3.60** -3.84(**NH**)	0.028	5.06,	*
Pennate diatoms (surface)	132	=**6.05** -0.12(PL) +0.26(**M<1**) +0.82(NO) -0.68(Si) +0.03(**AL**)	0.171	6.39,	***
Pennate diatoms (bottom)	132	=**4.36** -0.07(PL) +0.81(**M<1**) -0.60(**M1-2**) -1.25(**Si**) +0.06(S) +0.05(**AL**) +0.09(A) -0.38(V)	0.229	5.86,	***
Flagellates (surface)	168	=**9.79** +0.32(**M<1**) +0.30(NO) -0.87(**Si**) +0.13(**T**) -0.04(**F**)	0.259	12.69,	***
Flagellates (bottom)	168	=**10.81** +0.26(**M<1**) +0.82(NO) -1.81(PO) -0.92(**Si**) +0.10(**T**) -0.04(**F**)	0.220	8.83,	***
Nanoflagellates (surface)	132	=**16.00** -1.06(**BE**) -0.56(**M<1**) +5.36(**NH**) -2.10(**Si**) +3.89(PO) -0.06(S) +0.04(**AL**)	0.393	4.29,	***
Nanoflagellates (bottom)	132	=**16.18** -1.06(**M<1**) +4.75(**NH**) +5.46(**PO**) -2.29(Si) -0.08(S) +0.05(**AL**) +0.04(A) -0.01(F)	0.411	11.15,	***

Figure 5.1: Mean temperature, salinity and pH (± standard deviation) at the sea-surface (n = 2) and in tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

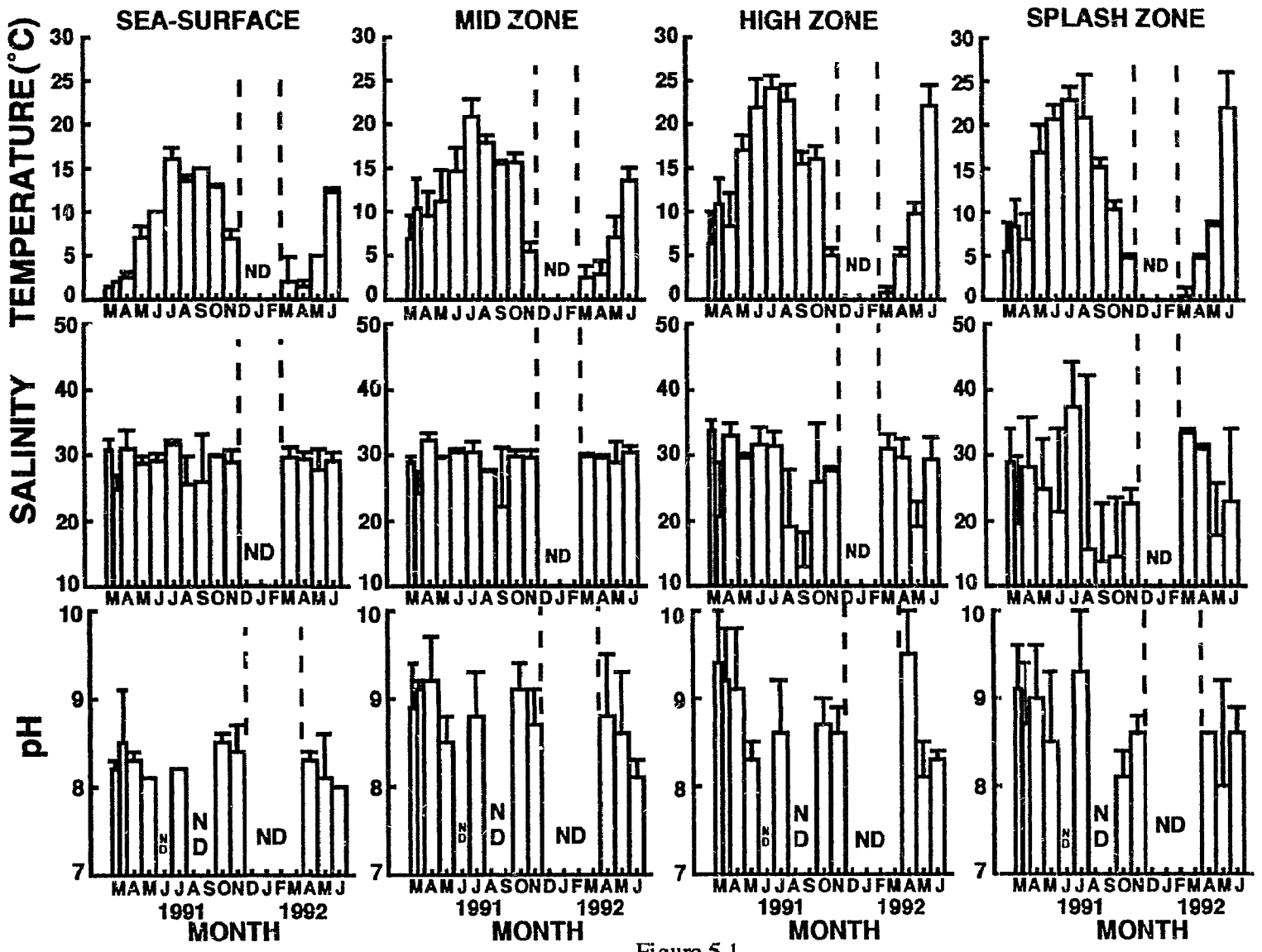
SEA-SURFACE
MID ZONE
HIGH ZONE
SPLASH ZONE
TEMPERATURE(°C)
SALINITY
pH
ND
MAMJJASONDJFMAMJ
1991
1992
MONTH

Figure 5.1

Figure 5.2: Mean abundance of total phytoplankton (± standard deviation) at the sea surface (n = 2) and at the surface and the bottom of tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

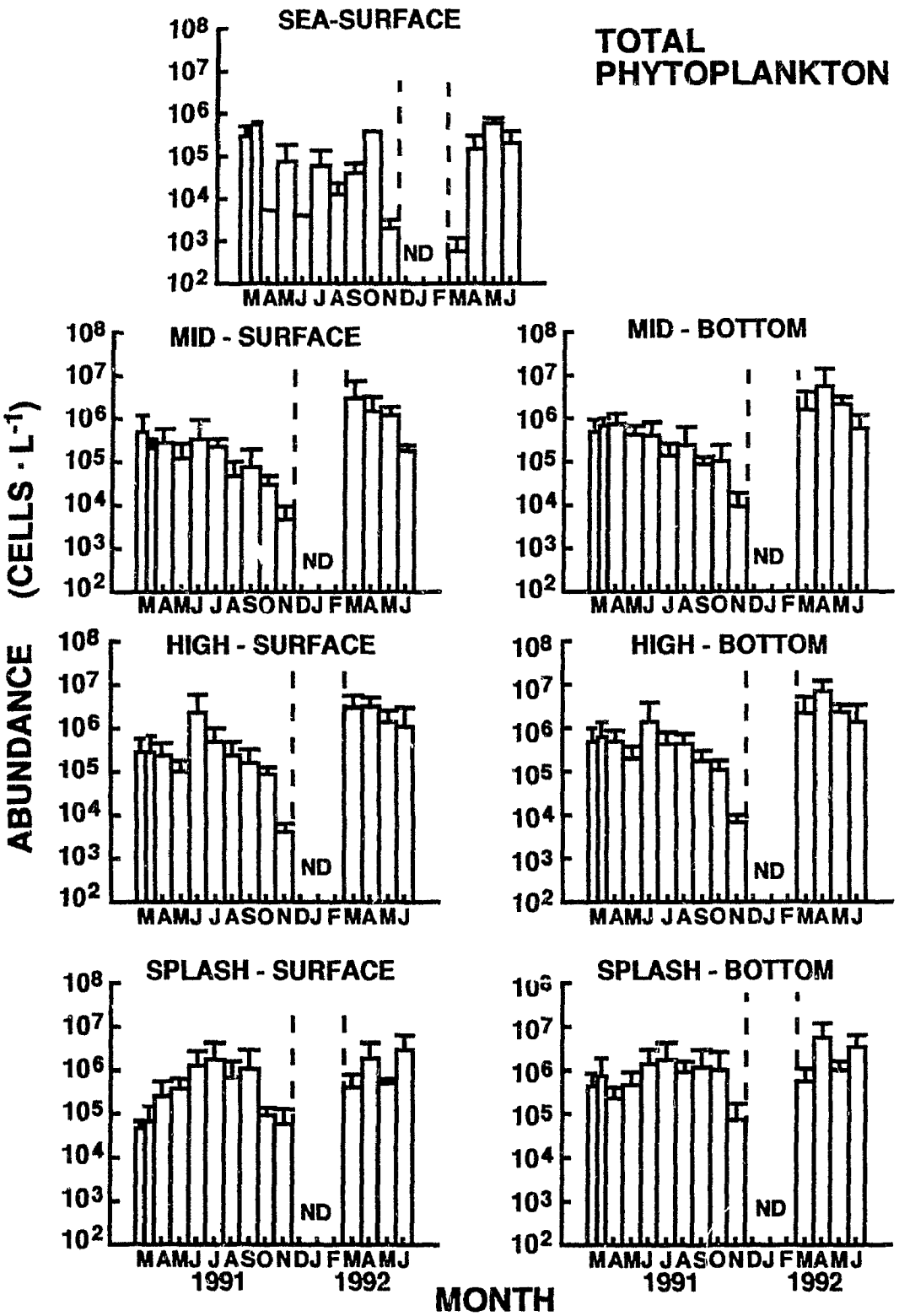
TOTAL PHYTOPLANKTON
SEA-SURFACE
MID - SURFACE
MID - BOTTOM
HIGH - SURFACE
HIGH - BOTTOM
SPLASH - SURFACE
SPLASH - BOTTOM
ABUNDANCE (CELLS · L-1)
ND
MAMJ JASONDJ FMAMJ
1991
1992
MONTH

Figure 5.2

Figure 5.3: Mean abundance of centric diatoms (± standard deviation) at the sea-surface (n = 2) and at the surface and the bottom of tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

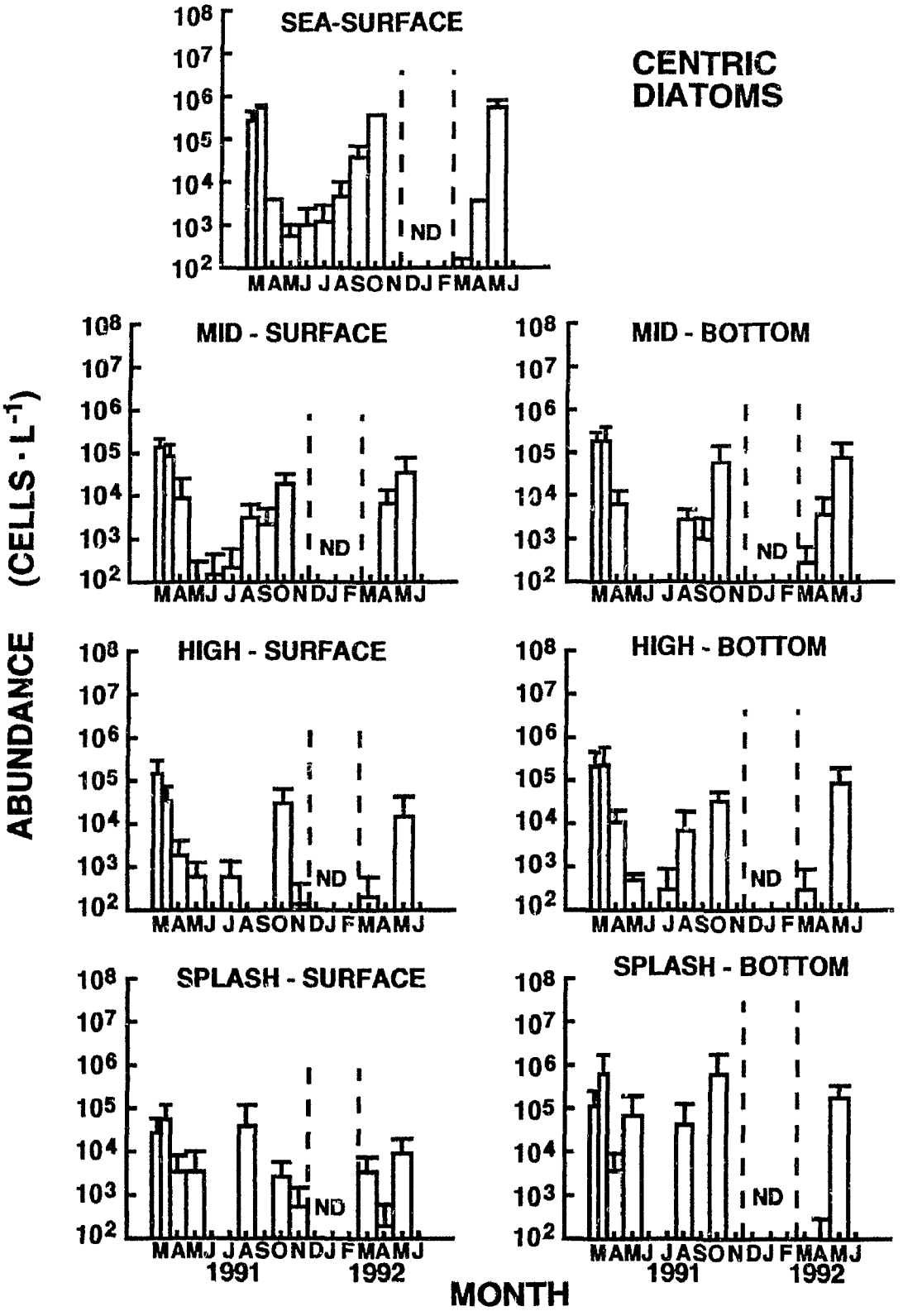
SEA-SURFACE
CENTRIC DIATOMS
MID - SURFACE
MID - BOTTOM
HIGH - SURFACE
HIGH - BOTTOM
SPLASH - SURFACE
SPLASH - BOTTOM
ABUNDANCE (CELLS · L-1)
MONTH
ND
M A M J J A S O N D J F M A M J
1991
1992

Figure 5.3

Figure 5.4: Mean abundance of pennate diatoms (± standard deviation) at the sea-surface (n = 2) and at the surface and the bottom of tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

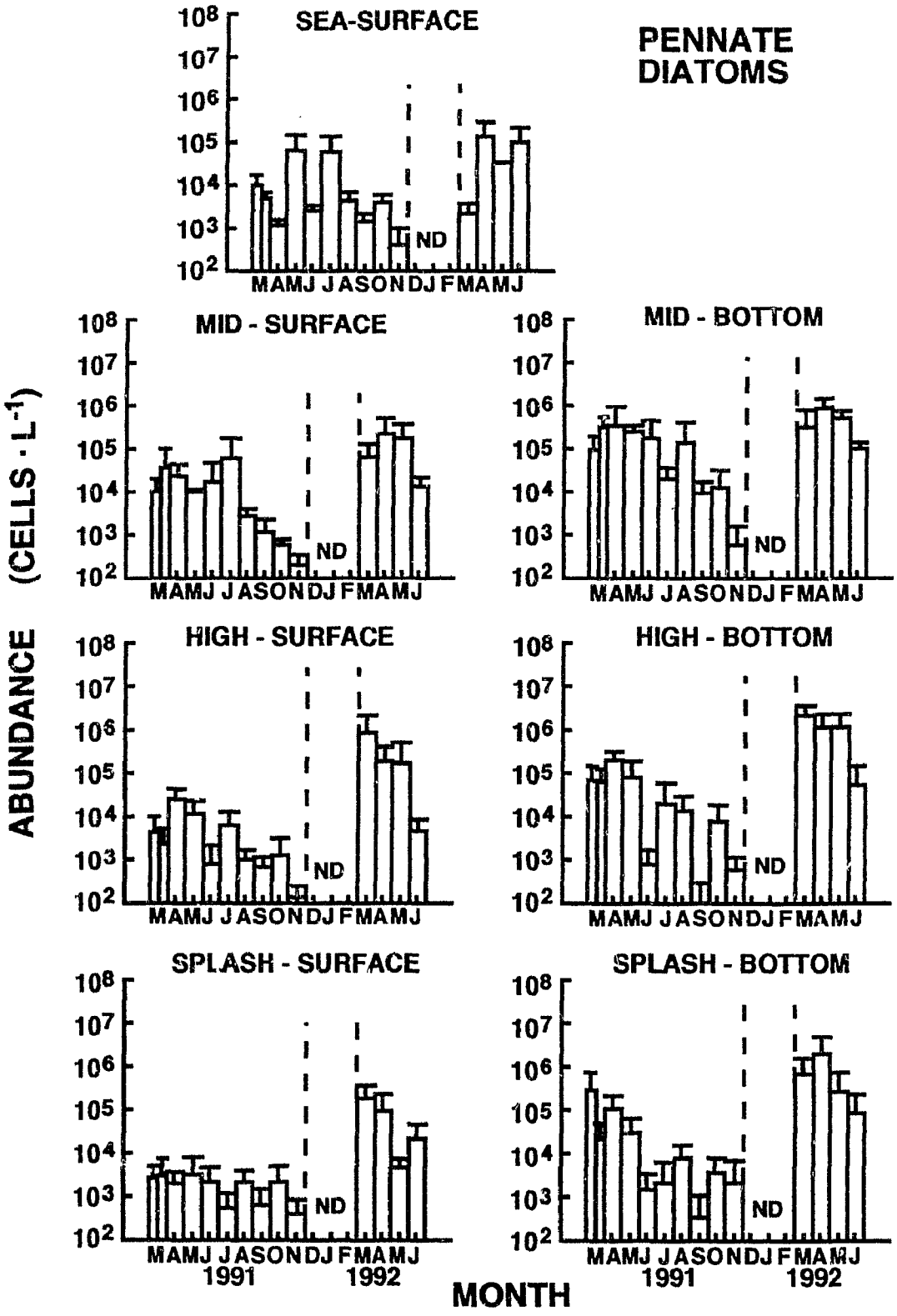
SEA-SURFACE
PENNATE DIATOMS
MID - SURFACE
MID - BOTTOM
HIGH - SURFACE
HIGH - BOTTOM
SPLASH - SURFACE
SPLASH - BOTTOM
ABUNDANCE (CELLS · L-1)
MONTH
ND
M A M J J A S O N D J F M A M J
1991
1992

Figure 5.4

Figure 5.5: Mean abundance of flagellates (± standard deviation) at the sea-surface (n = 2) and at the surface and the bottom of tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

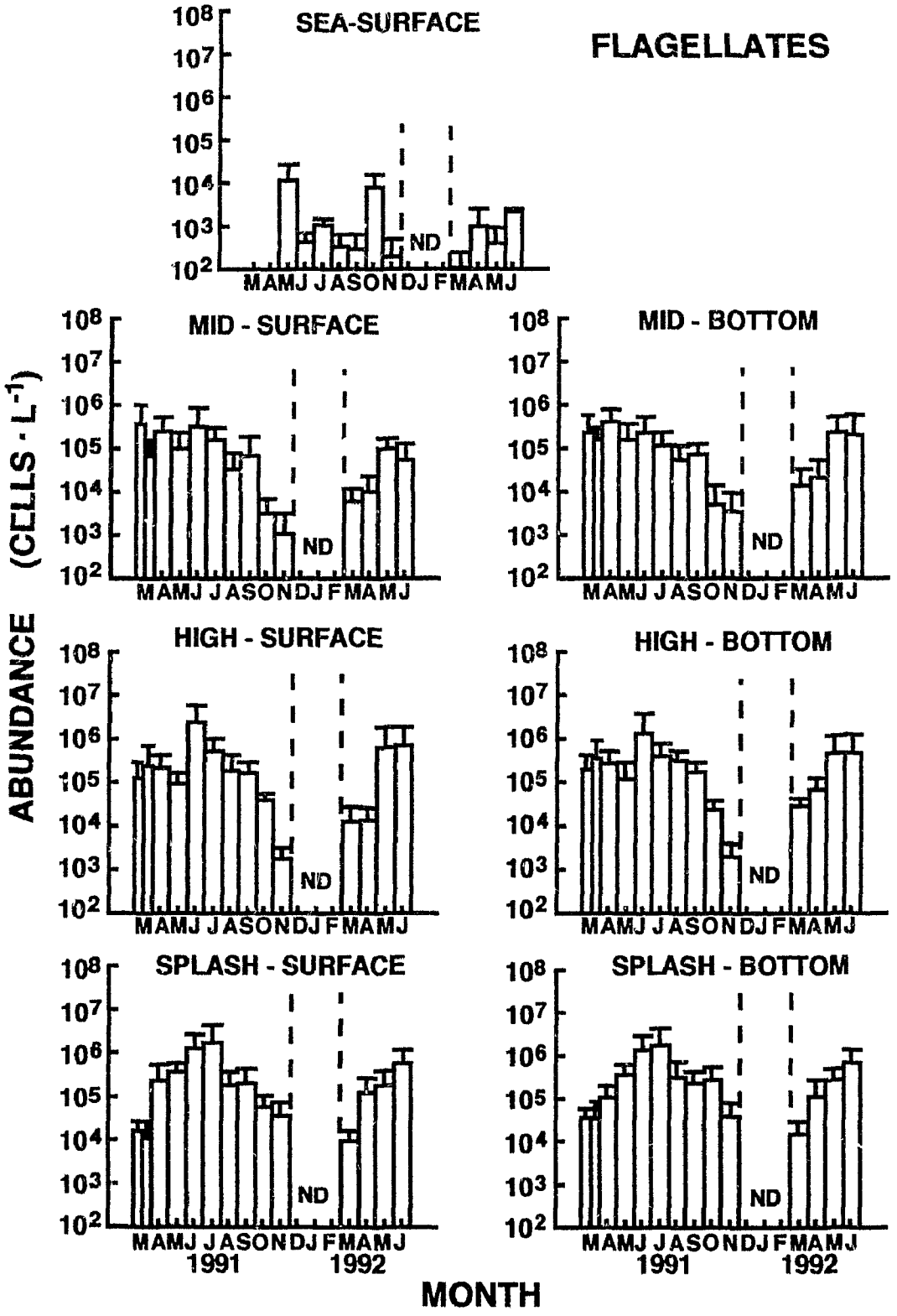
FLAGELLATES
SEA-SURFACE
MID - SURFACE
MID - BOTTOM
HIGH - SURFACE
HIGH - BOTTOM
SPLASH - SURFACE
SPLASH - BOTTOM
ABUNDANCE (CELLS · L-1)
MONTH
ND
M A M J J A S O N D J F M A M J
1991
1992

Figure 5.5

Figure 5.6: Mean abundance of nanoflagellates (±standard deviation) at the sea-surface (n = 2) and at the surface and the bottom of tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

