PHYTOPLANKTON SUCCESSION AND RESTING STAGE OCCURRENCE IN THREE REGIONS IN SECHELT INLET, BRITISH COLUMBIA

By

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ABSTRACT

Phytoplankton were monitored in three regions in Sechelt Inlet, British Columbia between June and September in 1989. The purpose was to compare the phytoplankton community (region I) transported into the inlet via a strong tidal jet to that which exists inside the inlet (region II) and in an inner shallow basin (region III). Core samples were also collected to compare the phytoplankton present at the water-sediment interface. In 1989 between June and September the temperature, salinity, and nutrient profiles show that the hydrographic conditions in region I were well-mixed, while those in region III were well-stratified. The conditions in region II fluctuated between mixed and stratified conditions. The depths of the 1 % light levels were generally deeper in region I. The depth of the 1 % light level fell above the nitricline in region II on September 25 and in region III on June 9 and July 8. In region III nitrogen and ammonium levels fell below 1 μM in the surface waters between June 25 and September 8. The nitrogen to phosphorus ratios in regions I, II, and III were 8.6, 7.5, and 7.2 respectively. Diatoms exhibited the highest relative biomass of the total phytoplankton groups in regions I and II. Fluctuations within each plankton group were more gradual in region III than those in region I. A reciprocal dominance of diatom to dinoflagellate biomass was observed from one sampling trip to another. The vertical distributions of dinoflagellates, photosynthetic flagellates, and diatoms reveal uniform profiles in region I and thin horizontal layers in region II and III. The biomass maxima of these phytoplankton groups in region III generally remain below the nutrient-depleted surface waters. A temporal succession was observed in region I. Small changes in the relative percent of successional phytoplankton stages in region II and III were observed over the sampling period. The distribution of potentially harmful phytoplankton such as *Heterosigma akashiwo*, *Protogonyaulax catenella* and *P. tamarensis*, *Prorocentrum minimum*, *Dinophysis fortii* and *D. acuminata*, *Chaetoceros convolutum* and *Ch. concavicorne*, and *Nitzschia pungens* are

discussed in the text. The water-sediment interface samples of region III contained the highest number of phytoplankton. *Chaetoceros* spp. resting spores were found only in region III. Auxospores of *Skeletonema costatum* were formed only in the incubated cores of region I and III. The mean diameter of sedimented *S. costatum* cells found in the core samples was significantly different than the mean cell diameter of the larger post-auxospore cells.

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1.1: INTRODUCTION

The development of a phytoplankton bloom inside a fjord may take place in three ways: the growth of a phytoplankton species resident within the fjord (autochthonous), the development of a bloom outside the fjord and subsequent transportation into the fjord via tidal jet (allochthonous), or the transportation of a low concentration ("inoculum") of phytoplankton species from outside the fjord or adjoining inlet into the fjord and subsequent bloom formation within the fjord (Gowen, 1984). In order to assess the origin of a phytoplankton bloom in a fjord an assessment of exchange rates and a comparison of species composition, resting stage distribution, species succession, water column stability, and nutrient availability between source and resident water is necessary.

The extent and rate at which exchange takes place in fjords will influence the species composition of the resident community. For example, Scottish fjords, such as Ardbhair, Craignish, and West Loch Tarbert, with rapid exchange rates of less than ten days, contain a resident phytoplankton community similar to that of their source water (Jones *et al.*, 1984). On the other hand, Loch Striven, another Scottish fjord, has a flushing rate of several weeks and has been observed to contain diatom blooms that were not observed in the sea area adjacent to the fjord (Tett *et al.*, 1981). Thus, the phytoplankton in fjords with slow flushing rates may not be expected to resemble that of their source water. In order to predict the development of phytoplankton blooms, Gowen (1984) classified fjords based on water column stability and flushing time. Fjords with larger tidal volume and smaller freshwater inflow relative to the volume of the fjord are type A fjords, while fjords with a smaller tidal and freshwater inflow volume relative to the volume of the fjord are on the other end of the scale and considered type E. The growth and biomass of phytoplankton inside a type E fjord will probably not be minimized by dilution of tidal and freshwater inflow.

Fjords have been observed to have a higher biomass of phytoplankton than the source water indicating that fjordic conditions are conducive for bloom formation (Tett *et al.*, 1981; Jones *et al.*, 1984). Therefore, fjords provide and optimal environment for shellfish farms by offering protection and a large food supply for the shellfish. However, if the resident phytoplankton community is dominated by harmful phytoplankton such as *Protogonyaulax catenella* and *P. tamarensis* (Paralytic Shellfish Poisoning; Gaines and Taylor, 1986; Larson and Moestrup, 1989), *Prorocentrum minimum* (Hepatic (Venerupin) Shellfish Poisoning; Hallegraeff, 1991), *Nitzschia pungens* (Amnesiac Shellfish Poisoning; Bates *et al.*, 1989), and *Dinophysis fortii* and *D. acuminata* (Diarrheic Shellfish Poisoning; Cembella, 1989; Lassus *et al.*, 1985) this increased biomass inside the fjord will pose a threat to the shellfish industry. Fish farms finding refuge in these protected areas are also threatened by fish-killing phytoplankton such as *Heterosigma akashiwo* (Chang *et al.*, 1990) and *Chaetoceros convolutum* (Bell, 1961; Kennedy *et al.*, 1976; Brett *et al.*, 1978) and *Ch. concavicorne* (pers. comm. F.J.R. Taylor). The barbs on the setae of *Chaetoceros concavicorne* are more developed than those of *Ch. convolutum* and therefore *Ch. concavicorne* is thought to be responsible for damage to fish gill tissue and subsequent fish losses to a greater extent than *Ch. convolutum.* In order to reduce mariculture losses by predicting the development of harmful phytoplankton blooms a comparison of species composition and succession in source and resident water is necessary.