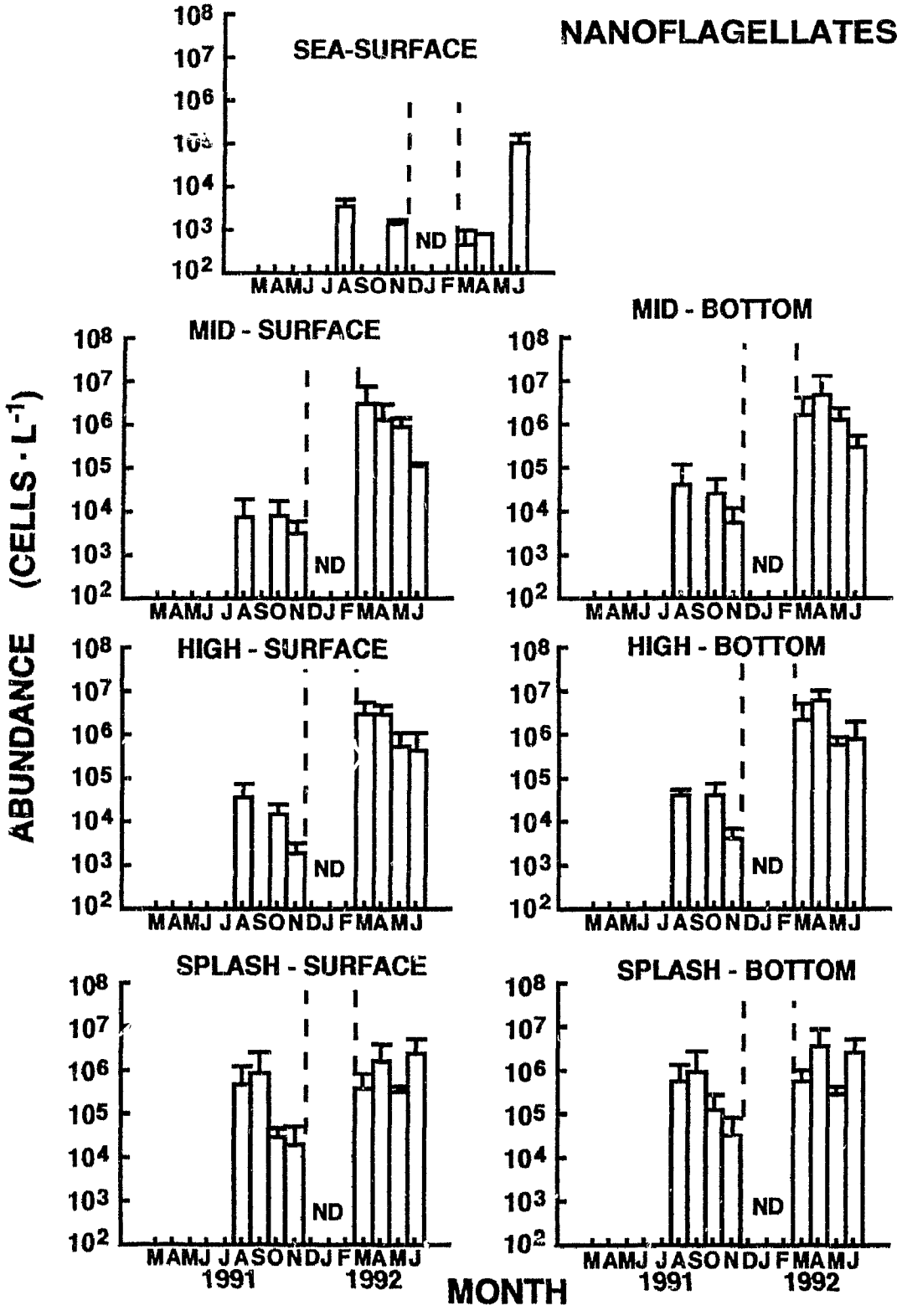
NANOFLAGELLATES
SEA-SURFACE
MID - SURFACE
MID - BOTTOM
HIGH - SURFACE
HIGH - BOTTOM
SPLASH - SURFACE
SPLASH - BOTTOM
ABUNDANCE (CELLS · L-1)
MONTH
ND
MAMJ JASONDJ FMAMJ
1991
1992

Figure 5.6

Figure 5.7: Magnitude of effects of each factor [Zone, Stratum, Pool (Zone)], as well as of the interaction terms [Zone * Stratum, Pool(Zone) * Stratum)], in the analyses of variance of the abundance of total phytoplankton and of each phytoplankton group for each sampling date. ND = no data.

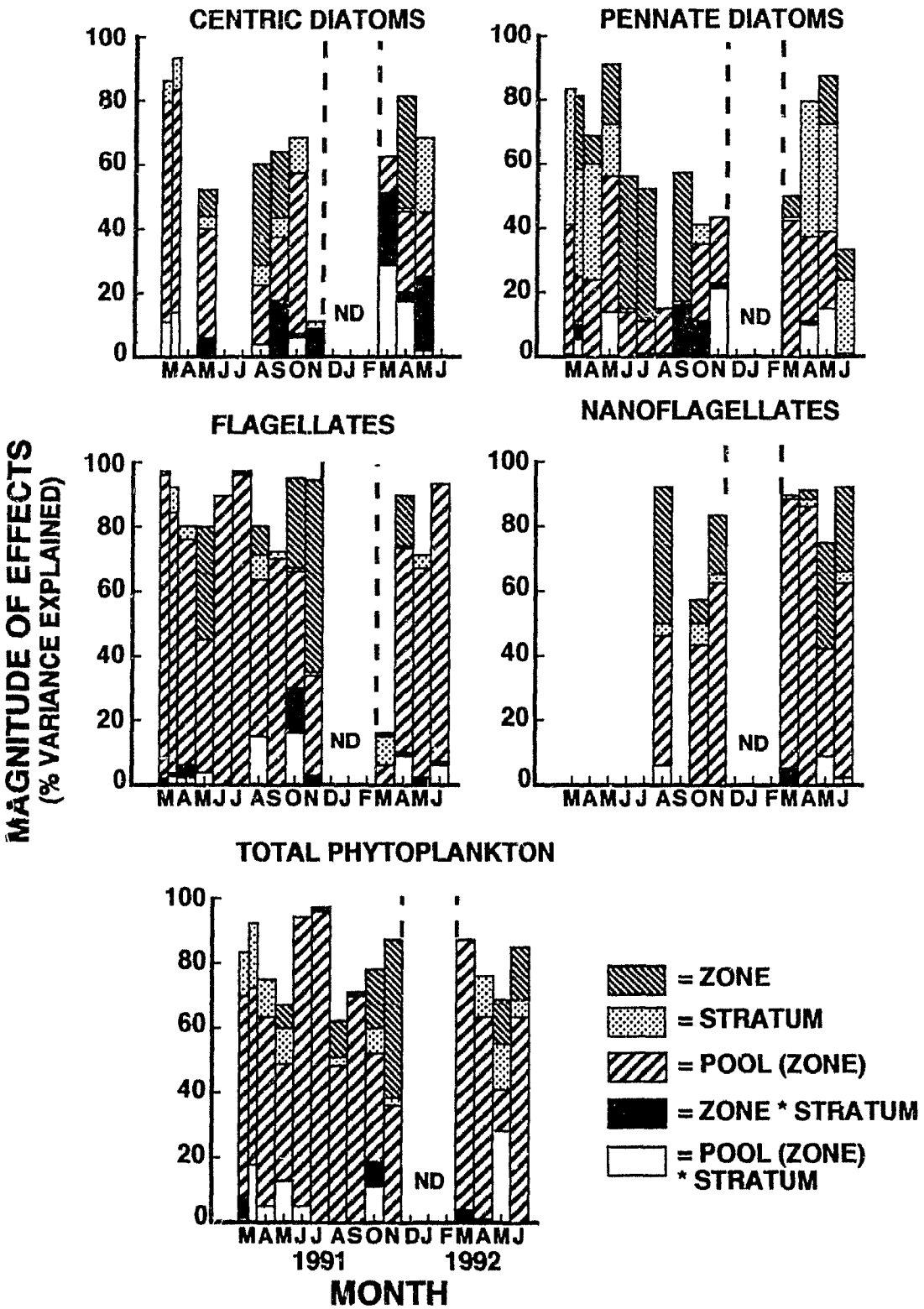
CENTRIC DIATOMS
PENNATE DIATOMS
FLAGELLATES
NANOFLAGELLATES
TOTAL PHYTOPLANKTON
MAGNITUDE OF EFFECTS
(% VARIANCE EXPLAINED)
100
80
60
40
20
0
ND
M A M J J A S O N D J F M A M J
1991
1992
MONTH
= ZONE
= STRATUM
= POOL (ZONE)
= ZONE * STRATUM
= POOL (ZONE)
* STRATUM

Figure 5.7

Figure 5.8: Mean density of planktonic and benthic micrograzers (±standard deviation) at the sea-surface (n = 2) and in tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and April and June 1992. ND = no data.

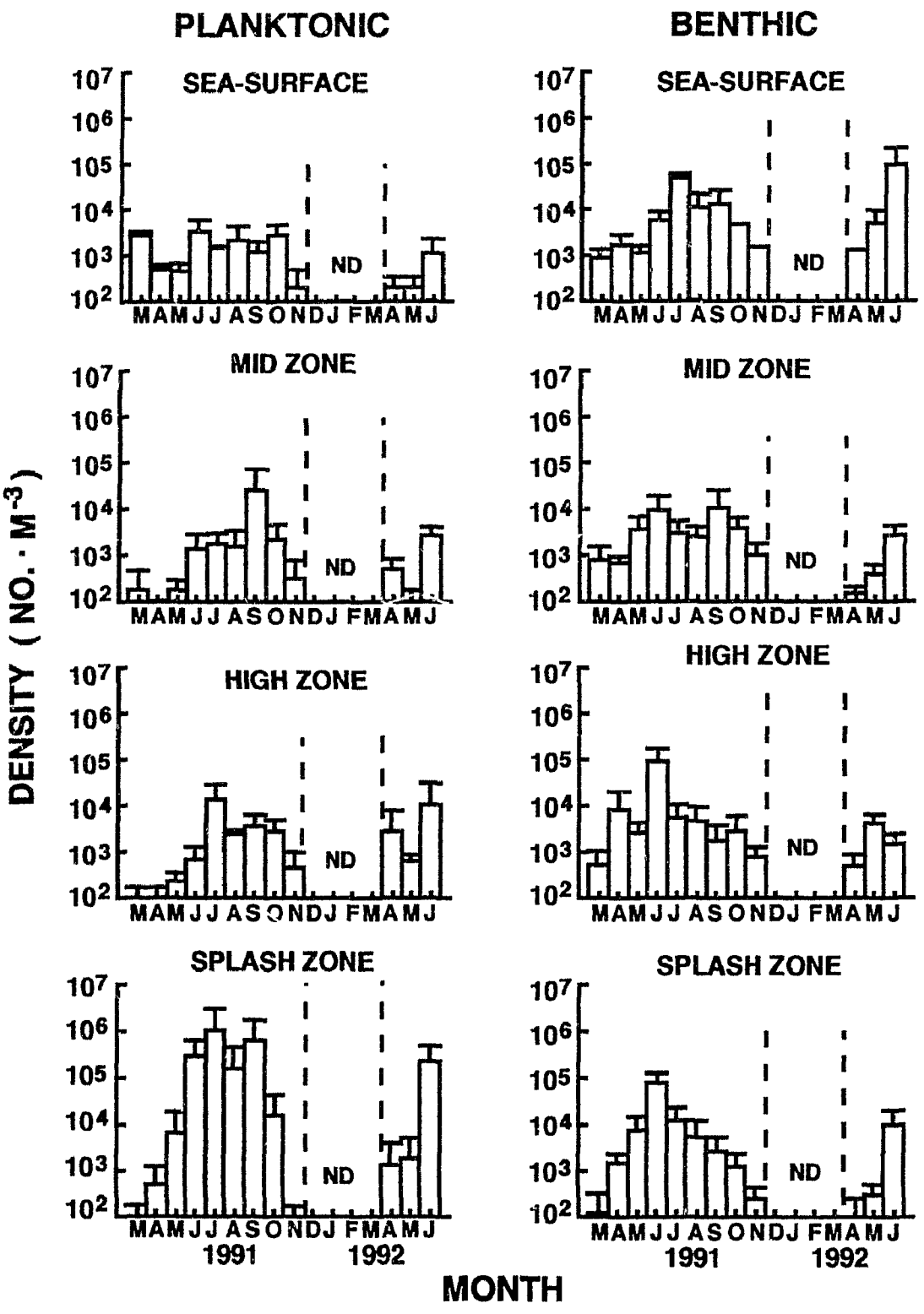
PLANKTONIC
BENTHIC
SEA-SURFACE
MID ZONE
HIGH ZONE
SPLASH ZONE
DENSITY (NO. · M-3)
10^7
10^6
10^5
10^4
10^3
10^2
ND
MAMJJASONDJFMAMJ
1991
1992
MONTH

Figure 5.8

Figure 5.9: Mean density of small, medium and large mussels in tidepools in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between June and October 1991 and in May and June 1992. ND = no data.

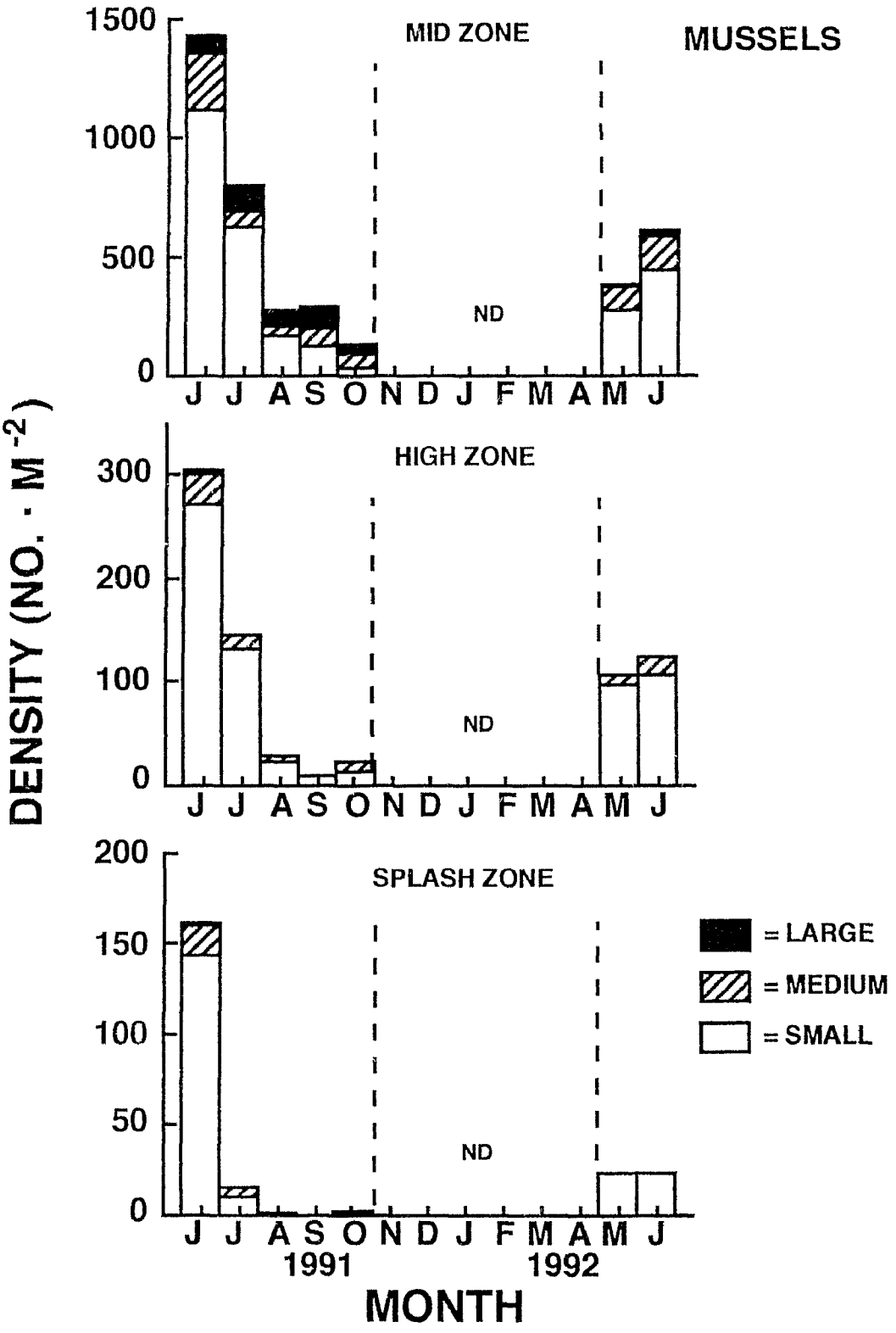
MUSSELS
MID ZONE
1500
1000
500
0
ND
J J A S O N D J F M A M J
HIGH ZONE
300
200
100
0
ND
J J A S O N D J F M A M J
SPLASH ZONE
200
150
100
50
0
ND
J J A S O N D J F M A M J
1991
1992
MONTH
DENSITY (NO. · M-2)
= LARGE
= MEDIUM
= SMALL

Figure 5.9

Figure 5.10: Mean concentration of nitrate+nitrite and ammonium (±standard deviation) at the sea-surface (n = 2) and in tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

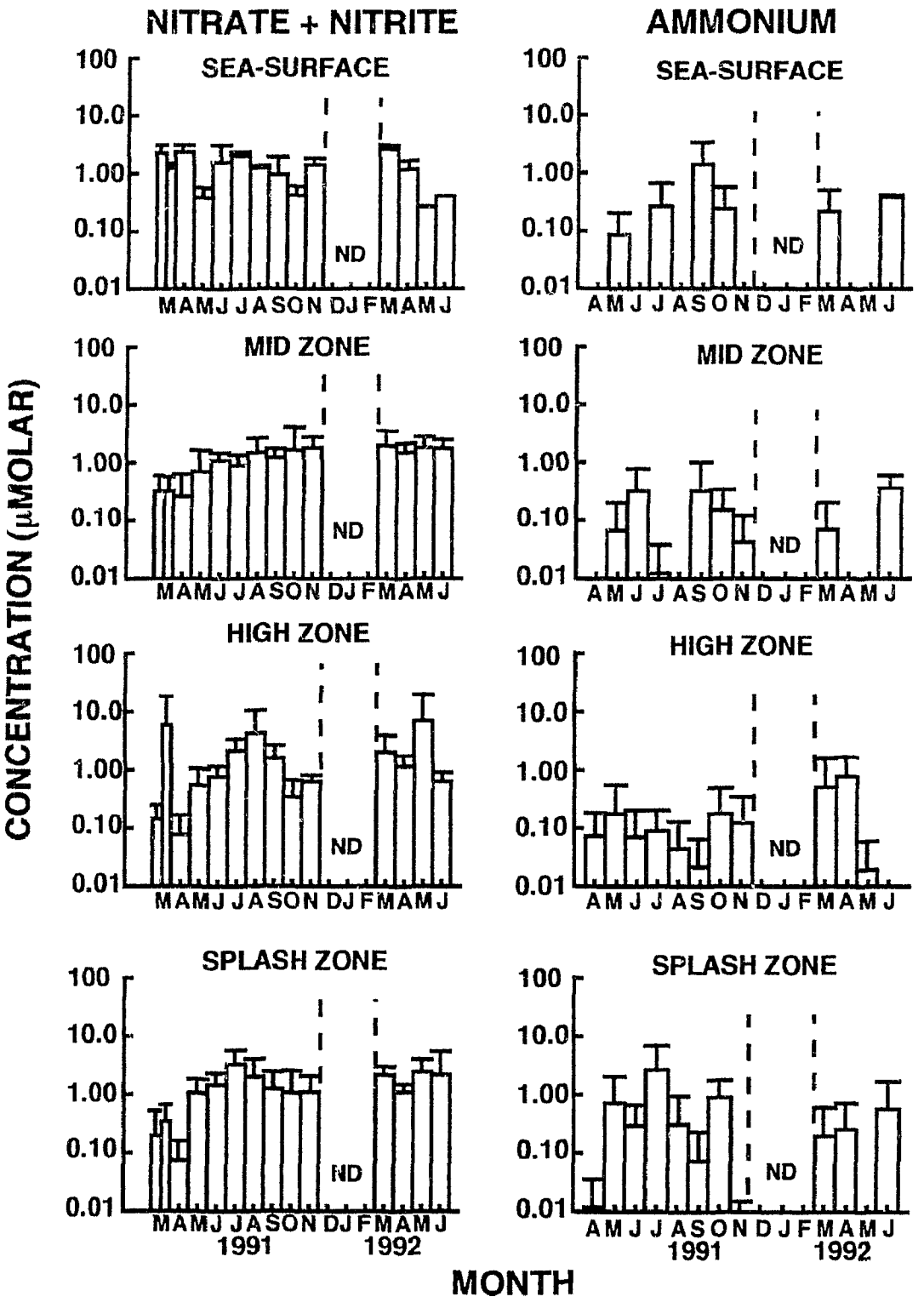
NITRATE + NITRITE
AMMONIUM
SEA-SURFACE
MID ZONE
HIGH ZONE
SPLASH ZONE
CONCENTRATION (μMOLAR)
100
10.0
1.00
0.10
0.01
ND
M A M J J A S O N D J F M A M J
A M J J A S O N D J F M A M J
1991
1992
MONTH

Figure 5.10

Figure 5.11: Mean concentration of silicate and phosphate (±standard deviation) at the sea-surface (n = 2) and in tidepools (n = 4) in 3 intertidal zones (mid, high and splash) at Cranberry Cove, Nova Scotia, sampled at approximately monthly intervals between March and November 1991 and March and June 1992 (I sampled twice during the bloom in March 1991). ND = no data.

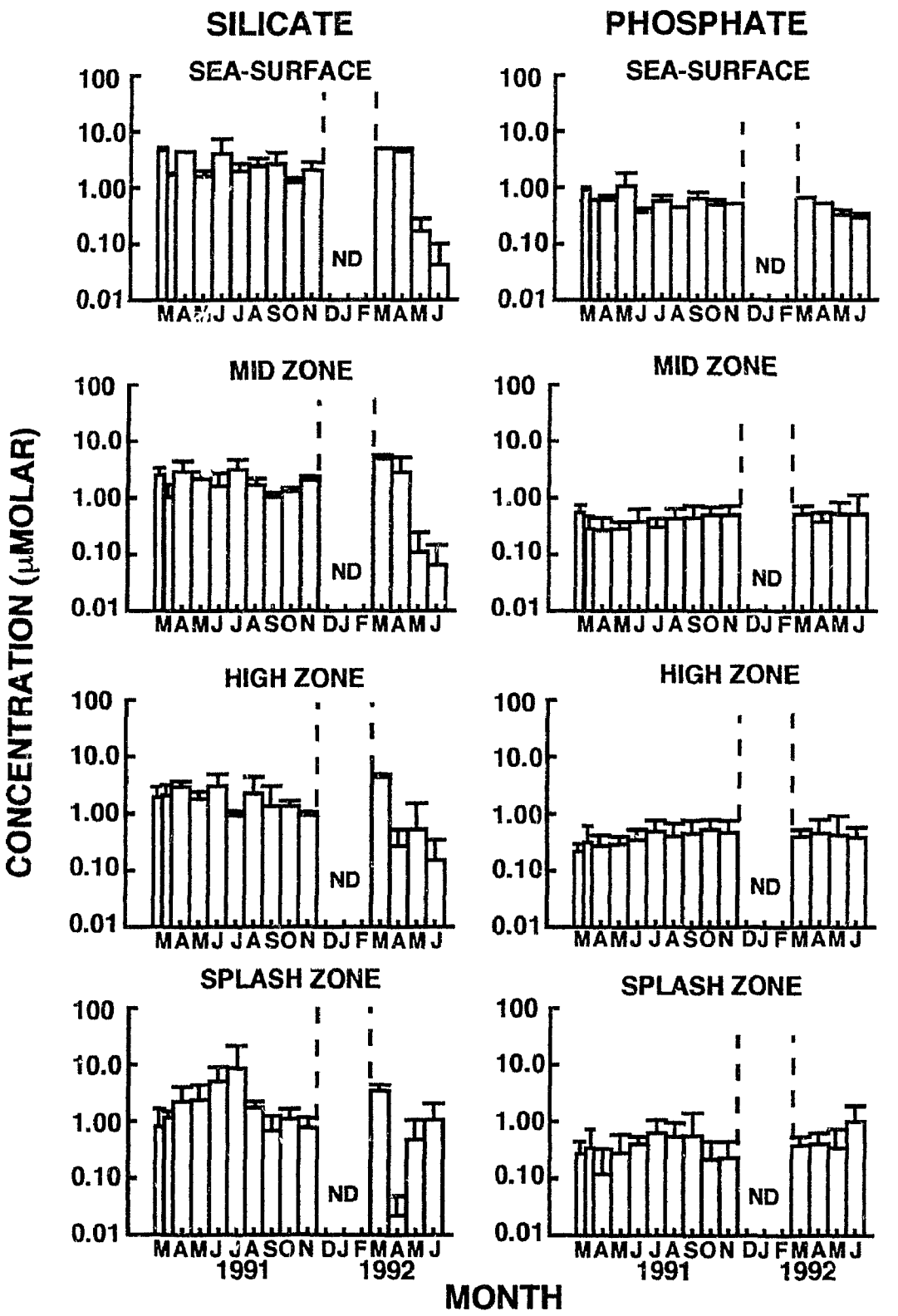
SILICATE
PHOSPHATE
SEA-SURFACE
MID ZONE
HIGH ZONE
SPLASH ZONE
CONCENTRATION (µMOLAR)
100
10.0
1.00
0.10
0.01
ND
MAMJ JASON DJ FMAMJ
1991
1992
MONTH

Figure 5.11

DISCUSSION

Phytoplankton succession at the sea-surface followed a pattern previously described for Nova Scotia (Côté & Platt 1983, Perry *et al.* 1989) and north temperate waters elsewhere (Harrison *et al.* 1983, Reid *et al.* 1990, Haigh *et al.* 1992, Weeks *et al.* 1993). The spring blooms in 1991 and 1992 were dominated by the centric diatoms *Chaetoceros* spp. and *Skeletonema costatum*, and the autumn bloom in 1991 was dominated by the centric diatom *Rhizosolenia*. After the spring blooms, the abundance of pennate diatoms, flagellates and nanoflagellates increased in May / June in both years.

In tidepools, flagellates and nanoflagellates were the numerically dominant groups of phytoplankton throughout the sampling period. Centric diatoms were introduced into pools during the blooms and their abundance subsequently decreased. Since tidepools and splash pools are less turbulent environments than the surrounding seawater the difference in dominance patterns between the sea-surface and the tidepools is consistent with Margalef's proposal (1978) that under conditions of high turbulence centric and pennate diatoms should dominate, whereas under low turbulence flagellates should dominate (see also Kiørbe 1993 for review). Cryptomonads (the dominant flagellate in my study) are characterized as opportunistic with wide temperature and salinity tolerances and low nutrient requirements (Klaveness 1988), which also may explain their numerical dominance in tidepools.

I examined 3 sources of spatial variability of the phytoplankton assemblages of tidepools: (1) between strata (the surface and bottom of pools), (2) among intertidal zones, and (3) among pools within zones. The magnitude of variability between strata differed among phytoplankton groups and reflected the characteristics of individual life-forms. The largest number of significant differences between strata were detected for pennate diatoms, a group which is mostly benthic. On most dates, the factor stratum

accounted for 30-40% of the variance in the abundance of pennate diatoms. In all cases except on 27 March 1991, the abundance of pennate diatoms was greater at the bottom than at the surface of the pools. I detected fewer differences in abundance between strata for centric diatoms and nanoflagellates than for pennate diatoms, probably because centric diatoms are more buoyant and nanoflagellates are more motile than pennate diatoms. In most cases, centric diatoms and nanoflagellates were more abundant at the bottom of the pools, probably because of sinking. The fewest significant differences in abundance between strata were detected for flagellates, reflecting the relatively greater motility of this phytoplankton group.

I found little indication of intertidal zonation of phytoplankton assemblages in tidepools. Centric diatoms showed significant variation among zones on 2 sampling dates and pennate diatoms on 4 dates: both groups were more abundant in mid than high and/or splash pools. Flagellates showed variation among zones on 1 sampling date (most abundant in splash pools) and nanoflagellates on 2 dates. Dethier (1982) recorded zonation of diatoms (mainly pennates) along the intertidal gradient which appeared to reverse during the year. She observed diatom blooms in lower pools in summer and in higher pools in winter which she attributed to reduced grazer densities in those zones during those periods (Dethier 1982, Dethier 1984). As in my study, Metaxas & Lewis (1992) observed a decline in the abundance of centric diatoms in pools of increasing intertidal height. However, Metaxas & Lewis (1992) also observed an increase in the abundance of pennates with increasing intertidal height which was not evident in my study. The difference between the two studies could be the result of wave exposure: the site described in Metaxas & Lewis (1992) was very protected, whereas my site was very exposed. Dethier (1984) also observed less zonation of microalgae in the more exposed sites of her study.

Significant differences among zones in abiotic and biotic factors that may affect phytoplankton abundance were observed on some sampling dates, and some of these differences were consistent with differences in phytoplankton abundance. For example, centric diatoms were more abundant in the mid pools in August 1991 and April 1992, when these pools were colder than high and splash pools. However, silicate concentration was greater in mid pools in April 1992, suggesting that the increased abundance of centric diatoms in these pools also could have been due to increased nutrient levels there. Pennate diatoms were more abundant in mid pools in March 1991, possibly because the concentration of phosphate was greatest in mid pools at that time. Flagellates were most abundant in the splash pools in November 1991 where salinity was lowest, and nanoflagellates were most abundant in mid pools in May 1992 where pH was lowest. The few detected differences among intertidal zones in the abundance of phytoplankton suggest that these assemblages do not show vertical zonation. Since there were even fewer differences among zones in the abiotic and biotic factors that potentially regulate these assemblages, I suggest that variability in these factors does not adequately explain the little variability in abundance of phytoplankton on the vertical spatial scale.

Spatial variability in the abundance of phytoplankton among pools within intertidal zones was detected consistently for all phytoplankton groups on most sampling dates. For total phytoplankton, and for flagellates and nanoflagellates, up to 96% of the variance in abundance was explained by variability along the horizontal scale. For centric and pennate diatoms, variability within zones was at least as large as variability among intertidal zones, and on some dates larger. The biotic factors that could affect phytoplankton abundance also varied significantly within zones on most sampling dates. I have documented previously that the hyperbenthic and macrobenthic assemblages of

these pools exhibit large variability within zones, suggesting that individual pools are unique in the combination of their biotic and abiotic characteristics (Chapters 2 & 3). Therefore, the factors regulating phytoplankton assemblages in tidepools probably operate more at the scale of the individual pool rather than the intertidal zone.

Multiple regressions showed significant relationships of all but one group of phytoplankton (centric diatoms), both at the surface and the bottom of the pools, with some biotic and abiotic characteristics of the pools. The lack of relationships with the abundance of centric diatoms is probably because they are more transient residents in the pools (they are mainly introduced during blooms in the surrounding seawater) than the other groups. Nutrients showed significant relationships with the abundance of most phytoplankton groups. The relationship between the abundance of phytoplankton and the concentration of silicate was negative for all phytoplankton groups. For pennate diatoms, the relationship may be attributed to nutrient uptake. Since flagellates and nanoflagellates do not require silicate for growth, no direct mechanism for the relationship can be suggested. Unlike silicate, the relationships between the abundance of nanoflagellates and the concentration of phosphate and ammonium were positive.

Certain grazers also showed significant relationships with the abundance of phytoplankton. The abundance of all phytoplankton groups varied significantly with the density of small mussels, but there was only 1 significant relationship with each of medium-sized mussels and benthic micrograzers, and none with large mussels and planktonic micrograzers. The relationships between the abundance of pennate diatoms and flagellates and the density of small mussels were positive, suggesting that mussels in that size class are more abundant in pools where a potential food source is more abundant or that both phytoplankton and small mussels are responding positively to some other factor. However, the relationships between the abundance of nanoflagellates

and the density of small mussels and benthic micrograzers, and the relationship between pennate diatoms and medium-sized mussels were negative, suggesting that these grazers may be significantly removing these two groups of phytoplankton by feeding. The lack of significant relationships between the abundance of phytoplankton and the density of planktonic grazers and large mussels suggest that these factors are not important and/or that their importance may vary during the year. The role of planktonic grazers such as calanoid copepods, cladocerans and rotifers, in determining phytoplankton community structure of oceanic systems has not been demonstrated consistently (e.g. Deason 1980, Estep *et al.* 1990, Hansen & van Boekel 1991, Morales *et al.* 1991, but see Conover & Mayzaud 1984). In contrast, the abundance of phytoplankton in restricted water masses can be reduced substantially by mussel beds during one tidal cycle (e.g. Wright *et al.* 1982, Frechette *et el.* 1989, Asmus & Asmus 1991).

Fewer significant relationships were detected between the abiotic characteristics of the pools and the abundance of phytoplankton. Temperature and flushing rate were important factors for flagellates, and percentage cover of macroalgae for pennate diatoms and nanoflagellates. A positive relationship between temperature and the abundance of flagellates reflects the increase in abundance of this group in summer. A negative relationship between flushing rate and the abundance of flagellates reinforces the suggestion that they are the dominant phytoplankton group in tidepools because pools are low-turbulence environments. A positive relationship between pennate diatoms and macroalgae suggests that macroalgae enhance settlement of this group by increasing the surface area upon which pennate diatoms (especially epiphytic species) can settle (see Round 1971 for review).

In summary, I examined the sources of vertical and horizontal spatial variability of phytoplankton assemblages in tidepools. I did not detect strong patterns of zonation

in tidepools across the intertidal gradient, and the potential abiotic and biotic factors regulating these assemblages did not adequately describe the observed variability at this spatial scale. Conversely, a large amount of the variance in phytoplankton abundance was attributed to variability on the horizontal spatial scale, within zones. At this scale, the biotic characteristics of individual pools explained some of the variability in phytoplankton abundance, although abiotic factors did not appear as important. Certain components of the grazer communities of each pool explained some of the variance in phytoplankton abundance for all phytoplankton groups except centric diatoms. The nutrient regime also was an important factor for all groups although the relative importance of different nutrients varied among phytoplankton groups. This study underscores the importance of assessing the different sources of spatial variability in the successful explanation of patterns of community organization.

CHAPTER 6: Top-down and bottom-up regulation of phytoplankton assemblages in tidepools

INTRODUCTION

Plant communities are regulated by top-down factors such as herbivory and bottom-up factors such as nutrient concentrations. Top-down regulation occurs when plant community structure (species composition and abundance) depends upon activities at higher trophic levels, whereas bottom-up regulation occurs when the structure depends upon resource availability. The importance of top-down and bottom-up factors in community regulation has been studied most extensively in lake systems (see Kerfoot & Sih 1987 for reviews). Some experimental and modelling studies have shown that top-down factors are most important in determining algal biomass, concentration of chlorophyll *a*, and phytoplankton size-distribution, either directly through grazing or indirectly through increased nutrient supply by excretion (e.g. Lynch & Shapiro 1981, Vanni & Findlay 1990, Hansson 1992, Carpenter & Kitchell 1984). Other studies have shown that zooplankton grazing is not important in regulating phytoplankton biomass (e.g. Threlkeld 1988, McQueen *et al.* 1989) but rather that concentration of chlorophyll *a* is directly related to nutrient concentration (e.g. McQueen *et al.* 1989, Hansson 1992). Lynch & Shapiro (1981) showed that nutrient enrichment can result in shifts in numerical dominance of phytoplankton species. In an empirical model of top-down and bottom-up forcing on the trophic structure of oligotrophic and eutrophic lakes, McQueen *et al.* (1986) showed that phytoplankton production is determined primarily by nutrients and the effect of herbivores is dependent on herbivore size. It is becoming increasingly evident that the relative importance of top-down and bottom-up regulation of primary

producers in a given community probably varies with season, the structure of the food-web, and phytoplankton and grazer species composition (e.g. Vanni 1987, Vanni & Temte 1990, Hansson 1992). Hunter & Price (1992) provide a model of top-down and bottom-up community regulation which incorporates the inherent heterogeneity in natural systems.

In marine systems, the importance of nutrients and grazers in regulating phytoplankton abundance and community structure is well documented (see Harrison *et al.* 1983, Hecky & Kilham 1988, Reid *et al.* 1990, Gervais 1991, Morales *et al.* 1991, Wassman 1991 for reviews). However, the relative importance of these two factors still remains unclear, mainly because of the difficulty in conducting experimental manipulations in the ocean. Recently, Kivi *et al.* (1993) manipulated the nutrient regime and abundance of grazers in factorial experiments in enclosures in the Baltic Sea and found that the relative importance of bottom-up and top-down regulation of the phytoplankton assemblages varied with season.

Community organization of rocky intertidal shores has been studied extensively and the importance of top-down regulating factors is well established (e.g. Paine 1966, Dayton 1971, 1984, Connell 1972, 1983, Menge 1976, Lubchenco & Menge 1978, Petraitis 1983, 1987, Sousa 1984b, Underwood & Denley 1984, Jernakoff 1985). Filter-feeders such as mussels and barnacles are often the dominant space occupiers on these shores. They feed on phytoplankton, the abundance and species composition of which depends on the concentration of nutrients. However, the effect of nutrient availability in the regulation of rocky intertidal communities remains largely unknown. Menge (1992) suggested that this gap in our knowledge is partly the result of the difficulty in experimentally manipulating the concentrations of nutrients in these systems. On shores with colonies of seabirds, guano can be a source of increased

nutrients (Ganning & Wulff 1969, Bosman & Hockey 1986) and a few descriptive studies have shown that the supply of guano may affect the abundance and community composition of macroalgae (Bosman & Hockey 1986, 1988, Wootton 1991). In an unreplicated experiment, Bosman *et al.* (1986) observed an increase in chlorophyll *a* when they increased the supply of guano to the high intertidal zone of a rocky shore in South Africa.

In this chapter, I examine the relative effects of bottom-up and top-down factors on the composition and abundance of phytoplankton assemblages in tidepools on a rocky intertidal shore. Tidepools facilitate the study of these processes because (1) they provide a habitat for plankton during the entire tidal cycle, (2) they have well defined boundaries, and (3) they are of manageable size to carry out manipulations. In Chapter 5, I found that phytoplankton assemblages of tidepools do not show a pronounced zonation along the intertidal gradient, but vary greatly among pools within intertidal zones in relation to the individual physical characteristics and biological processes within each pool. In this study, I manipulated the concentration of nutrients and the density of micrograzers in factorial experiments in tidepools. To my knowledge, this is the first study to examine experimentally the relative importance of bottom-up and top down factors in regulating the assemblages of primary producers on rocky intertidal shores.

MATERIALS AND METHODS

To examine the effects of nutrient addition and grazer removal on phytoplankton assemblages, 4 similar experiments were conducted in enclosures in tidepools in the high and splash zone at Cranberry Cove, near Halifax, Nova Scotia, Canada (44°28'N, 63°56'W). The physical characteristics of the 5 pools used in this study have been described in detail in Chapter 2: in this chapter, I refer to Pools 3 and 4 in the high zone in Table 2.1 as Pools 1 and 2; and to Pools 2, 3 and 4 in the splash zone in Table 2.1 as Pools 3, 4 and 5. The first experiment was conducted between 15 and 21 November 1992 in 4 replicate pools (Pools 1, 3, 4 and 5), the second between 31 May and 13 June 1993 in 1 pool (Pool 3), the third between 20 June and 3 July 1993 in 3 pools (Pools 1, 3 and 5), and the fourth between 1 and 15 August 1993 in 4 pools (Pools 1, 2, 3, and 5). The lower number of pools used in June and July 1993 was due to losses of experimental enclosures during storms. Four experimental treatments were set up in each pool in a factorial design: (1) grazers removed and nutrients enriched (G-N+); (2) grazers removed and nutrients at natural levels (G-No); (3) grazers at natural densities and nutrients enriched (GoN+); and (4) both grazers and nutrients at natural levels (GoNo). The water-column outside enclosures was used as a natural control to examine the artifactual effect of enclosures on the phytoplankton assemblages, as well as treatment efficacy. Two replicates per treatment or natural control were used in November 1992, and 3 replicates were used in June, July and August 1993. All treatments were randomly allocated to replicate enclosures; random locations within a pool were selected as natural controls.

The enclosures were made of clear acrylic pipe 12 cm in inner diameter (12.7 cm outer diameter) and 12 cm in height. At the base of the enclosure, a ring of closed-cell polyurethane foam was affixed to the pipe with silicone glue to provide an "o"-ring seal.

Bases for the enclosures were made of 3 cm high sections of sewer pipe (13 cm inner diameter) that were cemented to the rock bottom of the pools with an epoxy putty (A 788 Splash Zone Compound, Z*SPAR, Koppers Company Inc., CA). The enclosures were lowered slowly into the cemented bases to minimize disturbance of the water column and firmly attached to screws on the bases with cable ties. The top of each enclosure was loosely covered with a clear plastic sheet attached with the same putty. Each enclosure was positioned at 8 cm depth in the pools and contained 1 L of seawater. Incident light, measured using a Biospherical Instruments Inc. (San Diego, California) QSL-100 light meter, was 1,278 ± 70 μmol . m^{-2} . s^{-1} (mean ± standard deviation n = 2) on the rock adjacent to the enclosures, and 1,295 ± 764 and 1,411 ± 349 μmol . m^{-2} . s^{-1} in the water-column at mid depth inside and outside of the enclosures respectively.

The treatments were set up once the enclosures were in place. Micrograzers were removed by hand-pumping the seawater from the enclosure through a 60 μm net and then pouring the filtered water back into the enclosure. Nutrients (silicate, phosphate and nitrate) were enriched by adding small volumes (1-2 mL) of nutrient stocks (in the form of $Na_2SiO_3 \cdot 9H_2O$, $Na_2glyceroPO_4$ and $NaNO_3$) to reach the saturating nutrient levels in the ES medium of Harrison *et al.* (1980). The water in the enclosures was stirred to ensure homogeneous mixing of nutrients. A 60-mL sample of seawater was collected from each enclosure and control location at the beginning (immediately after the treatments were set up) and end of each experiment for nutrient analysis. These samples were collected stored and analyzed as described in Chapters 2 and 4 for silicate, phosphate, nitrate+nitrite and ammonium content. At the end of each experiment, after all sampling was completed, micrograzers were collected from each enclosure by hand-pumping all of the seawater as described in Chapter 3. Similarly, 1-

L samples were collected at each of the control locations in the pools to determine natural densities of micrograzers. Micrograzers were identified and enumerated as in Chapter 4.

A 20-mL sample of phytoplankton was collected with a polypropylene syringe at mid depth within each enclosure and from control locations. Phytoplankton samples were collected at the beginning and the end of each experiment on all dates, as well as at the mid points (i.e. after 7 days) of the experiments in July and August 1993. The phytoplankton samples were collected, processed and enumerated as in Chapter 4.

In order to test the efficacy of the treatment manipulations, I examined differences among treatments in the density of micrograzers at the end of each experiment, and in the concentration of nutrients at the beginning and end of each experiment, using 3-factor analyses of variance with 2 fixed factors, Grazer Density (natural, reduced) and Nutrient Concentration (natural, enriched), and 1 random factor, Pool (3 or 4 pools depending on date). In June 1993, I used a 2-factor analysis since I only sampled 1 pool. I also examined the effect of enclosures on the density of micrograzers at the end of each experiment, and on the concentration of nutrients at the beginning and end of each experiment, using 2-factor analyses of variance with Treatment (natural control, unmanipulated enclosure) as a fixed factor and Pool as a random factor. To assess the possibility of an increase in the concentration of nutrients in the water-column of the pools over the experimental period due to leakage of the enclosures, I examined changes in the concentration of nutrients in the natural controls over the same period using 2-factor analyses of variance with Time (beginning, end) as a fixed factor and Pool as a random factor. For the analyses, micrograzers were grouped as benthic and planktonic according to their functional morphology and mode of feeding (see Chapter 4).

For the statistical analyses, phytoplankton were assigned to 5 taxonomic groups: centric diatoms, pennate diatoms, cryptomonads, prasinophytes and chlorophytes. Because of large variability in phytoplankton abundance among pools (see Chapter 5) I examined differences among treatments in the percentage change in abundance of each group, calculated as: [(final abundance - initial abundance) / (initial abundance)] * 100. Percentage change in abundance was calculated for the entire experimental period, as well as separately for the first and second weeks of the experiments in July and August 1993. Using the same analyses as described above for the density of micrograzers and the concentration of nutrients, I examined differences in percentage change in abundance for each phytoplankton group at each sampling time. I also examined the effect of enclosures on percentage change in phytoplankton abundance.