Margalef (1978) proposed that the structure of a phytoplankton community is governed by turbulence and availability of nutrients (Fig. 1.0). The structure of the phytoplankton communities existing in Scottish, Norwegian, and Canadian west coast fjords are in agreement with this hypothesis since a greater diatom biomass is generally found in well-mixed waters while a greater dinoflagellate biomass is found in "transitional" and stratified waters of adjoining basins (Gowen, 1984; Taylor *et al.*, 1991). The long resident time of phytoplankton spent in fjords with low dilution rates

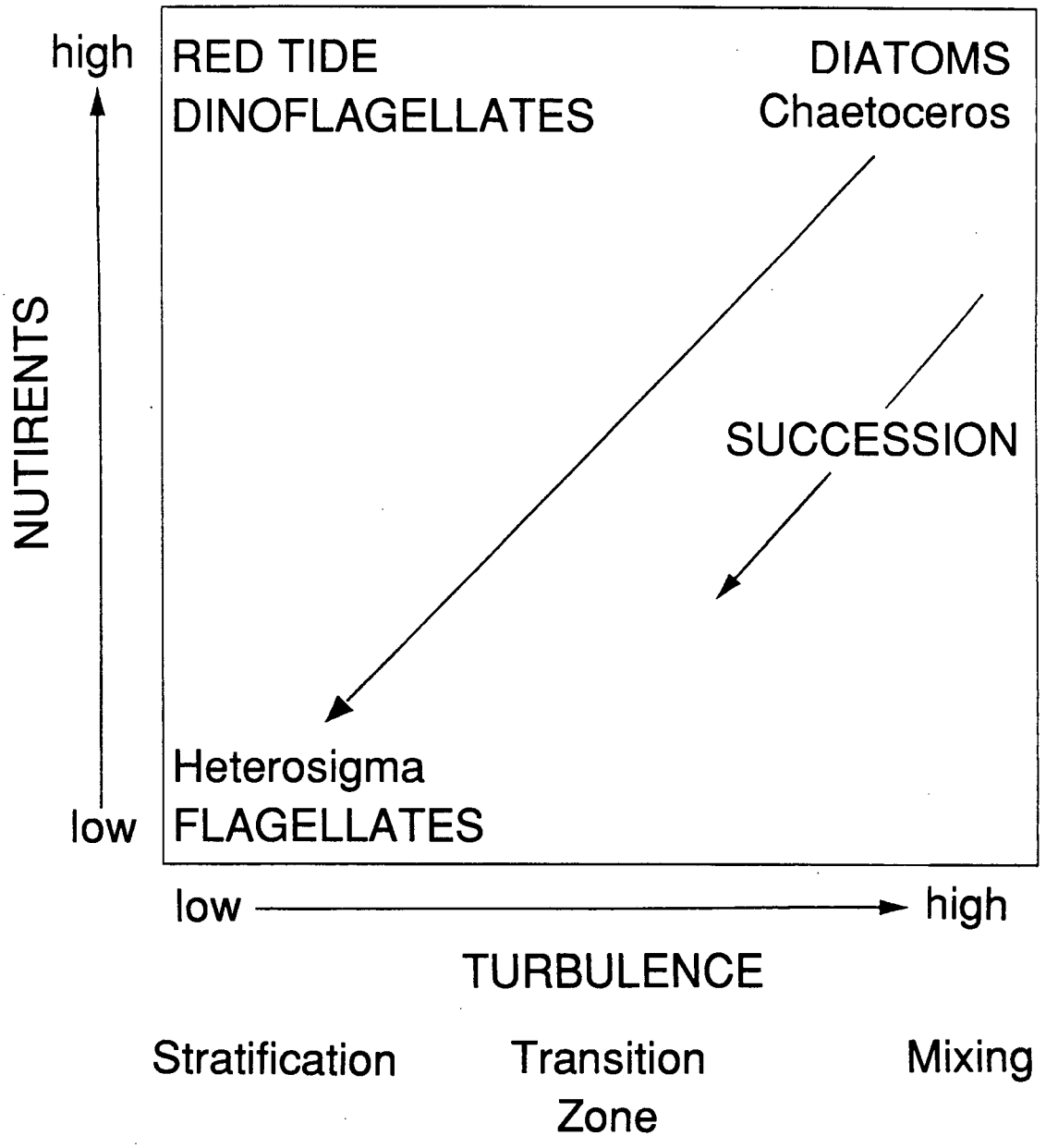

Figure 1.0: The influence of turbulence and nutrient availability on phytoplankton community structure. (Redrawn from Margalef, 1978.)

will allow persisting physical and chemical conditions to play an important role in governing the development of a bloom or "inoculum" of resident or source phytoplankton relative to that in a well-flushed fjord. Prediction of the development of a harmful source or resident "inoculum" within low-turbulent fjords will require the examination of hydrographic characteristics and an understanding of phytoplankton species successional patterns.