For all statistical analyses, variables were ln (x+1)-transformed to successfully remove heterogeneity of variance when detected using Cochran's test. Since percentage change in phytoplankton abundance could be either positive or negative, I transformed the absolute values of variables and replaced the sign after transformation to maintain the direction of change. Although the original experimental design was orthogonal and balanced, I lost some replicate enclosures during the experiments in June, July and August 1993. To maintain the largest possible number of degrees of freedom at the expense of an unbalanced design, I carried out least-squares analyses of variance with a posteriori comparisons by Student-Newman-Keuls tests (SNK) on arithmetic means for treatments with equal sample sizes and on harmonic means for treatments with unequal sample sizes (Winer 1971). The null hypothesis was rejected at $p < 0.05$ in all statistical tests (ANOVA and SNK). In the analyses of variance the main effects and the interaction terms of the fixed factors (Grazer Density, Nutrient Concentration, Grazer Density * Nutrient Concentration) were tested against the residual error when the

interaction terms that included the random factor (Grazer Density * Pool, Nutrient Concentration * Pool and Grazer Density * Nutrient Concentration * Pool) were not significant at $p > 0.150$ (Underwood 1981b). For the level of replication used in this study, and for $\alpha = 0.05$ and $\beta = 0.20$, the minimum detectable difference between treatment means, calculated as in Zar (1984), was between 2 and 34 % change in abundance over the entire experimental period for most phytoplankton groups in the experiments done in November 1992, and July and August 1993 (except for pennates in July and prasinophytes in August when it was ca. 120 % for both groups) All analyses were carried out using SYSTAT v. 5.2 (Wilkinson 1989) on a Macintosh SE 30 computer.

To qualitatively describe the relative importance of top-down versus bottom-up factors in experiments with significant treatment effects, I calculated the Top-Down Index as given by Rosemond *et al.* (1993): [(G-No) - (GoNo)] / [(GoN+) - (GoNo)]. This index was calculated for each pool and compares the strength of top-down (numerator) and bottom-up (denominator) effects, where the parameters are the means of percentage change of phytoplankton abundance for each treatment. The index is equal to 1 when the strengths of top-down and bottom-up effects are equal, it is > 1 when top-down effects are stronger, and it is < 1 when bottom-up effects are stronger.

RESULTS

Experimental manipulations

(a) Experimental artifacts

Artifactual effects of the experimental enclosures on the percentage change in abundance of each phytoplankton group were examined by comparing changes in the natural control and the GoNo treatment as a procedural control. There were no differences in percentage change in abundance of any phytoplankton group between the natural and procedural controls in the experiments in November 1992 and June 1993. In July 1993, a few differences were detected between the 2 treatments but not in all pools: the change in abundance was less in the procedural control (where abundance decreased) than in natural control (where abundance increased) in most cases (Table 6.1). The largest number of differences between the 2 treatments were detected in August 1993, when the change in abundance of most phytoplankton groups was greater in the procedural control (where abundance increased in all cases) in most pools. For pennate diatoms and total phytoplankton, the effect of the enclosures on percentage change in abundance was significant in the second week of the experiment in August (8-14 d and 1-14 d), whereas for prasinophytes, it was significant only in the first week (1-7d).

The effects of experimental enclosures on the density of micrograzers at the end of the experiments, and on the concentration of nutrients both at the beginning and the end of each experiment also were examined by comparing natural and procedural controls (Figs. 6.1-6.4). The density of planktonic micrograzers was less in the procedural than the natural controls in the experiments in July and August 1993, but only in some pools (Figs. 6.3 & 6.4, Table 6.2). Conversely, the density of benthic

micrograzers was greater in the procedural than the natural controls in all pools in November 1992 (Fig. 6.1).

The largest number of differences in nutrient concentration between natural and procedural controls at the beginning of the experiments were recorded in June 1993, when the concentration of all manipulated nutrients was greater in the procedural than natural controls (Fig. 6.2, Table 6.3). However, there were no significant differences between the 2 treatments at the end of the experiment. In the other experiments, the few significant differences in the concentration of manipulated nutrients between natural and procedural controls were not consistent among nutrients, nor were they consistent between the beginning and end of the experimental periods among experiments (Figs. 6.1, 6.3 & 6.4). In July and August 1993, the concentration of ammonium (which was not manipulated) at the end of the experiment was greater in the procedural than the natural controls in 2 pools.

The concentrations of the manipulated nutrients in the natural controls varied little over the experimental periods; when they did vary significantly, they tended to decrease. In November 1992 and June 1993, no significant changes in the concentrations of nutrients were detected over the experimental period (in all cases, $F_{1,8} < 5.32$, $p > 0.05$ in November 1992, and $F_{1,4} < 7.71$, $p > 0.05$ in June 1993). Significant interactions between Time and Pool were detected for the concentration of silicate and phosphate in July (silicate: $MS_{error} = 0.007$, $F_{2,12} = 12.78$, $p = 0.001$; phosphate: $MS_{error} = 0.009$, $F_{2,12} = 118.1$, $p < 0.001$) and August 1993 (silicate: $MS_{error} = 0.073$, $F_{3,16} = 5.80$, $p < 0.01$; phosphate: $MS_{error} = 0.013$, $F_{3,16} = 6.14$, $p < 0.01$). The concentration of both these nutrients decreased between the beginning and the end of the experiments but not in all pools.

(b) Efficacy of manipulations

In all experiments, the density of planktonic and benthic micrograzers in most pools was less in the grazer removal treatments (G-No, G-N+) than in the treatments where grazers were not manipulated (GoNo, GoN+) (Figs. 6.1-6.4). However, there were no statistically significant differences between treatments in the density of planktonic micrograzers in November 1992 and August 1993, and in the density of benthic micrograzers in June and July 1993 (Table 6.4). In July 1993, the density of planktonic and benthic micrograzers was less in the grazer removal treatments than in the treatments where grazers were not manipulated, except in 1 pool (Pool 3), where density was greater in the grazer removal treatments (although the difference was not statistically significant). However, marine water-boatmen (corixids) were abundant in this pool, whereas due to my grazer manipulations they were reduced in the grazer removal treatments. These corixids are carnivorous and probably consumed more micrograzers in the treatments where grazers were not manipulated, resulting in lower grazer densities in these treatments than in the grazer removal treatments.

At the beginning of the experiments, the concentrations of the manipulated macronutrients (silicate, phosphate and nitrate) in all pools were significantly greater in the nutrient enrichment treatments than in the treatments where nutrients were not manipulated, except for the concentration of phosphate in November 1992 (Figs. 6.1-6.4, Tables 6.5-6.8). Differences in nutrient concentration between the 2 nutrient treatments were maintained until the end of the experiment for silicate and nitrate+nitrite in most pools in November 1992 (Table 6.5) and August 1993 (Table 6.8), and for phosphate in 1 pool in July 1993 (Table 6.7). The concentrations of ammonium in June 1993 and of phosphate in July 1993 were less in the grazer removal treatments than in treatments where grazers were not manipulated at the end of the experiment in 1 pool.

Effects of grazer density and nutrient concentration on the abundance of phytoplankton

The effects of grazer density and nutrient concentration on percentage change in abundance of the different phytoplankton groups varied over the period of individual experiments, and among pools and experiments. In November 1992 and June 1993, pennate diatoms and chlorophytes were the most abundant phytoplankton groups in the pools (Figs. 6.5 & 6.6). There were no significant effects of grazer density or nutrient concentration over the period of the experiment on any phytoplankton group in either November 1992 or June 1993 (Tables 6.9 & 6.10). In November 1992, although the percentage change in abundance of centric diatoms varied significantly among pools, SNK tests did not reveal significant differences among pool means.

In July 1993, pennate diatoms, cryptomonads, chlorophytes, and prasinophytes were abundant in most pools at the beginning of the experiment (Fig. 6.7). I detected significant effects of grazer density on the percentage change in abundance of most phytoplankton groups over the entire experimental period, but the effects of nutrient concentration only became significant in the second week of the experiment (Table 6.11). The effects of these 2 factors varied among phytoplankton groups and among pools. The change in abundance of pennate diatoms in the first week of the experiment was less in the grazer removal treatments (where abundance decreased) than in the treatments where grazers were not manipulated (where abundance increased), but only in 1 pool. However, in the second week, the increase in the abundance of this group was greater in the treatments with reduced grazer densities in all pools (grazer removal treatment for Pools 1 and 5, and treatment where grazers were not manipulated for Pool 3, see above). In the second week of the experiment. the increase in the abundance of

pennate diatoms was greater in the treatments where nutrients were not manipulated than in the nutrient enriched treatments, but only in 1 pool. The change in the abundance of cryptomonads in the first week of the experiment was greater in the treatments where grazers were not manipulated (where abundance increased) than in the grazer removal treatments (where abundance decreased) in 1 pool; in the second week, it was greater in the nutrient enriched treatments (where abundance increased) than in the treatments where nutrients were not manipulated (where abundance decreased) in the same pool. The increase in the abundance of prasinophytes over the entire experimental period was greater in the treatments with reduced grazer densities than those with natural grazer densities in 2 pools. The change in the abundance of this group in the second week of the experiment was greater in the nutrient enriched treatments (where abundance increased) than in the treatments where nutrients were not manipulated in 1 pool; however, there was a greater increase in abundance in the treatments where nutrients were not manipulated than in the nutrient enriched treatments in another pool. The change in the abundance of chlorophytes over the entire experimental period was less in the treatments with reduced grazer densities (where abundance decreased) than those with natural grazer densities (where abundance increased) in 2 pools, and it was greater in the nutrient enriched treatments (where abundance increased) than in the treatments where nutrients were not manipulated (where abundance decreased) in all pools. The change in the abundance of total phytoplankton in the second week of the experiment was greater in the treatments with reduced grazer densities (where abundance increased) than those with natural grazer densities (where abundance decreased) in 2 pools; there was a greater increase in abundance in the nutrient enriched treatments than in the treatments where nutrients were not manipulated in all pools.

In August 1993, although th same phytoplankton groups were present in the pools as in July 1993, their abundance was generally lower than in July (Fig. 6.8). There were significant effects of grazer density on the percentage change in abundance of all phytoplankton groups except prasinophytes (Table 6.12). Although these effects varied among pools and between weeks of the experiment for pennate diatoms and cryptomonads, the change in abundance of most groups was significantly greater in the treatments where grazers were not manipulated (where abundance generally increased) than in the grazer removal treatments (where abundance generally decreased) (except for cryptomonads in the first week of the experiment in 1 pool). The change in the abundance of pennate diatoms in the first week of the experiment was greater in the nutrient enriched treatments (where abundance increased) than in the treatments where nutrients were not manipulated (where abundance decreased) in 1 pool. There was also a significant effect of nutrient concentration on percentage change in the abundance of prasinophytes in the first week of the experiment, but the direction of the effect varied among pools. There was a significant interaction between Grazer Density and Nutrient Concentration in the percentage change in abundance of pennate diatoms in the first week of the experiment.

The Top-Down Index was used to compare qualitatively the strengths of top-down and bottom-up effects on the percentage change in abundance of the phytoplankton groups for the experiments in July and August 1993 (Fig. 6.9). In July, the values of this index ranged widely among pools but the mean values across all pools suggest that top-down effects were stronger than bottom-up effects for all phytoplankton groups throughout the experiment. In August, bottom-up effects were stronger than top-down effects for pennate diatoms throughout the experiment, whereas top-down effects were stronger than bottom-up effects for cryptomonads. For prasinophytes,

bottom-up effects were stronger than top-down effects in the first week of the experiment, but this was reversed in the second week. Over the entire experimental period, bottom-up effects were stronger than top-down effects for this group. For chlorophytes, top-down effects were stronger than bottom-up effects in the first week of the experiment, but this was reversed in the second week. Over the entire experimental period, top-down effects were stronger than bottom-up effects for this group.

Table 6.1: Significant analyses of variance of percentage change in abundance of different phytoplankton groups between procedural controls (unmanipulated enclosures, treatment GoNo) and natural controls (C) in the experiments in November 1992 and June, July and August 1993. Degrees of freedom are: July 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 2, 9$; if $p_{TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 9$; if $p_{F\,TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 2$; August 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 3, 14$; if $p_{F\,TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 14$; if $p_{F\,TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 3$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$. MS = mean square. + = the factor Treatment was tested against the interaction Treatment * Pool.

DATE	GROUP	PERIOD (d)	ERROR MS	TREATMENT * POOL F, p	POOL F, p	TREATMENT F, p	COMPARISON
JUL 1993	PENNATES	1-14	28.54	5.36, *	1.93, NS	0.01, NS +	POOL 3: GoNo < C
	CRYPTOMONADS	1-7	1.31	75.49, ***	22.14, ***	0.02, NS +	POOL 1: GoNo > C
	CHLOROPHYTES	1-14	1.80	22.49, ***	44.41, ***	1.13, NS +	POOL 3: GoNo < C
	TOTAL	1-14	5.86	5.41, *	14.27, **	2.05, NS +	POOL 3: GoNo < C
AUG 1993	PENNATES	8-14	40.42	1.33, NS	0.14, NS	5.29, *	ALL POOLS: GoNo > C
	CRYPTOMONADS	1-7	7.37	8.35, **	4.95, *	1.65, NS +	POOLS 1, 2, 5: GoNo < C POOL 3: GoNo > C
	CRYPTOMONADS	8-14	16.35	1.51, NS	1.65, NS	8.13, *	ALL POOLS: GoNo > C
	CRYPTOMONADS	1-14	5.14	14.22, ***	9.50, **	0.70, NS +	POOLS 1, 3: GoNo > C POOL 5: GoNo < C
	PRASINOPHYTES	1-7	1.14	67.76, ***	83.89, ***	1.47, NS +	POOLS 2, 3: GoNo > C
	CHLOROPHYTES	1-7	7.86	1.72, NS	6.00, **	30.61, ***	ALL POOLS: GoNo > C
	CHLOROPHYTES	8-14	11.31	0.67, NS	3.12, NS	13.35, **	ALL POOLS: GoNo > C
	CHLOROPHYTES	1-14	8.46	0.85, NS	0.44, NS	67.93, ***	ALL POOLS: GoNo > C
	TOTAL	8-14	9.27	1.17, NS	2.82, NS	23.22, ***	ALL POOLS: GoNo > C
	TOTAL	1-14	5.33	4.56, *	1.99, NS	10.49, * +	POOLS 1, 2, 3: GoNo > C

Table 6.2: Significant analyses of variance of the nsity of micrograzers between procedural controls (unmanipulated enclosures, treatment GoNo) and natural controls (C) at the end of the experiments in November 1992, and June, July and August 1993. Degrees of freedom are: November 1992: $F_{TREATMENT * POOL}$, $F_{POOL} = 3, 8$; if $p_{F\ TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 8$; if $p_{F\ TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 3$; July 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 2, 9$; if $p_{F\ TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 9$; if $p_{F\ TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 2$; August 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 3, 14$; if $p_{F\ TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 14$; if $p_{F\ TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 3$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = the factor Treatment was tested against the interaction Treatment * Pool.

DATE	GROUP	ERROR MS	TREATMENT * POOL		POOL		TREATMENT		COMPARISON
			F.	p	F.	p	F.	p	
NOV 1992	BENTHIC	0.54	0.28.	NS	3.64.	NS	10.92.	*	ALL POOLS: GoNo > C
JUL 1993	PLANKTONIC	1.33	6.02.	*	12.45.	**	0.75.	NS +	POOL 1: GoNo < C
AUG 1993	PLANKTONIC	0.37	25.98.	***	70.45.	***	0.91.	NS +	POOLS 2, 3: GoNo < C

Table 6.3: Significant analyses of variance of the concentrations of nutrients between procedural controls (unmanipulated enclosures, treatment GoNo) and natural controls (C) at the beginning (BEG) or end of the experiments in November 1992, and June, July and August 1993. Degrees of freedom are: November 1992: $F_{TREATMENT \times POOL}$, $F_{POOL} = 3, 8$; if $p\ F_{TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 8$; if $p\ F_{TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 3$; June 1993: $F_{TREATMENT} = 1, 4$; July 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 2, 9$; if $p\ F_{TREATMENT \times POOL} > 0.150$, $F_{TREATMENT} = 1, 9$; if $p\ F_{TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 2$; August 1993: $F_{TREATMENT * POOL}$, $F_{POOL} = 3, 14$; if $p\ F_{TREATMENT * POOL} > 0.150$, $F_{TREATMENT} = 1, 14$; if $p\ F_{TREATMENT * POOL} < 0.150$, $F_{TREATMENT} = 1, 3$. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = the factor Treatment was tested against the interaction Treatment * Pool.

DATE	NUTRIENT	TIME	ERROR MS	TREATMENT * POOL F, p	POOL F, p	TREATMENT F, p	COMPARISON
NOV 1992	SILICATE	BEG	137	1.04, NS	2.31, NS	6.36, *	ALL POOLS: GoNo > C
JUN 1993	SILICATE	BEG	61.77	-	-	79.82, **	ALL POOLS: GoNo > C
	PHOSPHATE	BEG	1.14	-	-	42.17, **	ALL POOLS: GoNo > C
	NITRATE	BEG	1788	-	-	61.15, **	ALL POOLS: GoNo > C
JUL 1993	SILICATE	END	0.01	6.56, *	6.40, *	0.80, NS +	POOL 3: GoNo < C
	AMMONIUM	BEG	0.07	5.37, *	41.08, ***	0.14, NS +	POOL 3: GoNo > C POOL 5: GoNo < C
	AMMONIUM	END	0.06	7.86, *	12.09, **	5.57, NS +	POOLS 3, 5: GoNo > C
AUG 1993	SILICATE	END	0.03	6.14, **	13.49, **	0.57, NS +	POOL 1: GoNo > C POOLS 2, 5: GoNo < C
	PHOSPHATE	BEG	0.003	3.50, *	101.8, ***	0.60, NS +	POOL 1: GoNo > C POOL 2: GoNo < C
	PHOSPHATE	END	0.02	1.51, NS	2.19, NS	5.96, *	ALL POOLS: GoNo > C
	AMMONIUM	END	4.34	5.79, **	8.89, **	6.01, NS +	POOLS 3, 5: GoNo > C

Table 6.4: Analyses of variance of the density of micrograzers in the different treatments in the end of the experiments in November 1992 and June, July and August 1993. In November 1992, and July and August 1993, factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P); in June 1993, factors are Grazer Density (G) and Nutrient Concentration (N). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No = treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: November 1992: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 16; if $p_{FG*N*P,\ G*P,\ N*P} > 0.150$, $F_{G*N,\ G,\ N}$ = 1, 16; if $p_{FG*N*P,\ G*P,\ N*P} < 0.150$, $F_{G*N,\ G,\ N}$ = 1, 3; June 1993: F_{G*N}, F_G, F_N = 1, 7; July 1993: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 2, 14; if $p_{FG*N*P,\ G*P,\ N*P} > 0.150$, $F_{G*N,\ G,\ N}$ = 1, 14; if $p_{FG*N*P,\ G*P,\ N*P} < 0.150$, $F_{G*N,\ G,\ N}$ = 1, 2; August 1993: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 22; if $p_{FG*N*P,\ G*P,\ N*P} > 0.150$, $F_{G*N,\ G,\ N}$ = 1, 22; if $p_{FG*N*P,\ G*P,\ N*P} < 0.150$, $F_{G*N,\ G,\ N}$ = 1, 3.
*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

Table 6.4 (continued)

DATE	GROUP	ERROR	G * N * P		G * P		N * P		G * N	
		MS	F,	p	F,	p	F,	p	F,	p
NOV 1992	PLANKTONIC	0.50	0.55,	NS	1.89,	NS	1.84,	NS	0.45,	NS
	BENTHIC	0.10	1.16,	NS	4.57,	*	10.22,	**	0.12,	NS
JUN 1993	PLANKTONIC	0.79	-		-		-		0.05,	NS
	BENTHIC	0.45	-		-		-		0.36,	NS
JUL 1993	PLANKTONIC	2.56	0.50,	NS	3.03,	NS	0.004,	NS	1.40,	NS
	BENTHIC	0.65	0.14,	NS	1.83,	NS	0.07,	NS	0.33,	NS
AUG 1993	PLANKTONIC	0.97	0.29,	NS	2.06,	NS	0.09,	NS	0.23,	NS
	BENTHIC	0.92	0.54,	NS	2.04,	NS	1.10,	NS	0.02,	NS

Table 6.4 (continued)

DATE	GROUP	P		G		N		COMPARISON
		F,	p	F,	p	F,	p	
NOV 1992	PLANKTONIC	10.41,	***	3.39,	NS	0.22,	NS	-
	BENTHIC	41.59,	***	0.44,	NS +	0.68	NS +	POOL 3: Go > G-
JUN 1993	PLANKTONIC	-		12.83,	**	0.97,	NS	Go > G-
	BENTHIC	-		2.49,	NS	2.95,	NS	-
JUL 1993	PLANKTONIC	17.20,	***	0.79,	NS +	1.12,	NS	POOL 1: Go > G-
	BENTHIC	11.88,	***	1.08,	NS	5.03,	NS	ALL POOLS: N+ > No
AUG 1993	PLANKTONIC	43.67,	***	1.00,	NS +	3.75,	NS	-
	BENTHIC	3.89,	*	0.65,	NS +	2.16,	NS	POOL 2: Go > G-

Table 6.5: Analyses of variance of the concentrations of nutrients in the different treatments at the beginning (BEG) and end of the experiment in November 1992. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No = treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 16; if p $_{FG*N*P, G*P, N*P}$ > 0.150, $F_{G*N, G, N}$ = 1, 16; if p $_{FG*N*P, G*P, N*P}$ < 0.150, $F_{G*N, G, N}$ = 1, 3. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

TIME	NUTRIENT	ERROR	G * N * P		G * P		N * P		G * N	
		MS	F,	p	F,	p	F,	p	F,	p
BEG	SILICATE	131	2.91,	NS	1.68,	NS	1.95,	NS	4.78,	NS +
	PHOSPHATE	0.03	0.60,	NS	0.55,	NS	0.29,	NS	1.82,	NS +
	NITRATE	1.00	2.46,	NS	1.96,	NS	1.02,	NS	1.85,	NS +
	AMMONIUM	0.34	3.07,	NS	1.66,	NS	2.25,	NS	0.02,	NS +
END	SILICATE	211	0.55,	NS	0.45,	NS	0.04,	NS	1.06,	NS +
	PHOSPHATE	0.13	0.63,	NS	0.38,	NS	0.25,	NS	0.08,	NS
	NITRATE	2.34	1.03,	NS	0.15,	NS	0.60,	NS	0.27,	NS +
	AMMONIUM	0.46	0.60,	NS	1.68,	NS	1.91,	NS	4.69,	*

Table 6.5 (continued)

TIME	NUTRIENT	P		G		N		COMPARISON
		F,	p	F,	p	F,	p	
BEG	SILICATE	3.02,	NS	0.03,	NS	362.7,	***	Go,G-: N+ > No
	PHOSPHATE	0.99,	NS	3.50,	NS +	0.88,	NS +	-
	NITRATE	1.34,	NS	3.07,	NS	92.11,	***+	Go,G-: N+ > No
	AMMONIUM	1.00,	NS	0.99,	NS	4.66,	NS	-
END	SILICATE	0.14,	NS	0.16,	NS	5.79,	*	N+ > No
	PHOSPHATE	1.72,	NS	0.09,	NS	4.26,	NS	-
	NITRATE	0.34,	NS	0.77,	NS +	14.21,	* +	N+ > No
	AMMONIUM	3.29,	*	0.01,	NS	0.21,	NS	Go,G-: N+ = No

Table 6.6: Analyses of variance of the concentrations of nutrients in the different treatments at the beginning (BEG) and end of the experiment in June 1993. The factors are Grazer Density (G) and Nutrient Concentration (N). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No = treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N}, F_G, F_N = 1, 7 . *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square.

TIME	NUTRIENT	ERROR	G * N		G		N		COMPARISON
		MS	F,	p	F,	p	F,	p	
BEG	SILICATE	501	2.09,	NS	1.93,	NS	91.90,	***	N+ > No
	PHOSPHATE	5.31	7.57,	*	0.28,	NS	16.80,	**	Go,G-: N+ > No
	NITRATE	$2.8x10^4$	1.50,	NS	0.37,	NS	43.93,	***	N+ > No
	AMMONIUM	0.31	0.06,	NS	1.06,	NS	0.74,	NS	-
END	SILICATE	0.06	1.12,	NS	3.77,	NS	0.07,	NS	-
	PHOSPHATE	0.004	0.05,	NS	1.37,	NS	0.00,	NS	-
	NITRATE	89.77	0.65,	NS	1.80,	NS	0.96,	NS	-
	AMMONIUM	0.12	0.00,	NS	5.82,	*	2.18,	NS	Go > G-

Table 6.7: Analyses of variance of the concentrations of nutrients in the different treatments at the beginning (BEG) and end of the experiment in July 1993. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No = treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 2, 14; if p $_{FG*N*P, G*P, N*P}$ > 0.150, $F_{G*N, G, N}$ = 1, 14; if p $_{FG*N*P, G*P, N*P}$ < 0.150, $F_{G*N, G, N}$ = 1, 2. *** = p < 0.001; ** = p < 0.01; * = p < 0.05, NS = p > 0.05. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

TIME	NUTRIENT	ERROR MS	G * N * P F.	p	G * P F.	p	N * P F.	p	G * N F.	p
BEG	SILICATE	0.19	0.40.	NS	0.75.	NS	0.38.	NS	0.58.	NS
	PHOSPHATE	0.02	0.68.	NS	1.15.	NS	110.1.	***	1.02.	NS
	NITRATE	0.30	1.14.	NS	1.63.	NS	2.10.	NS	0.12.	NS
	AMMONIUM	0.10	0.26.	NS	4.41.	*	5.98.	*	23.75.	* +
END	SILICATE	0.01	4.07.	*	2.76.	NS	1.60.	NS	0.00.	NS +
	PHOSPHATE	0.01	695.2.	***	652.0.	***	679.8.	***	1.02.	NS +
	NITRATE	1.04	0.39.	NS	0.73.	NS	1.01.	NS	0.23.	NS
	AMMONIUM	0.24	0.33.	NS	1.93.	NS	0.13.	NS	0.01.	NS

Table 6.7 (continued)

TIME	NUTRIENT	P		G		N		COMPARISON
		F,	p	F,	p	F,	p	
BEG	SILICATE	0.78,	NS	0.45,	NS	399.8,	***	ALL POOLS: N+ > No
	PHOSPHATE	45.38,	***	2.54,	NS	2.60,	NS +	POOLS 1, 5: N+ > No
	NITRATE	2.62,	NS	0.05,	NS +	306.0,	***	ALL POOLS: N+ > No
	AMMONIUM	41.18,	***	0.06,	NS +	0.28,	NS +	POOL 1: N+ < No
								POOL 3: Go > G-
END	SILICATE	4.08,	*	0.03,	NS +	2.78,	NS	ALL POOLS: N+ = No
	PHOSPHATE	629.7,	***	1.06,	NS +	1.12,	NS +	POOL 1: N+ > No
								POOL 2: N+ < No
								POOL 1: Go > G-
	NITRATE	2.41,	NS	0.48,	NS	0.28,	NS	-
	AMMONIUM	10.38,	**	0.03,	NS	1.84,	NS	-

Table 6.8: Analyses of variance of the concentrations of nutrients in the different treatments at the beginning (BEG) and end of the experiment in August 1993. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No = treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 22; if p $_{FG*N*P, G*P, N*P}$ > 0.150, $F_{G*N, G, N}$ = 1, 22; if p $_{FG*N*P, G*P, N*P}$ < 0.150, $F_{G*N, G, N}$ = 1, 3. *** = p < 0.001; ** = p < 0.01; * = p < 0.05, NS = p > 0.05. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

TIME	NUTRIENT	ERROR MS	G * N * P F.	p	G * P F.	p	N * P F.	p	G * N F.	p
BEG	SILICATE	0.02	0.40.	NS	0.31.	NS	6.53.	**	0.02.	NS
	PHOSPHATE	0.01	0.40.	NS	1.00.	NS	100.0.	***	1.04.	NS
	NITRATE	0.07	0.56.	NS	0.31.	NS	7.94.	**	0.02.	NS
	AMMONIUM	2.86	0.35.	NS	2.26.	NS	1.58.	NS	0.01.	NS
END	SILICATE	0.09	0.98.	NS	1.07.	NS	10.32.	***	0.15.	NS
	PHOSPHATE	0.12	0.53.	NS	0.43.	NS	0.55.	NS	2.03.	NS
	NITRATE	1.60	0.62.	NS	0.45.	NS	4.21.	*	0.27.	NS
	AMMONIUM	75.98	0.94.	NS	0.48.	NS	0.64.	NS	1.25.	NS

Table 6.8 (continued)

TIME	NUTRIENT	P		G		N		COMPARISON
		F,	p	F,	p	F,	p	
BEG	SILICATE	21.19,	***	0.97,	NS	1,031,	***+	ALL POOLS: N+ > No
	PHOSPHATE	81.41,	***	2.72,	NS	7.62,	NS +	ALL POOLS: N+ > No
	NITRATE	29.45,	***	0.85,	NS	393.9,	***+	ALL POOLS: N+ > No
	AMMONIUM	18.23,	***	0.00,	NS	0.51,	NS	-
END	SILICATE	11.82,	***	0.43,	NS	6.75,	NS +	POOLS 1,3,5: N+ > No
	PHOSPHATE	2.69,	NS	0.65,	NS	1.33,	NS	-
	NITRATE	2.59,	NS	0.13,	NS	7.94,	NS +	POOLS 1,3,5: N+ > No
	AMMONIUM	2.99,	NS	1.66,	NS	1.39,	NS	-

Table 6.9: Analyses of variance of the percentage changes in the abundance of phytoplankton in the different treatments during the experiment in November 1992. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 16; if $p_{FG*N*P, G*P, N*P} > 0.150$, $F_{G*N, G, N}$ = 1, 16; if $p_{FG*N*P, G*P, N*P} < 0.150$, $F_{G*N, G, N}$ = 1, 3. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

GROUP	ERROR	G * N * P		G * P		N * P		G * N		P		G		N	
	MS	F,	p	F,	p	F,	p	F,	p	F,	p	F,	p	F,	p
CENTRICS	17.27	0.47,	NS	0.18,	NS	1.30,	NS	0.31,	NS	3.94,	*	0.96,	NS	4.08,	NS
PENNATES	14.13	0.20,	NS	0.28,	NS	2.50,	NS	0.02,	NS	1.68,	NS	3.44,	NS	0.28,	NS +
CRYPTOMONADS	15.76	0.35,	NS	0.39,	NS	1.18,	NS	0.02,	NS	2.01,	NS	0.11,	NS	0.01,	NS
CHLOROPHYTES	16.19	0.34,	NS	2.43,	NS	1.40,	NS	0.07,	NS	2.45,	NS	0.15,	NS +	1.22,	NS
TOTAL	14.35	0.76,	NS	1.28,	NS	2.40,	NS	0.46,	NS	0.94,	NS	0.15,	NS	0.53,	NS +

Table 6.10: Analyses of variance of the percentage changes in the abundance of phytoplankton in the different treatments during the experiment in June 1993. The factors are Grazer Density (G) and Nutrient Concentration (N). Degrees of freedom are: F_{G*N}, F_G, F_N = 1, 7. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square.

GROUP	ERROR	G * N		G		N	
	MS	F,	p	F,	p	F,	p
PENNATES	47.43	0.09,	NS	0.17,	NS	1.42,	NS
CRYPTOMONADS	28.45	0.03,	NS	1.24,	NS	1.32,	NS
PRASINOPHYTES	30.37	0.08,	NS	0.47,	NS	0.13,	NS
CHLOROPHYTES	0.18	0.33,	NS	1.37,	NS	0.04,	NS
TOTAL	5.60	0.31,	NS	0.90,	NS	0.51,	NS

Table 6.11: Analyses of variance of the percentage changes in the abundance of phytoplankton in the first week (1-7 d), the second week (8-14 d) and over the entire experimental period (1-14 d) in the different treatments in the experiment in July 1993. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No treatments with naturalnutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 2, 14; if $p_{FG*N*P,\ G*P,\ N*P} > 0.150$, $F_{G*N,\ G,\ N}$ = 1, 14; if $p_{FG*N*P,\ G*P,\ N*P} < 0.150$, $F_{G*N,\ G,\ N}$ = 1, 2. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + G*N tested against G*N*P; G tested against G*P; N tested against N*P.

GROUP	PERIOD (d)	ERROR MS	G * N * P F,	p	G * P F,	p	N * P F,	p	G * N F,	p
PENNATES	1-7	21.37	0.04,	NS	4.92,	*	0.36,	NS	0.05,	NS
PENNATES	8-14	7.47	5.74,	*	20.17,	***	1.12,	NS	0.09,	NS +
PENNATES	1-14	16.07	1.08,	NS	0.67,	NS	0.87,	NS	0.19,	NS
CRYPTO MONADS	1-7	13.84	0.17,	NS	5.32,	*	0.26,	NS	1.42,	NS
CRYPTO MONADS	8-14	8.45	4.23,	*	0.80,	NS	5.32,	*	0.61,	NS +
CRYPTO MONADS	1-14	8.65	0.41,	NS	4.39,	**	6.73,	**	0.00,	NS
PRASINO PHYTES	1-7	11.93	1.20,	NS	1.02,	NS	1.16,	NS	0.24,	NS
PRASINO PHYTES	8-14	5.55	0.31,	NS	27.44,	***	5.92,	*	0.16,	NS
PRASINO PHYTES	1-14	17.79	2.85,	NS	14.39,	***	1.83,	NS	0.90,	NS +
CHLORO PHYTES	1-7	1.80	0.14,	NS	28.11,	***	0.17,	NS	0.08,	NS
CHLORO PHYTES	8-14	7.97	0.06,	NS	0.44,	NS	3.12,	NS	1.17,	NS
CHLORO PHYTES	1-14	5.33	2.48,	NS	11.13,	**	0.06,	NS	1.82,	NS +
TOTAL	1-7	4.09	1.02,	NS	13.06,	***	0.37,	NS	0.06,	NS
TOTAL	8-14	6.06	0.81,	NS	6.27,	**	2.16,	NS	0.04,	NS
TOTAL	1-14	5.36	0.49,	NS	7.60,	**	3.89,	*	1.02,	NS

Table 6.11 (continued)

GROUP	PERIOD (d)	P F,	p	G F,	p	N F,	p	COMPARISON
PENNATES	1-7	1.60,	NS	1.01,	NS +	0.87,	NS	POOL 5: Go > G-
PENNATES	8-14	9.35,	**	0.52,	NS +	4.60,	NS	POOLS 1, 5: Go < G- POOL 3: Go > G- POOL 5: N+ < No
PENNATES	1-14	12.05,	***	0.70,	NS	0.42,	NS	-
CRYPTO-MONADS	1-7	1.71,	NS	0.01,	NS +	0.53,	NS	POOL 1: Go > G-
CRYPTO-MONADS	8-14	9.43,	**	0.15,	NS	0.15,	NS +	POOL 1: N+ > No
CRYPTO-MONADS	1-14	5.56,	*	0.16,	NS +	0.02,	NS +	POOL 1: N+ > No
PRASINO PHYTES	1-7	2.91,	NS	0.56,	NS	0.69,	NS	-
PRASINO-PHYTES	8-14	80.47,	***	1.29,	NS +	0.98,	NS +	POOL 5: Go < G- POOL 1: N+ > No POOL 5: N+ < No
PRASINO-PHYTES	1-14	0.79,	NS	0.63,	NS +	0.06,	NS	POOL 3: Go > G- POOL 5: Go < G-
CHLORO-PHYTES	1-7	25.96,	***	0.85,	NS +	0.23,	NS	POOL 3: Go < G-
CHLORO-PHYTES	8-14	9.64,	*	0.30,	NS	2.81,	NS +	-
CHLORO-PHYTES	1-14	7.01,	**	0.02,	NS +	21.17,	***	POOL 3: Go < G- POOL 5: Go > G- ALL POOLS: N+>No
TOTAL	1-7	6.83,	**	0.37,	NS +	1.25,	NS	POOL 3: Go < G-
TOTAL	8-14	7.11,	**	0.13,	NS +	8.10,	*	POOL 1: Go < G- POOL 3: Go > G- ALL POOLS: N+>No
TOTAL	1-14	8.55,	**	0.26,	NS +	3.62,	NS +	POOL 3: Go < G- POOL 1: N+ > No

Table 6.12: Analyses of variance of the percentage changes in the abundance of phytoplankton in the first week (1-7 d), the second week (8-14 d) and over the entire experimental period (1-14 d) in the different treatments in the experiment in August 1993. The factors are Grazer Density (G), Nutrient Concentration (N) and Pool (P). Comparisons show the results from Student-Newman-Keuls comparisons of treatment means. [Go = treatments with natural density of grazers (GoNo and GoN+); G- = treatments with reduced density of grazers (G-No and G-N+); N+ = treatments with enriched nutrient concentrations (GoN+ and G-N+); No treatments with natural nutrient concentrations (GoNo and G-No)]. Degrees of freedom are: F_{G*N*P}, F_{G*P}, F_{N*P}, F_P = 3, 22; if $p_{FG*N*P,\ G*P,\ N*P} > 0.150$, $F_{G*N,\ G,\ N}$ = 1, 22; if $p_{FG*N*P,\ G*P,\ N*P} < 0.150$, $F_{G*N,\ G,\ N}$ = 1, 3. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = $p > 0.05$. MS = mean square. + = G*N tested against G*N*P; G tested against G*P; N tested against N*P.

GROUP	PERIOD	ERROR	G * N * P		G * P		N * P		G * N	
	(d)	MS	F_s	p	F_s	p	F_s	p	F_s	p
PENNATES	1-7	20.97	4.66,	*	0.33,	NS	0.42,	NS	0.08,	NS +
PENNATES	8-14	40.27	0.48,	NS	0.21,	NS	0.54,	NS	0.02,	NS
PENNATES	1-14	18.29	0.86,	NS	3.78,	*	0.91,	NS	0.50,	NS
CRYPTO MONADS	1-7	6.75	0.23,	NS	10.02,	***	0.60,	NS	0.84,	NS
CRYPTO MONADS	8-14	10.68	0.76,	NS	4.72,	*	1.24,	NS	5.25,	+
CRYPTO MONADS	1-14	12.59	1.29,	NS	1.89,	NS	1.12,	NS	2.39,	NS
PRASINO PHYTES	1-7	18.76	2.06,	NS	0.12,	NS	9.32,	***	0.12,	NS +
PRASINO PHYTES	8-14	32.59	2.44,	NS	1.08,	NS	1.19,	NS	0.55,	NS +
PRASINO PHYTES	1-14	30.13	4.79,	**	1.05,	NS	0.73,	NS	0.13,	NS +
CHLORO PHYTES	1-7	10.98	0.39,	NS	1.57,	NS	1.66,	NS	0.94,	NS
CHLORO PHYTES	8-14	5.36	0.22,	NS	10.14,	***	1.69,	NS	0.15,	NS
CHLORO PHYTES	1-14	1.25	1.00,	NS	0.48,	NS	0.97,	NS	0.79,	NS
TOTAL	1-7	10.11	1.10,	NS	1.23,	NS	0.82,	NS	1.71,	NS
TOTAL	8-14	4.43	1.00,	NS	10.16,	***	1.08,	NS	0.72,	NS
TOTAL	1-14	2.35	0.72,	NS	1.22,	NS	0.58,	NS	2.49,	NS

Table 6.12 (continued)

GROUP	PERIOD (d)	P F,	p	G F,	p	N F,	p	COMPARISON
PENNATES	1-7	2.71,	NS	4.39,	*	7.32,	*	POOL 5: Go > G- POOL 3: N+ > No GoN+ > G-No
PENNATES	8-14	0.88,	NS	0.20,	NS	0.00,	NS	-
PENNATES	1-14	4.80,	*	1.27,	NS +	1.10,	NS	POOL 5: Go > G-
CRYPTO-MONADS	1-7	18.16,	***	0.01,	NS +	0.79,	NS	POOL 1: Go < G- POOL 3: Go > G-
CRYPTO-MONADS	8-14	2.33,	NS	0.34,	NS +	0.01,	NS	POOL 1: Go > G-
CRYPTO-MONADS	1-14	7.69,	**	2.99,	NS	0.25,	NS	-
PRASINO-PHYTES	1-7	7.38,	**	0.81,	NS	0.03,	NS +	POOL 1: N+ > No POOL 2: N+ < No
PRASINO-PHYTES	8-14	8.20,	***	0.10,	NS	0.50,	NS	-
PRASINO-PHYTES	1-14	9.63,	***	0.02,	NS	0.78,	NS	-
CHLORO-PHYTES	1-7	13.89,	***	2.53,	NS	0.00,	NS	-
CHLORO-PHYTES	8-14	12.93,	***	0.85,	NS +	0.04,	NS	POOL 1: Go > G-
CHLORO-PHYTES	1-14	8.77,	***	6.68,	*	0.01,	NS	ALL POOLS: Go>G-
TOTAL	1-7	11.99,	***	0.58,	NS	0.29,	NS	-
TOTAL	8-14	12.03,	***	0.44,	NS +	0.46,	NS	POOL 1: Go > G-
TOTAL	1-14	2.76,	NS	5.16,	*	1.90,	NS	ALL POOLS: Go>G-

Figure 6.1: Mean density of micrograzers at the end (DAY 7) of the experiment and mean concentration of nutrients at the beginning (DAY 1) and end of the experiment in November 1992 in the different treatments (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 4).

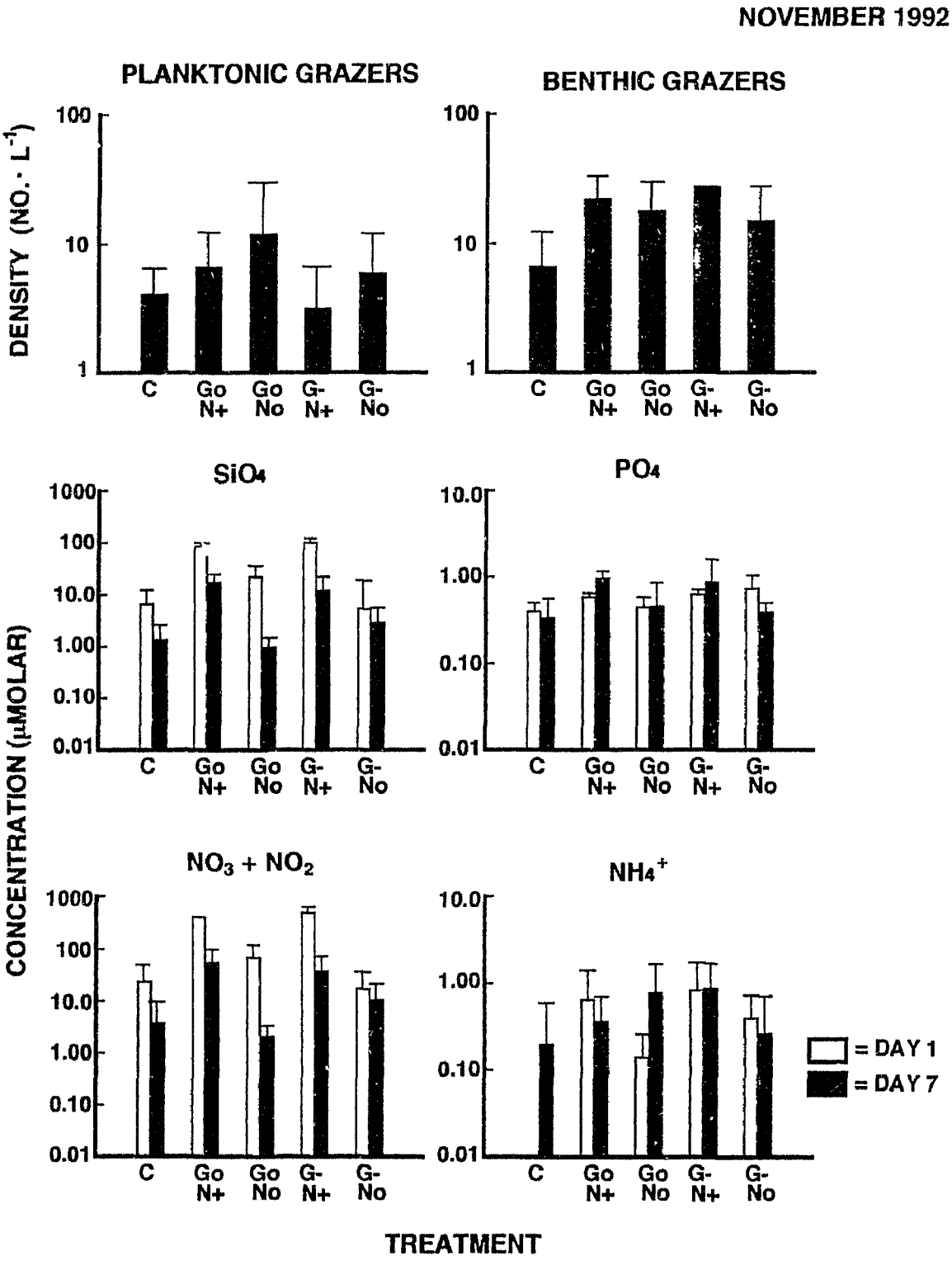
NOVEMBER 1992
PLANKTONIC GRAZERS
BENTHIC GRAZERS
DENSITY (NO. · L⁻¹)
100
10
1
C
Go N+
Go No
G- N+
G- No
SiO4
PO4
CONCENTRATION (µMOLAR)
1000
100
10.0
1.00
0.10
0.01
NO3 + NO2
NH4+
= DAY 1
= DAY 7
TREATMENT

Figure 6.1

Figure 6.2: Mean density of micrograzers at the end (DAY 14) of the experiment and mean concentration of nutrients at the beginning (DAY 1) and end of the experiment in June 1993 in the different treatments (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 2: G-No treatments; n = 3: all other treatments).

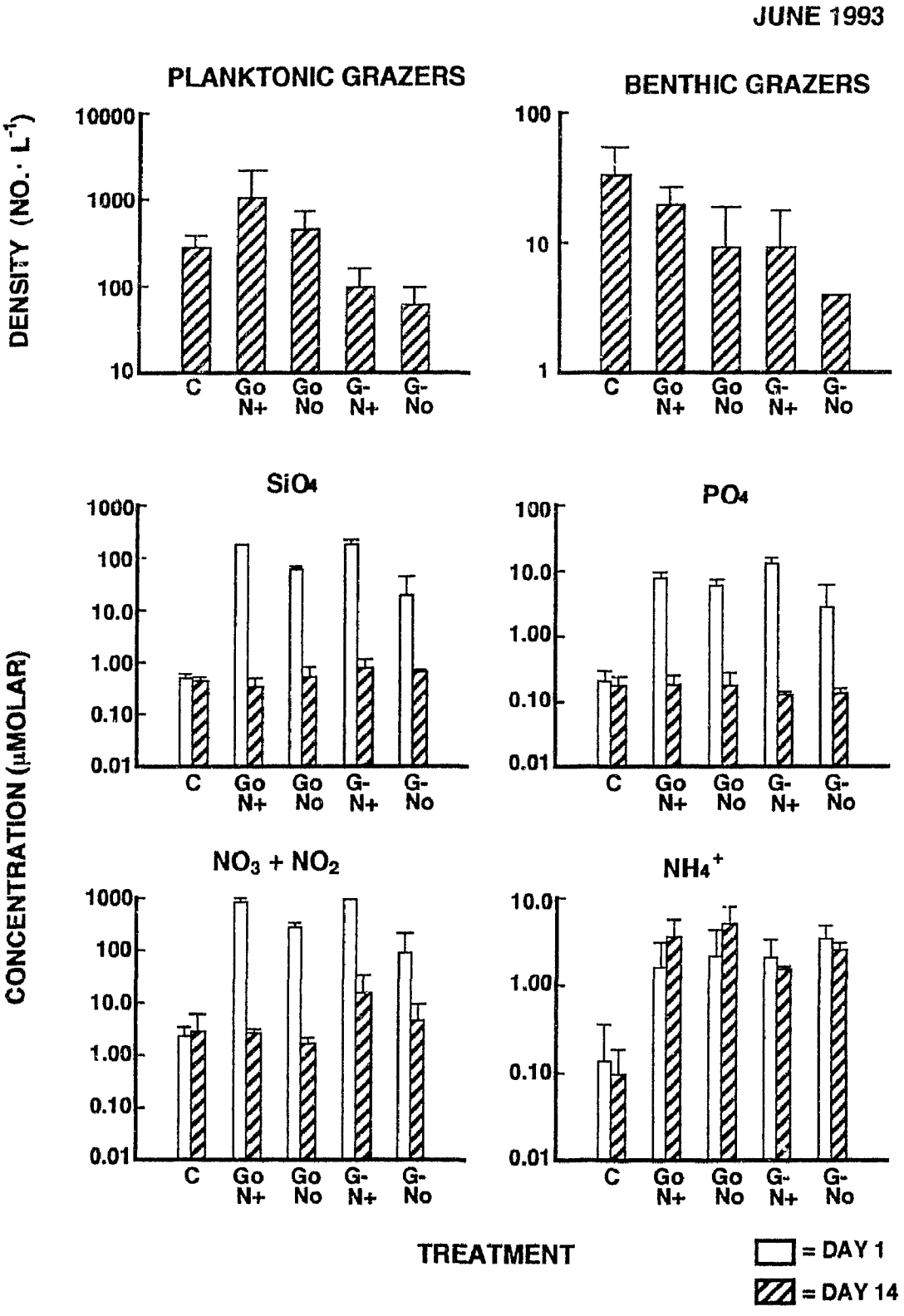
JUNE 1993
PLANKTONIC GRAZERS
BENTHIC GRAZERS
DENSITY (NO. · L⁻¹)
10000
1000
100
10
100
10
1
C
Go N+
Go No
G- N+
G- No
SiO4
PO4
NO3 + NO2
NH4+
CONCENTRATION (µMOLAR)
1000
100
10.0
1.00
0.10
0.01
TREATMENT
= DAY 1
= DAY 14

Figure 6.2

Figure 6.3: Mean density of micrograzers at the end (DAY 14) of the experiment and mean concentration of nutrients at the beginning (DAY 1) and end of the experiment in July 1993 in the different treatments (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 3).

JULY 1993

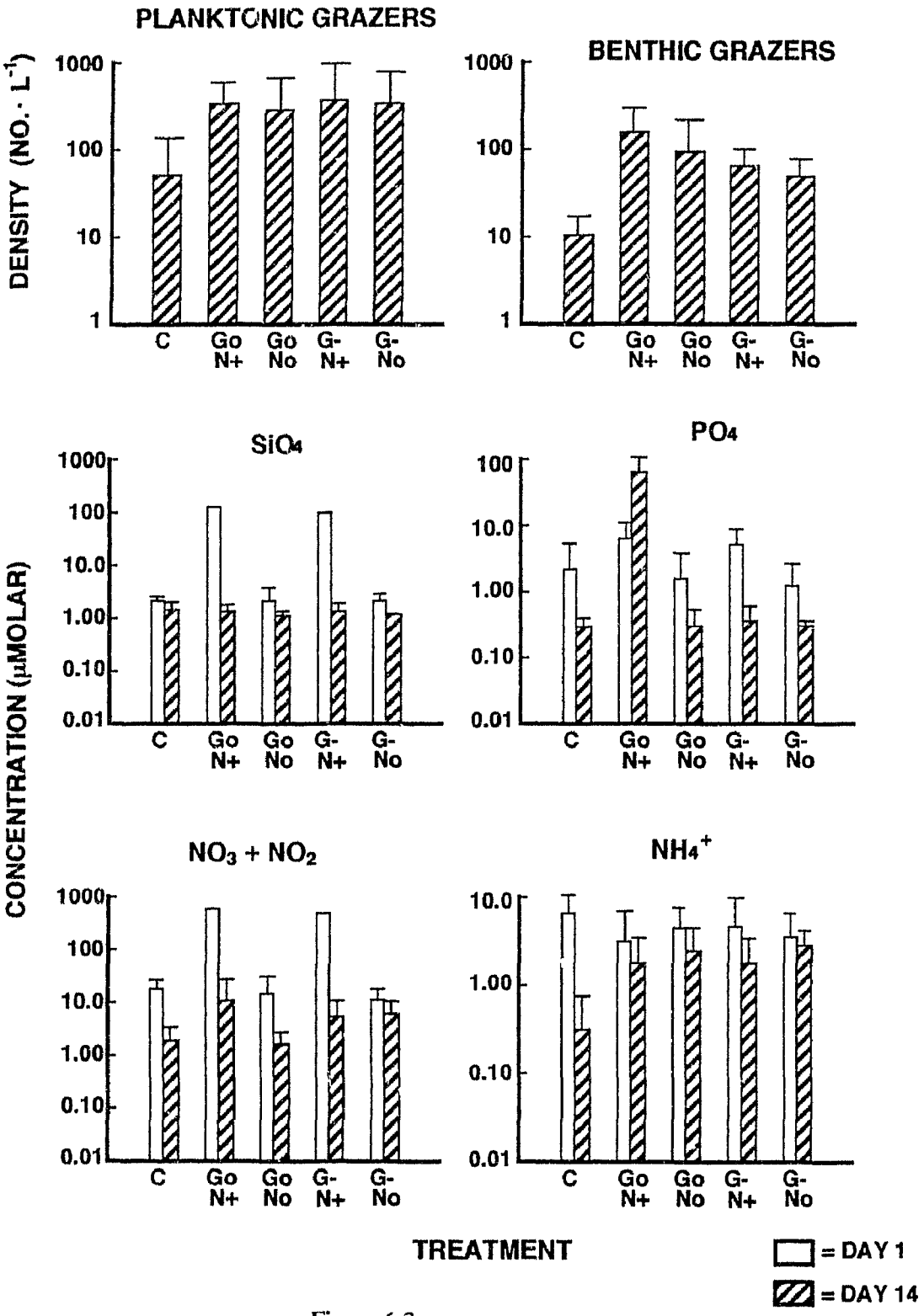

Figure 6.3

Figure 6.4: Mean density of micrograzers at the end (DAY 14) of the experiment and mean concentration of nutrients at the beginning (DAY 1) and end of the experiment in August 1993 in the different treatments (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 4).

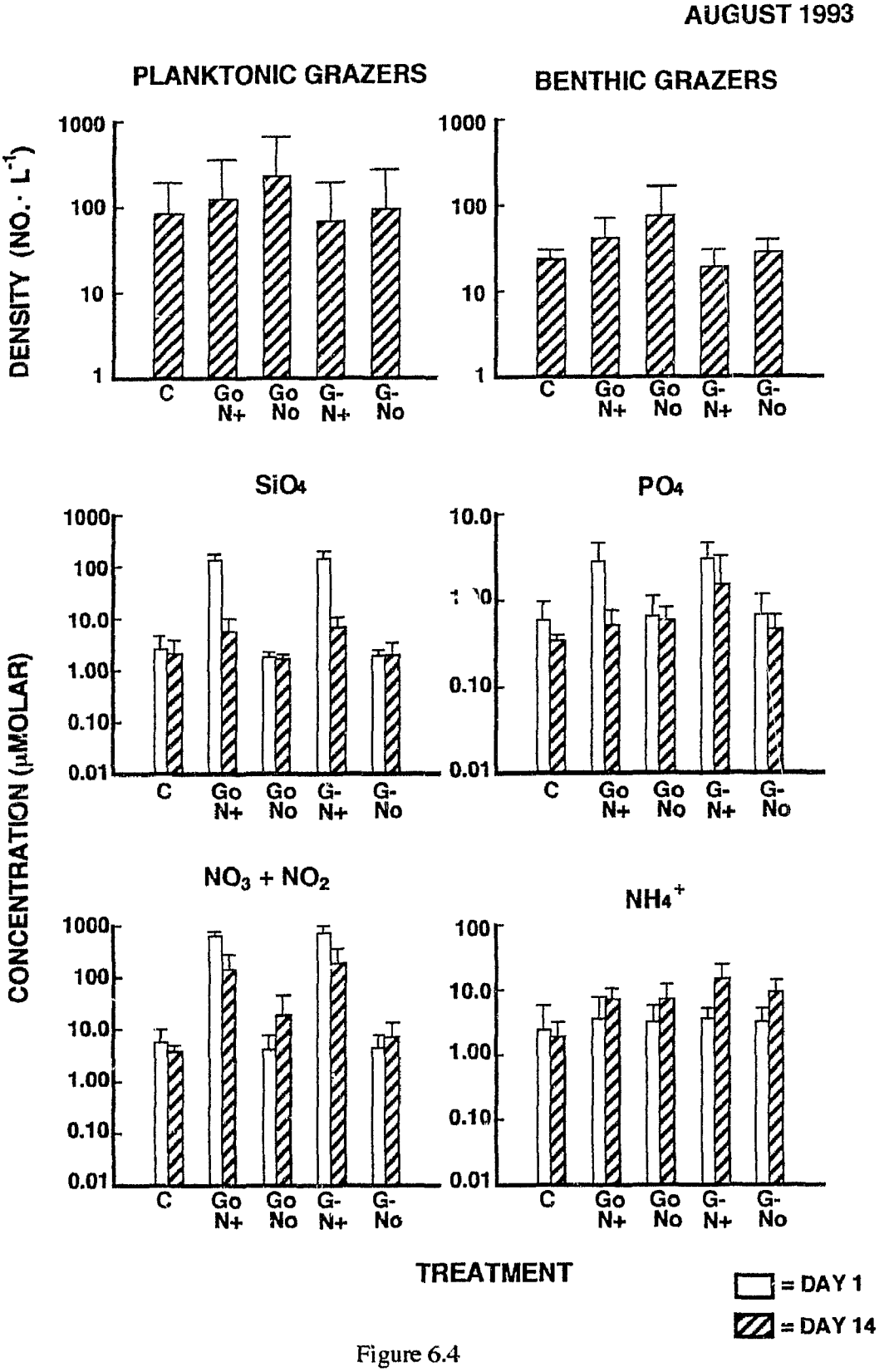
AUGUST 1993
PLANKTONIC GRAZERS
BENTHIC GRAZERS
DENSITY (NO. · L⁻¹)
1000
100
10
1
C
Go N+
Go No
G- N+
G- No
SiO4
PO4
10.0
0.10
0.01
NO3 + NO2
NH4+
CONCENTRATION (µMOLAR)
TREATMENT
= DAY 1
= DAY 14

Figure 6.4

Figure 6.5: Mean abundance of total phytoplankton and 4 phytoplankton groups in the different treatments in Pools (P) 1, 3, 4 and 5 at the beginning (DAY 1) and end (DAY 7) of the experiment in November 1992 (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 3).

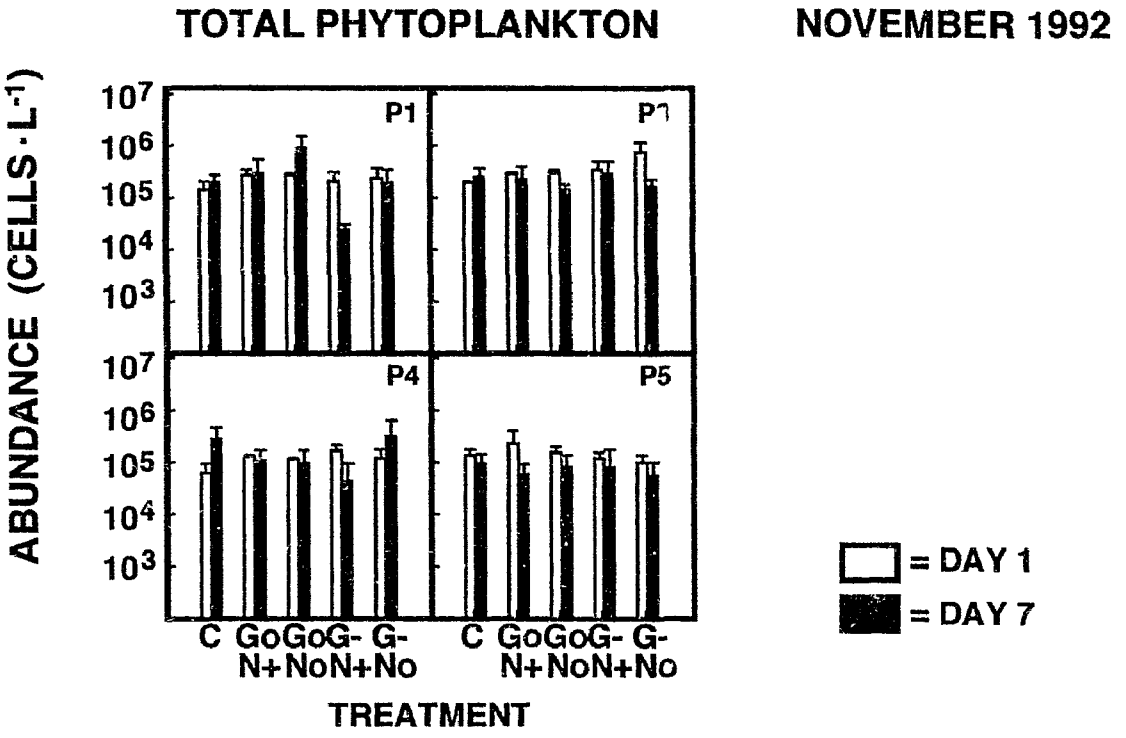
TOTAL PHYTOPLANKTON
NOVEMBER 1992
ABUNDANCE (CELLS·L-1)
P1
P4
P5
C GoGoG- G-
N+NoN+No
TREATMENT
= DAY 1
= DAY 7

Figure 6.5

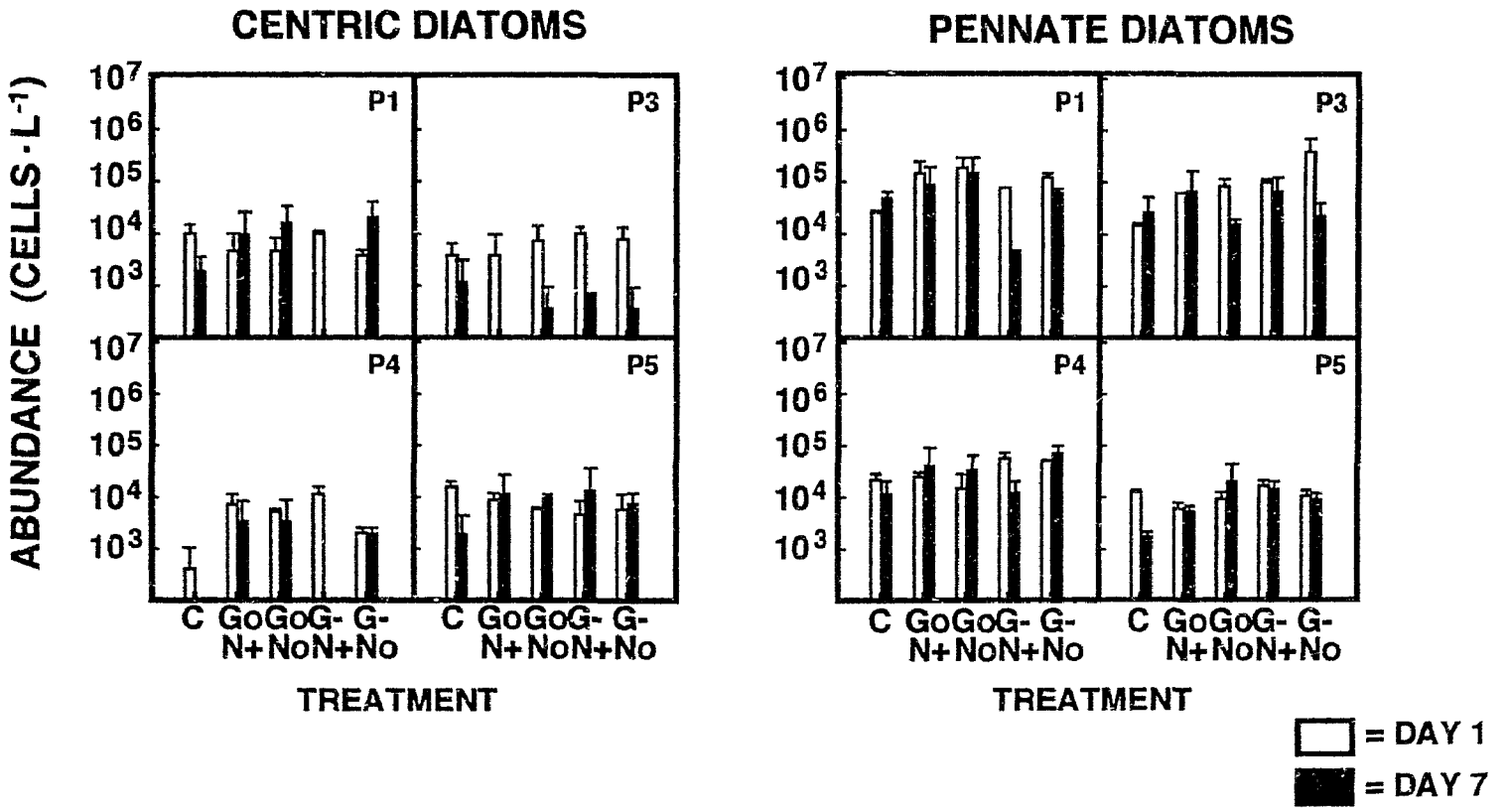

Figure 6.5 (continued)

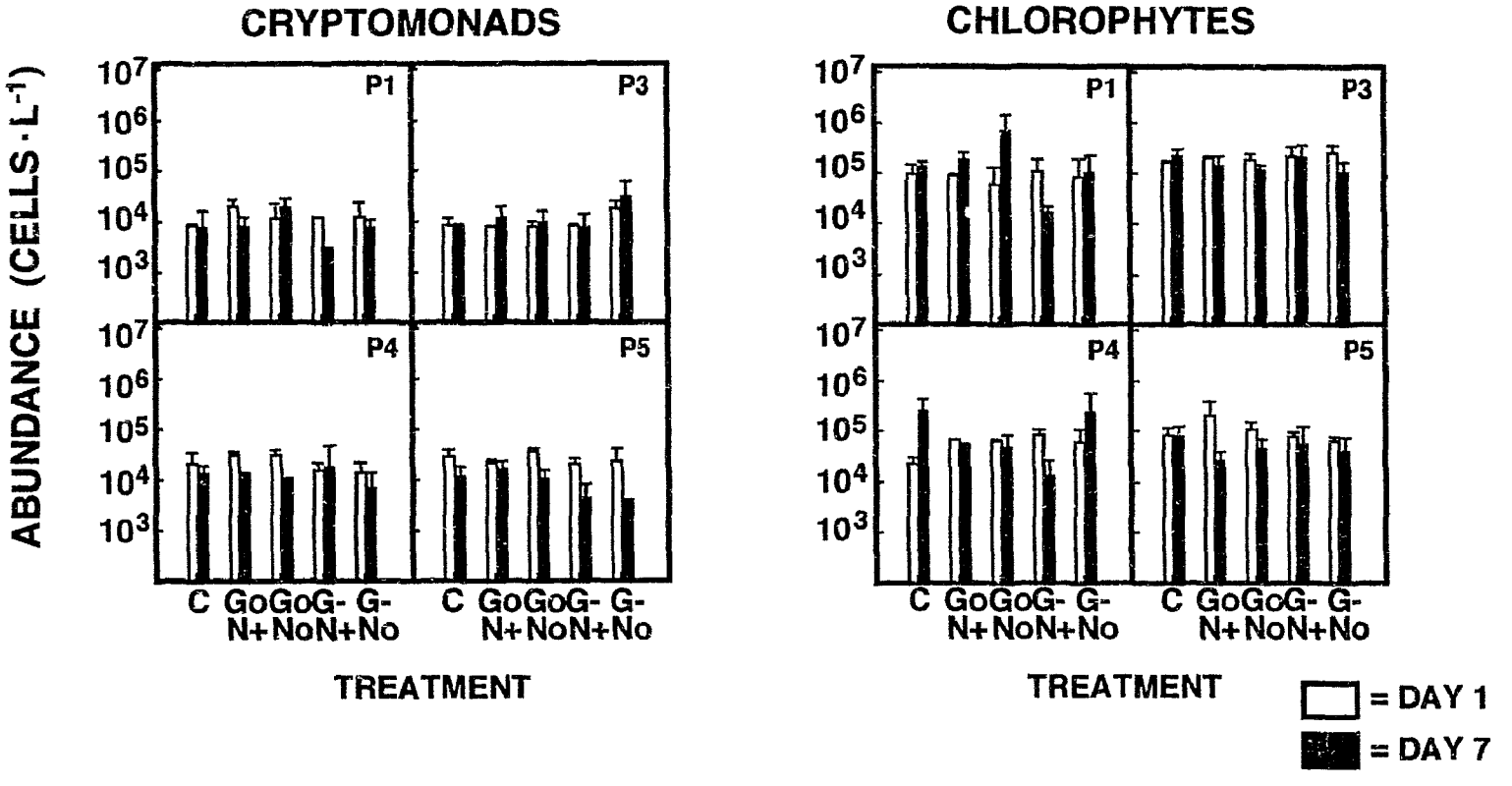

Figure 6.5 (continued)

Figure 6.6: Mean abundance of total phytoplankton and 4 phytoplankton groups in the different treatments in Pool 3 at the beginning (DAY 1) and end (DAY 14) of the experiment in June 1993 (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 2: G-No treatments; n = 3: all other treatments).

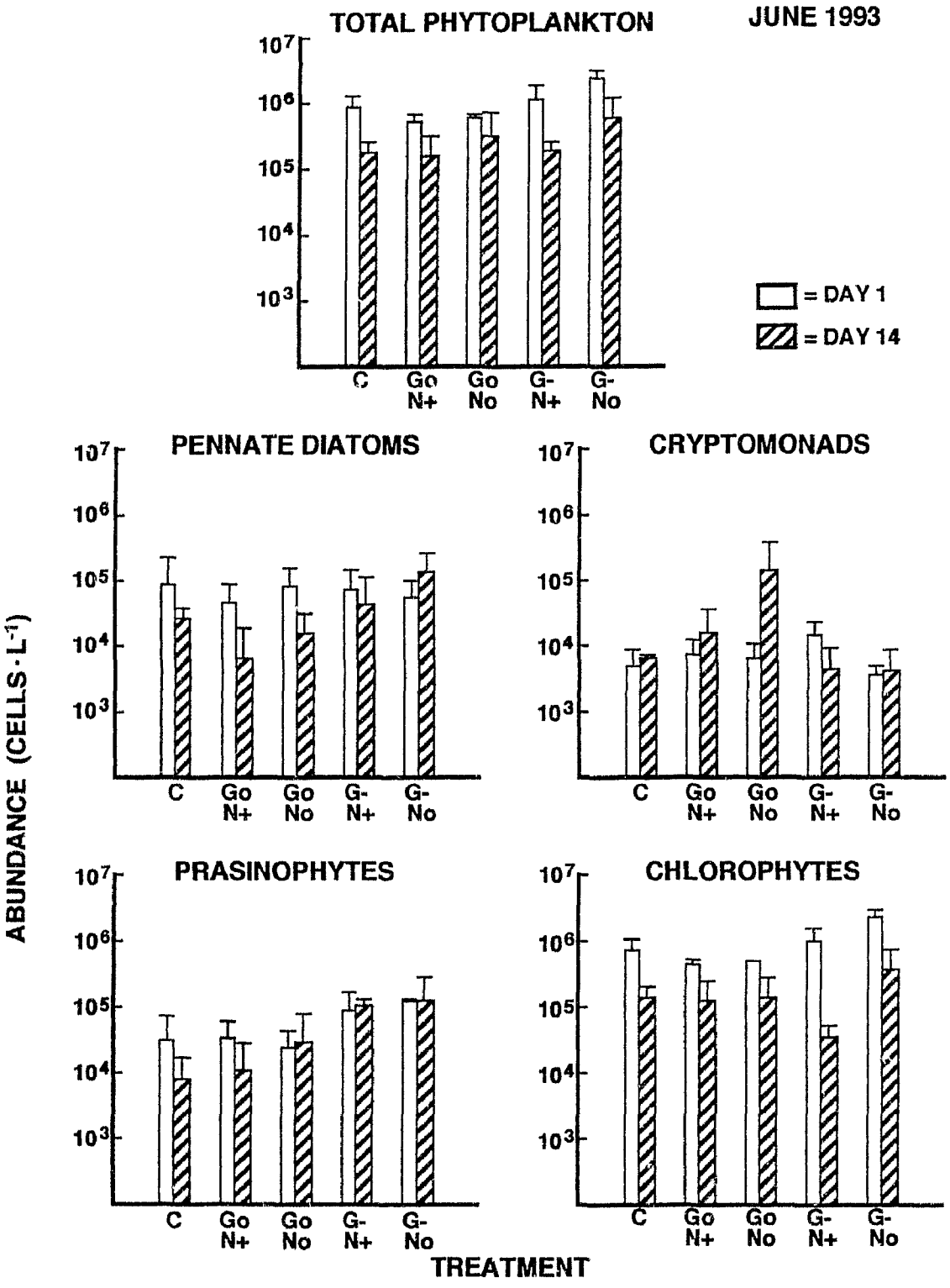
TOTAL PHYTOPLANKTON
JUNE 1993
= DAY 1
= DAY 14
PENNATE DIATOMS
CRYPTOMONADS
PRASINOPHYTES
CHLOROPHYTES
ABUNDANCE (CELLS·L-1)
TREATMENT
C
Go N+
Go No
G- N+
G- No

Figure 6.6

Figure 6.7: Mean abundance of total phytoplankton and 4 phytoplankton groups in the different treatments in Pools (P) 1, 3 and 5 at the beginning (DAY 1), middle (DAY 7) and end (DAY 14) of the experiment in July 1993 (C = natural controls, GoN+ = treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G-N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G-No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 2: GoNo, G-N+ treatments in Pools 3 and 5; G-No treatments in Pool 5; n = 3: all other treatments).

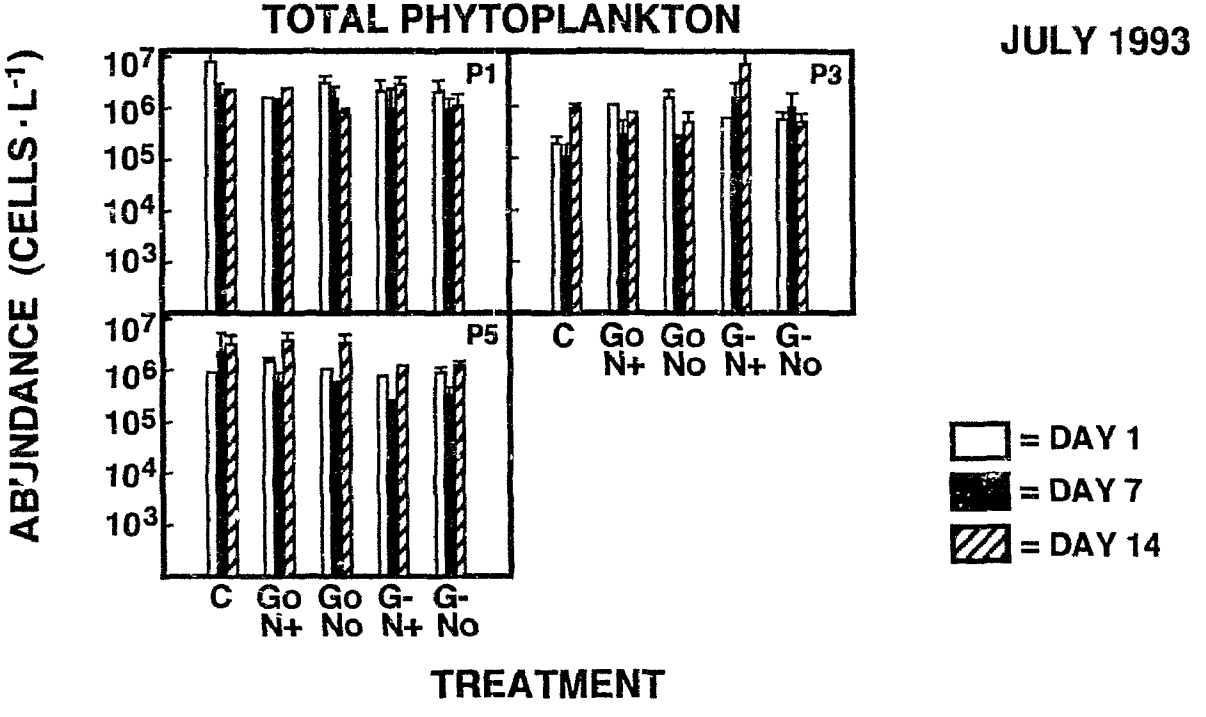
TOTAL PHYTOPLANKTON
JULY 1993
AB'JNDANCE (CELLS·L-1)
P1
P3
P5
C
Go N+
Go No
G- N+
G- No
TREATMENT
= DAY 1
= DAY 7
= DAY 14

Figure 6.7

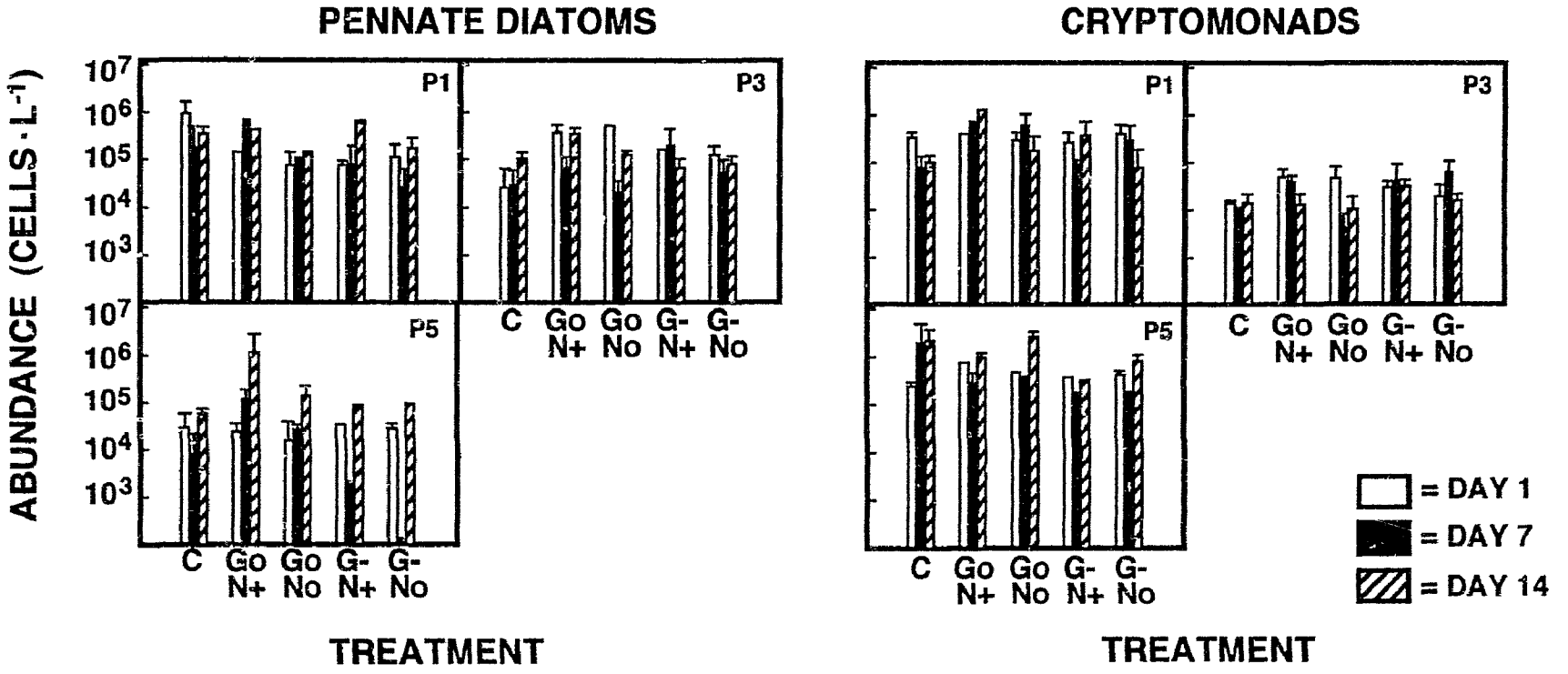

Figure 6.7 (continued)

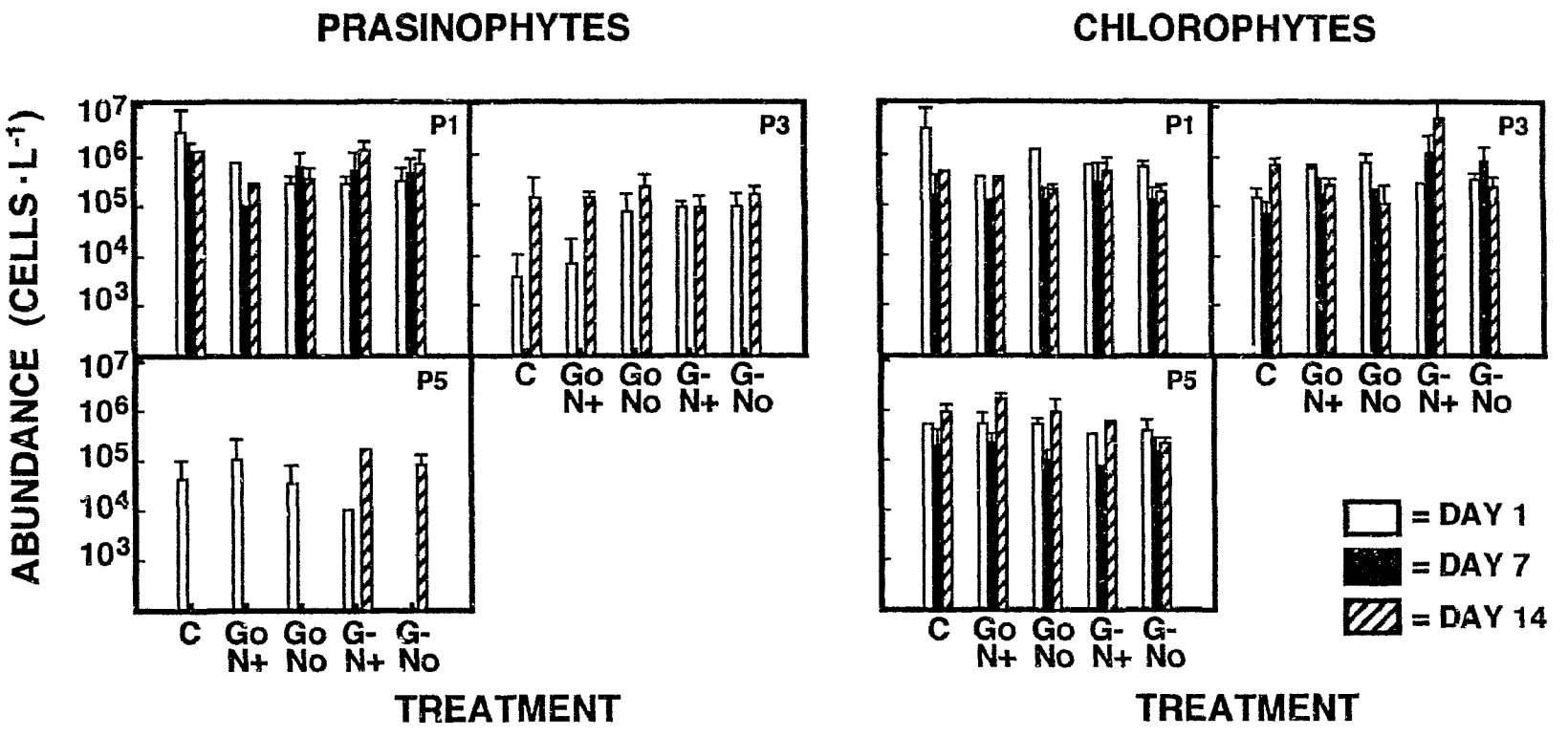

Figure 6.7 (continued)

Figure 6.8: Mean abundance of total phytoplankton and 4 phytoplankton groups in the different treatments in Pools (P) 1, 2, 3 and 5 at the beginning (DAY 1), middle (DAY 7) and end (DAY 14) of the experiment in August 1993 (C = natural controls, GoN+ treatments with natural density of grazers and enriched concentration of nutrients, GoNo = treatments with natural density of grazers and natural concentration of nutrients, G N+ = treatments with reduced density of grazers and enriched concentration of nutrients, G No = treatments with reduced density of grazers and natural concentration of nutrients). Error bars represent standard deviations (n = 2: GoN+ treatments in Pool 3; GoNo, G N+ treatments in Pools 3 and 5; G-No treatments in Pools 2 and 3; n = 3: all other treatments).

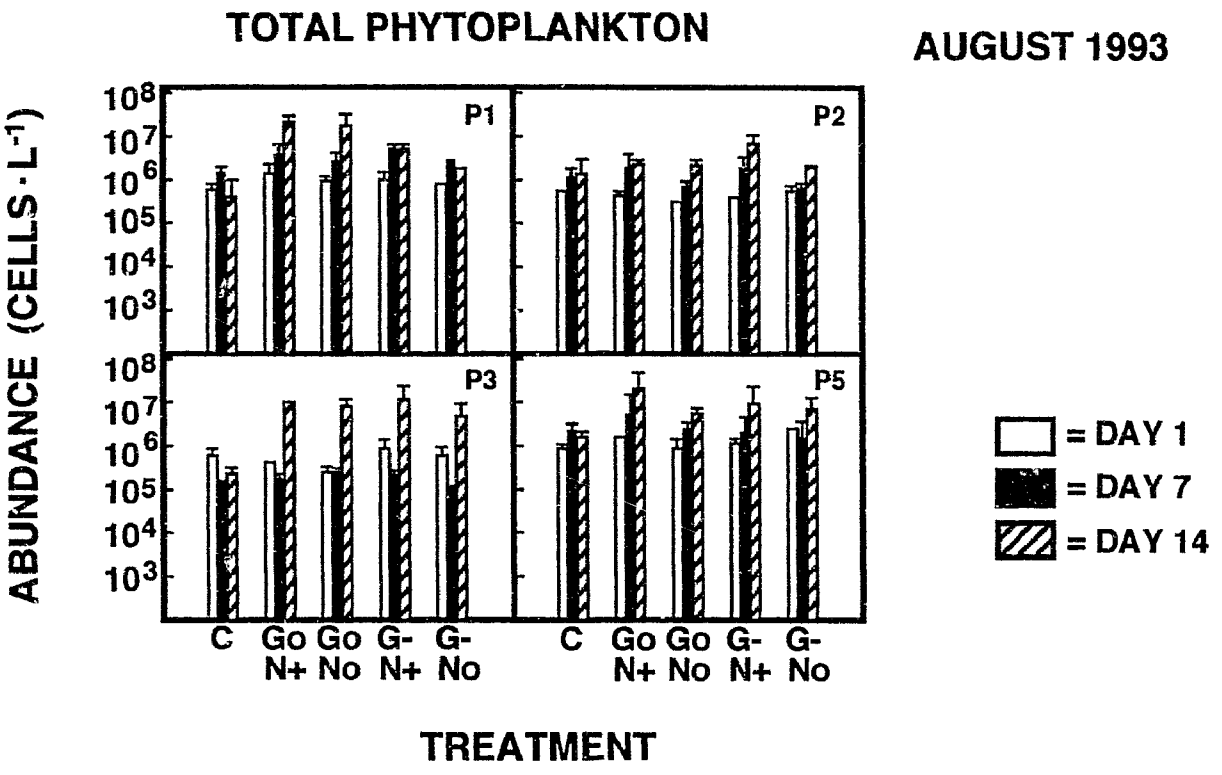
TOTAL PHYTOPLANKTON
AUGUST 1993
ABUNDANCE (CELLS·L-1)
P1
P2
P3
P5
C
Go N+
Go No
G- N+
G- No
TREATMENT
= DAY 1
= DAY 7
= DAY 14

Figure 6.8

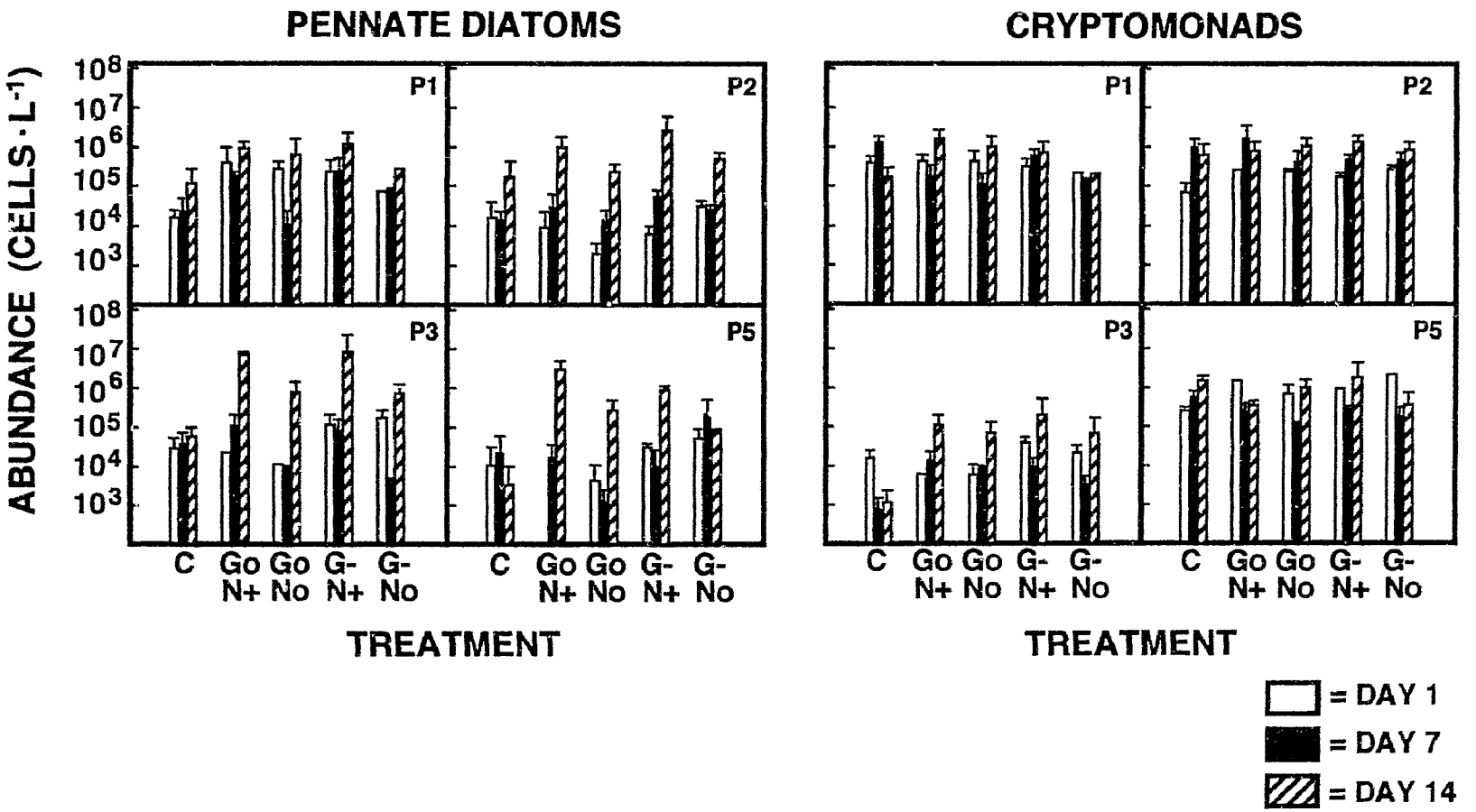

Figure 6.8 (continued)

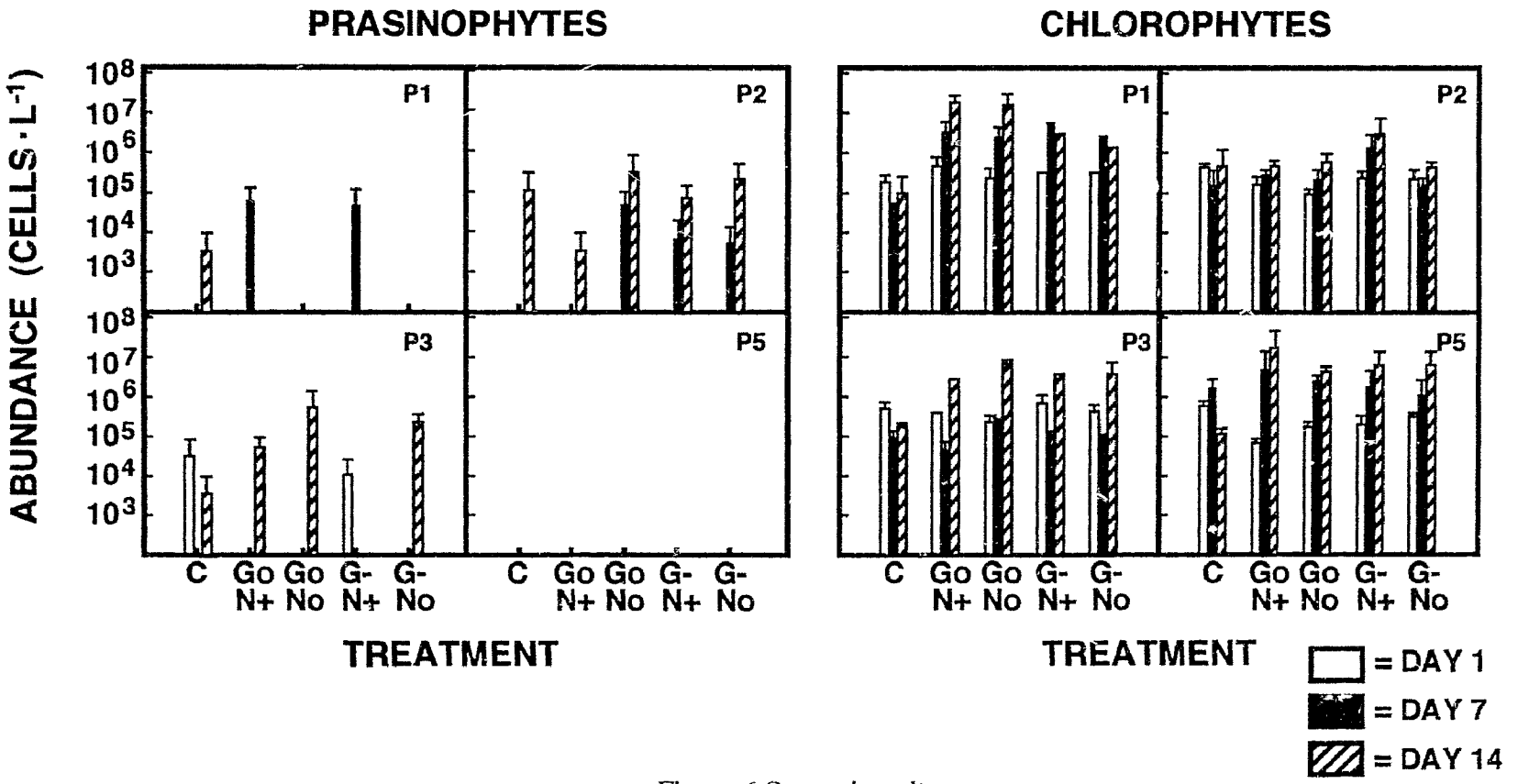

Figure 6.8 (continued)

Figure 6.9: Top-down Index (TDI) in each pool for percentage change in abundance of total phytoplankton and of 4 phytoplankton groups in the first week (1-7 d), the second week (8-14 d), and over the entire experimental period (1-14 d) of the experiments in July and August 1993.

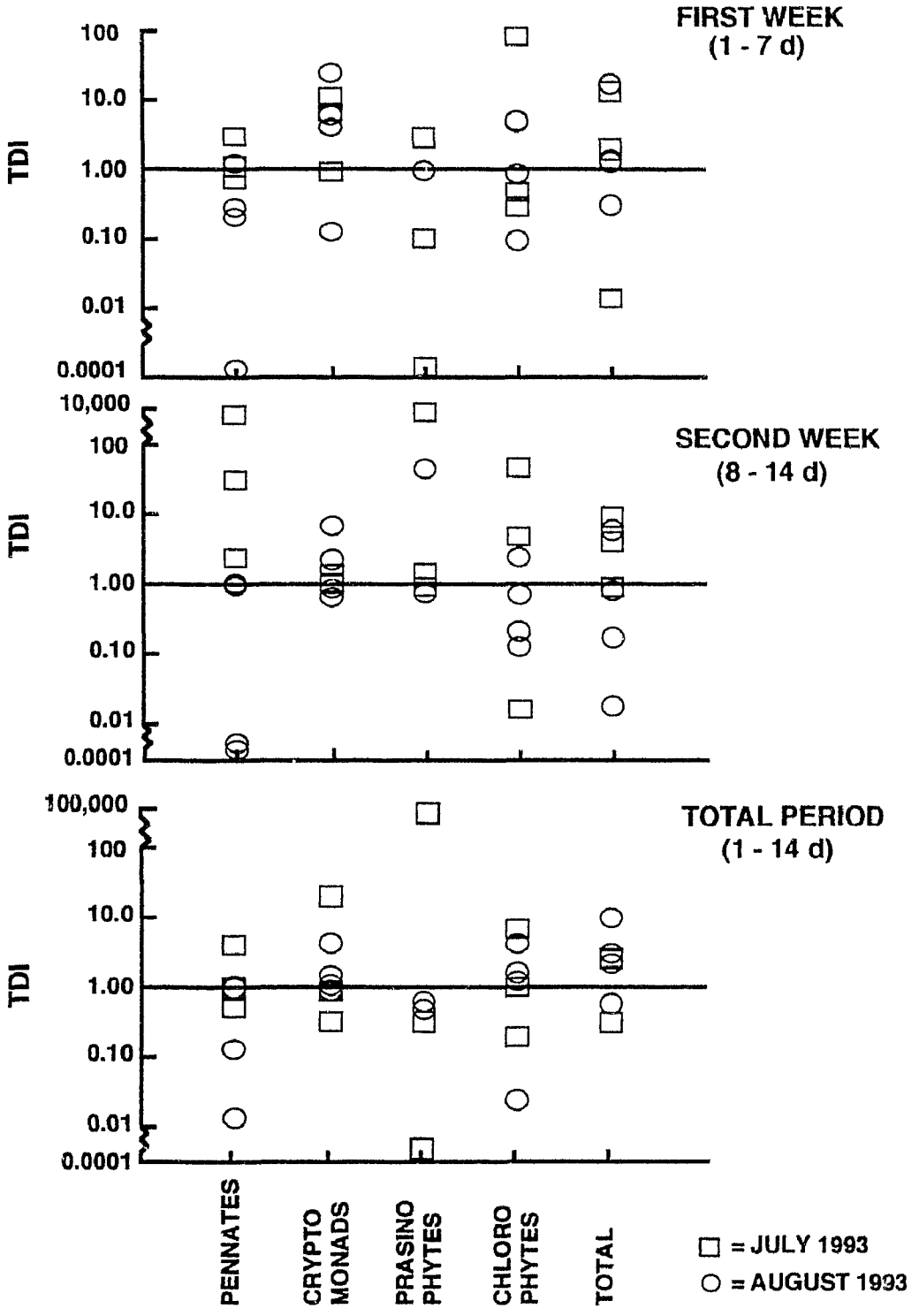
FIRST WEEK
(1 - 7 d)
SECOND WEEK
(8 - 14 d)
TOTAL PERIOD
(1 - 14 d)
TDI
100
10.0
1.00
0.10
0.01
0.0001
10,000
100,000
PENNATES
CRYPTO MONADS
PRASINO PHYTES
CHLORO PHYTES
TOTAL
□ = JULY 1993
○ = AUGUST 1993

Figure 6.9

DISCUSSION

Experimental manipulations

The artifactual effects of the experimental enclosures on the response variable (percentage change in the abundance of phytoplankton) and on both of the manipulated variables (density of micrograzers and the concentration of nutrients) showed no consistent pattern among experiments, between weeks within experiments, and among pools. There were few or no significant effects of the enclosures on the change in abundance of phytoplankton in the experiments in November 1992 and in June and July 1993. In the experiment in August 1993, changes in the abundance of most phytoplankton groups were greater in enclosures compared to natural controls, suggesting that the observed responses of phytoplankton to the treatment manipulations have been intensified in the enclosures. The experimental effect of planktonic micrograzers may have been damped at least in some pools in the experiments in July and August 1993. The concentrations of silicate in November 1992 and of all manipulated nutrients in June 1993 at the beginning of the experiments were greater in the enclosures in all pools, probably due to procedural contamination. Therefore, it is possible that the absence of a significant effect of nutrient enrichment on percentage change in phytoplankton abundance in these two experiments was the result of insufficient differences in the initial concentration of nutrients between the nutrient enriched treatments and those in which nutrients were not manipulated.

Another potential artifact of the experimental procedure was nutrient contamination of the pools (i.e. natural controls) during the experiment through leaking from the enriched enclosures. However, there were no differences at the beginning of the experiments in the nutrient concentrations between the natural controls and the unmanipulated enclosures (except for 1 pool in August 1993 where the concentration of

phosphate was greater in the natural controls although the difference was small). Furthermore, the concentrations of nutrients in the natural controls did not increase over the experimental period during any of the experiments. Therefore, there was no evidence of nutrient contamination of the natural controls in any of my experiments.

In all experiments, the density of planktonic and benthic micrograzers in most pools was less in the treatments where grazers were reduced than those where grazers were not manipulated. Also, the concentration of all manipulated nutrients at the beginning of all experiments was greater in the nutrient enriched treatments than in those that were not manipulated. Therefore, the experimental manipulations of grazer density and nutrient concentration were effective.

Effects of grazer density on the abundance of phytoplankton

Manipulation of the density of grazers only affected the abundance of phytoplankton in the experiments in July and August 1993, and the effect varied among phytoplankton groups. Reduction in grazer density generally increased the abundance of pennate diatoms and prasinophytes in July suggesting that these two groups of phytoplankton are limited by grazing, especially during the period when grazers are abundant (Chapter 5). Conversely, reduction in grazer density generally decreased the abundance of cryptomonads in July, and of pennate diatoms, cryptomonads and chlorophytes in August. Grazers may have beneficial effects for particular phytoplankton groups by increasing nutrient concentrations through excretion. For example, Vanni & Findlay (1990) demonstrated that increased fish excretion resulted in increased abundance of nutrient-limited phytoplankton. Grazers also may enhance the abundance of certain phytoplankton groups by selectively feeding on their potential competitors (e.g. pennate diatoms and prasinophytes in July 1993). The importance of

grazers in influencing the phytoplankton assemblage was greatest in the experiment conducted in August, a period of low ambient nutrient concentrations (Chapter 5) and potentially increased competition for nutrients. Other studies also have shown that a reduction in the density of grazers can have a negative effect on the abundance of some phytoplankton groups but not others, thereby changing phytoplankton community structure (Lynch & Shapiro 1981, Vanni 1987, Vanni & Temte 1990, Rosemond *et al.* 1993).

Effects of nutrient concentration on the abundance of phytoplankton

As with the manipulations of the density of grazers, nutrient enrichment only affected the abundance of phytoplankton in the experiments in July and August 1993, and the effect varied among phytoplankton groups. Previous studies in freshwater and marine systems have shown that nutrient regulation of phytoplankton assemblages is more important in summer than in spring or fall (Vanni & Temte 1990, Kivi *et al.* 1993). Nutrient enrichment had a positive effect on the abundance of chlorophytes in all pools and of cryptomonads and prasinophytes in 1 pool in July, and on the abundance of pennate diatoms and prasinophytes in 1 pool in August. Conversely, nutrient enrichment had a negative effect on the abundance of pennate diatoms and prasinophytes in 1 pool in July, and of prasinophytes in 1 pool in August. My results suggest that some groups of phytoplankton that may have been nutrient-limited (e.g. chlorophytes in July) grew in the enriched nutrient concentrations, probably at the expense of other groups (e.g. pennate diatoms and prasinophytes which decreased in the nutrient enriched treatments). Experimental studies in lakes also have shown that nutrient enrichment can have differential effects on the abundance of different phytoplankton species (Lynch & Shapiro 1981, Vanni 1987). Tilman (1977) and

Tilman *et al.* (1982) suggested that because species have different nutrient requirements, the composition of phytoplankton communities is determined by the ratio in which different macronutrients are available: species can only co exist at certain nutrient ratios and they outcompete one another as the ratios change.

Relative importance of top-down and bottom-up regulation

The relative importance of top-down (grazing) and bottom-up (nutrients) factors in regulating phytoplankton assemblages varied among phytoplankton groups and among experiments in different months. Neither of the two factors affected changes in phytoplankton abundance in November 1992 or June 1993, when there was little or no phytoplankton growth. Both factors affected the abundance of all phytoplankton groups in July when the concentration of nutrients was low and the density of grazers was high. In August, however, most phytoplankton groups were affected only by the density of grazers, except for prasinophytes that were only affected by nutrients. The top-down index indicated that, over the entire experimental period, the effect of grazing was greater than that of nutrient availability for all groups of phytoplankton in July, but only for cryptomonads and chlorophytes in August. Previous studies in other systems also have found that the relative importance of nutrients and grazing as regulatory factors of phytoplankton community structure varies seasonally and depends upon the species composition of the phytoplankton communities and the dominant zooplankters present (Vanni & Temte 1990, Kivi *et al.* 1993). Vanni & Temte (1990) suggested that the two factors are important simultaneously only in summer.

Under simulatenous dual regulation by top-down and bottom-up factors, an interaction between grazing and nutrient availability is expected such that the greatest change in abundance should be observed in the G-N+ treatments. I detected a

significant 3 way interaction between Grazer Density, Nutrient Concentration and Pool for pennate diatoms and cryptomonads in July, and for pennate diatoms and prasinophytes in August, but in no case was the largest change in abundance observed in the G-N+ treatment. Contrary to my results, Rosemond *et al.* (1993) showed strong simultaneous dual control on chlorophyll *a* in experimental manipulations in streams: nutrient enrichment had a stronger effect in the absence of grazers than in their presence.

There was large variability among tidepools in the response of phytoplankton to grazer and nutrient manipulations, as indicated by the large number of significant 2-way interactions involving Pool effects in the experiments in July and August 1993. In some cases, significant effects of grazer density or nutrient enrichment were recorded only in 1 pool (e.g. the effect of grazer density on cryptomonads and prasinophytes in July, or the effect of nutrient concentration on prasinophytes in August). In other cases, the directions of the effects of grazer density or nutrient enrichment differed among pools (e.g. the effect of grazer density on cryptomonads in August, or the effect of nutrient enrichment on prasinophytes in July). These results suggest that the importance of grazing and nutrients as regulating factors of the phytoplankton assemblages may vary among individual tidepools for individual phytoplankton groups. In other chapters, I have shown that the phytoplankton and micrograzer assemblages, and the nutrient regime are highly variable among individual tidepools (Chapters 3 & 5). Hunter and Price (1992) suggested two models that describe the role of bottom-up and top-down community regulation and incorporate the natural heterogeneity of communities. My results reinforce the suggestion that the inherent heterogeneity of the environment should be accounted for in the determination of the factors regulating a community.

This is the first study to examine the relative importance of bottom up and top down factors in regulating phytoplankton assemblages in the rocky intertidal environment. I showed that the phytoplankton assemblages in this system are regulated by both types of factors. However, the relative importance of the each type of factor varies both spatially and temporally, and this probably reflects the variability in the nutrient regime and composition of the phytoplankton and micrograzer assemblages in these systems.

CHAPTER 7: General Discussion

This thesis examined the temporal and spatial dynamics of phytoplankton assemblages in tidepools on a temperate rocky shore over a 2 yr period. The abundance of these assemblages fluctuated little over the period of tidal isolation of the pools, but showed pronounced changes on longer temporal scales (Chapter 4). Over the period of tidal isolation, the abundance of one phytoplankton group decreased probably due to grazing, whereas that of another group increased due to population growth. Over periods of months, different factors affected the fluctuations in abundance of different members of the assemblages (Chapter 5). For example, centric diatoms were only abundant in pools during the spring and autumn phytoplankton blooms in the surrounding sea-water, suggesting that the presence and temporal dynamics of this group in pools depended mainly upon tidal input. Other groups, such as flagellates, despite their consistently low abundance in the surrounding sea-water, were present throughout the year and reached high abundances in pools in summer. These results suggest that the temporal dynamics of these groups depended mainly upon processes that occur within the pools.

There was no pronounced vertical zonation along the intertidal gradient in the abundance or composition of phytoplankton assemblages in tidepools. Rather, the abundance of the numerically dominant groups of phytoplankton varied widely among pools within zones, and this pattern was maintained throughout the entire sampling period (Chapter 5). For transient groups of phytoplankton, such as centric diatoms, the lack of zonation is probably the result of uniform input into the pools from the surrounding sea-water during the spring and autumn blooms. For more permanent residents, such as flagellates, the lack of zonation suggests that their abundance was

affected by the physical characteristics of individual pools and the biological processes within them.

The lack of pronounced vertical zonation of phytoplankton assemblages in tidepools is not surprising considering the variability in the other biological assemblages of the pools. I also found little evidence of zonation but great variability among pools in the macrobenthic and hyperbenthic assemblages (Chapters 2 and 3), both of which can have an effect on phytoplankton. Macroalgae may provide an alternate food source for potential grazers of phytoplankton and alter the nutrient regime in pools. Macroalgae also provide physical structure that may enhance attachment of epiphytic microalgal species and reduce the probability of benthic species of phytoplankton being flushed out of the pools. Macrofauna such as littorinids, may consume phytoplankton that have sunk to the bottom of the pools and most members of the hyperbenthos are micrograzers of phytoplankton throughout the water-column. Alternatively, the macrofauna and hyperbenthos may increase the concentration of nutrients and therefore enhance the abundance of phytoplankton in pools.

Like in tidepools, spatial variability has been detected in both the distributions of organisms and the mechanisms that establish them on emergent substrata of rocky shores (e.g. Underwood 1975, Little & Smith 1980, McGuinness 1987a, b, Menge 1983, Petraitis 1987, Fairweather 1988, Hill & Hawkins 1991). However, unlike tidepools, zonation of biological assemblages on emergent substrata along the intertidal gradient is striking and ubiquitous on most temperate rocky shores (e.g. Stephenson & Stephenson 1950, 1952, 1954a, b, Dayton 1971, Lubchenco & Menge 1978, Underwood 1981a, Janke 1990) providing evidence of the overriding effect of the tide on the organization of these assemblages. The lack of biological zonation in tidepools may be explained by differences in the manner in which the tide affects the physical

regime, and therefore the biological assemblages of these habitats, compared to emergent substrata. The daily rise and fall of the tide define the intertidal gradient by dramatically changing the physical conditions between submergence and emergence. Like emergent substrata, tidepools with similar periods of isolation are affected by the tide with similar frequency, however, the magnitude of submergence, as well as the frequency, define the tidal influence on tidepools. The magnitude of tidal influence (i.e. the water-exchange rate of the pool with the surrounding seawater during the ascent of the tide) affects the amplitude of fluctuations in physical conditions in pools. This exchange rate will depend upon the orientation, volume, surface area and drainage pattern of individual pools. These physical characteristics can vary widely among pools with similar periods of isolation, making tidal influence more variable among pools than emergent substrata and thus, not having an overriding effect on biological zonation.

The large variability among pools in phytoplankton community organization that I observed could be the result of founder effects on the composition of the micrograzer assemblages resulting from differences in tidal influence among pools. The abundance of the hyperbenthic assemblages (which are the main potential grazers of phytoplankton in high and splash pools) increased in summer but varied widely among pools (Chapter 3). The effects of grazing and nutrient availability on the abundance of phytoplankton in the factorial experiments also were most pronounced in summer (Chapter 6). Furthermore, for most phytoplankton groups the top-down effects (grazing) on abundance were stronger than bottom-up effects (nutrient availability). Reducing the number of grazers had a positive effect on the abundance of some phytoplankton groups but a negative effect on others, suggesting that the grazer field is important in regulating the structure of phytoplankton assemblages. However, the importance of

grazing in regulating the abundance of phytoplankton was largely variable among pools. In the high intertidal and splash zones, different pools were dominated by different but dense, single-taxon assemblages of hyperbenthos that persisted interannually and can have differential effects on the abundance of phytoplankton. The variability among pools in the abundance of different groups of hyperbenthos could be the result of variability in recruitment rates. Although there is large spatial variability in settlement and recruitment of organisms on emergent substrata of rocky shores (e.g. Caffey 1985, Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Petraitis 1991), little is known about spatial variability in recruitment to tidepools. Hyperbenthic organisms can be introduced into tidepools mainly with the incoming tide and, given the large variability in tidal influence among pools, recruitment of these organisms probably is also highly variable. Therefore, the dominant populations of hyperbenthos that I observed probably are established by founder effects and persist due to low flushing rates. In turn, differences in the composition of micrograzers may contribute to the variation among pools in the composition and abundance of phytoplankton.

One avenue for future research on the mechanisms of community organization in tidepools is experimental manipulation of initial conditions of community structure. Individual pools can be considered as islands, and recruitment of sessile and planktonic organisms to each "island" occurs from the surrounding sea-water. Uniformity in initial conditions can be achieved by manipulation of the abundance of different species and the rates of recruitment, to reflect similar tidal influence among pools. Such manipulations can address the following questions: Under similar initial conditions does large variability in community structure and organization develop among pools? If so, on what temporal scales do the communities and their regulatory factors diverge

among pools? If communities with similar initial conditions diverge, what are the mechanisms that caused the divergence? Answers to these questions will allow us to determine the causes of spatial variability in community organization in tidepools and possibly allow extrapolation of the results to other aquatic systems.

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