Advection of resting stages of phytoplankton from the benthos may also serve as an "inoculum" for the development of resident phytoplankton blooms (Smayda, 1977). Phytoplankton succession may be delayed by the vertical mixing of phytoplankton cells or the advection of seed populations into the euphotic zone (Malone, 1977). It is important to avoid selecting a shellfish or fish farm site that may overlay a "seed bed" of over-wintering cysts of toxic dinoflagellates or a shallow site where resuspension of harmful diatoms may be a regular event. Harmful phytoplankton species repeatedly reached their highest cell concentrations at the same stations over the three year study in Sechelt Inlet, British Columbia posing a threat to the mariculture industry (Taylor *et al.*, 1991).

Fjords act as sediment traps and retain large amounts of fine-grained material such as cysts (Dale, 1976). Cysts act as fine sediment particles and collect with other fine grain materials in the deeper basins of estuaries or fjords (Dale, 1976; Lewis, 1985; Anderson and Keafer, 1985). This accumulation and localization of flagellate or diatom resting stages is defined as a "seed bed" (Steidinger, 1975, 1983; Walker and Steidinger, 1979).

The excystment or germination of phytoplankton from a "seed bed" and consequent introduction to overlying waters has been suggested as the source of initiation of phytoplankton blooms (Walsh et al., 1978; Anderson, 1979, 1983; Owen, 1982; Steidinger, 1983; Lewis, 1985; Binder, 1987; Imai and Itoh, 1987; Marasovic, 1989 Sancetta, 1989; Nakamura, 1990). Only a small percentage of an encysted benthic

population is required to excyst and seed reoccurring estuarine blooms each year (Anderson et al., 1983; Lewis, 1985). However, excysted or germinated cells act only as an "inoculum" and must undergo accelerated vegetative growth under the appropriate hydrographic conditions in order to create a phytoplankton bloom (Steidinger, 1983).

Although the normal development of a phytoplankton succession in waters changing from mixed toward stable conditions are clearly complex, knowledge of regional hydrographic conditions and of regular seasonal patterns of progressive phytoplankton stages will aid as a tool in the prediction of the occurrence of harmful phytoplankton species. In this study the source and resident species composition, succession and cyst distribution was examined in a fjord, Sechelt Inlet, British Columbia, with low flushing rates and freshwater inflow. The distribution and occurrence of harmful phytoplankton species in mixed, stratified and transition zones are compared.

1.2 DESCRIPTION OF THE STUDY SITE, SECHELT INLET, BRITISH COLUMBIA

Sechelt Inlet (49° 40'N, 123° 45'W) is a southern British Columbian fjord located 43 km northwest of Vancouver (Fig. 1.1). The main inlet has a length of 29 km, an average width of 1.2 km and a maximum depth of 300 m. The shallow-silled entrance, U-shaped basin, and parallel sides with bordering high altitude mountains give Sechlet Inlet its fjordic characteristics (Pickard, 1961; Lazier, 1963; Thomson, 1981). Two adjoining inlets, Salmon Inlet and Narrows Inlet, enter the main inlet on the eastern border.

Salmon Inlet (19 km) is treated as the head of Sechelt Inlet because substantial freshwater input exists at the tip of Salmon Inlet compared to that at the southern tip of Sechelt Inlet (Lazier, 1963). As a result, the connection between Salmon Inlet and the town of Sechelt does not contribute significantly to estuarine flow. However, the Clowhom River at the head of Salmon Inlet was dammed in 1957 by B.C. Hydro and as a consequence power requirements regulate water release from this region.

Freshwater runoff and precipitation are responsible for a two-layer flow system that drives the estuarine circulation in fjords. As the brackish surface water flows seaward, a subsurface dense oceanic water mass flows into the estuary, to compensate for the loss of surface water entrained into the outflow of freshwater (Fig. 1.2). However, in Sechelt Inlet there is relatively little estuarine circulation due to the low freshwater drainage (annual mean 110 $m^3 \cdot s^{-1}$; Pickard, 1961). Flushing of deep water will therefore depend largely on intrusion of dense water from a tidal jet over the sill, in addition to the estuarine circulation (Fig. 1.3) (Lazier, 1963).

The entrance to Sechelt Inlet, Skookumchuck Narrows, is a narrow channel 80 m deep and 0.5 km wide (Fig. 1.4). Sechelt Rapids is located near a shallow sill (14 m) and a series of small islands traversing one end of Skookumchuck Narrows. Tidal exchange through Sechelt Rapids is predominantly unidirectional at any one time and the tidal flow (maximum 17 knots; Anon., 1989) enters or leaves the inlet in a turbulent jet (Lazier,

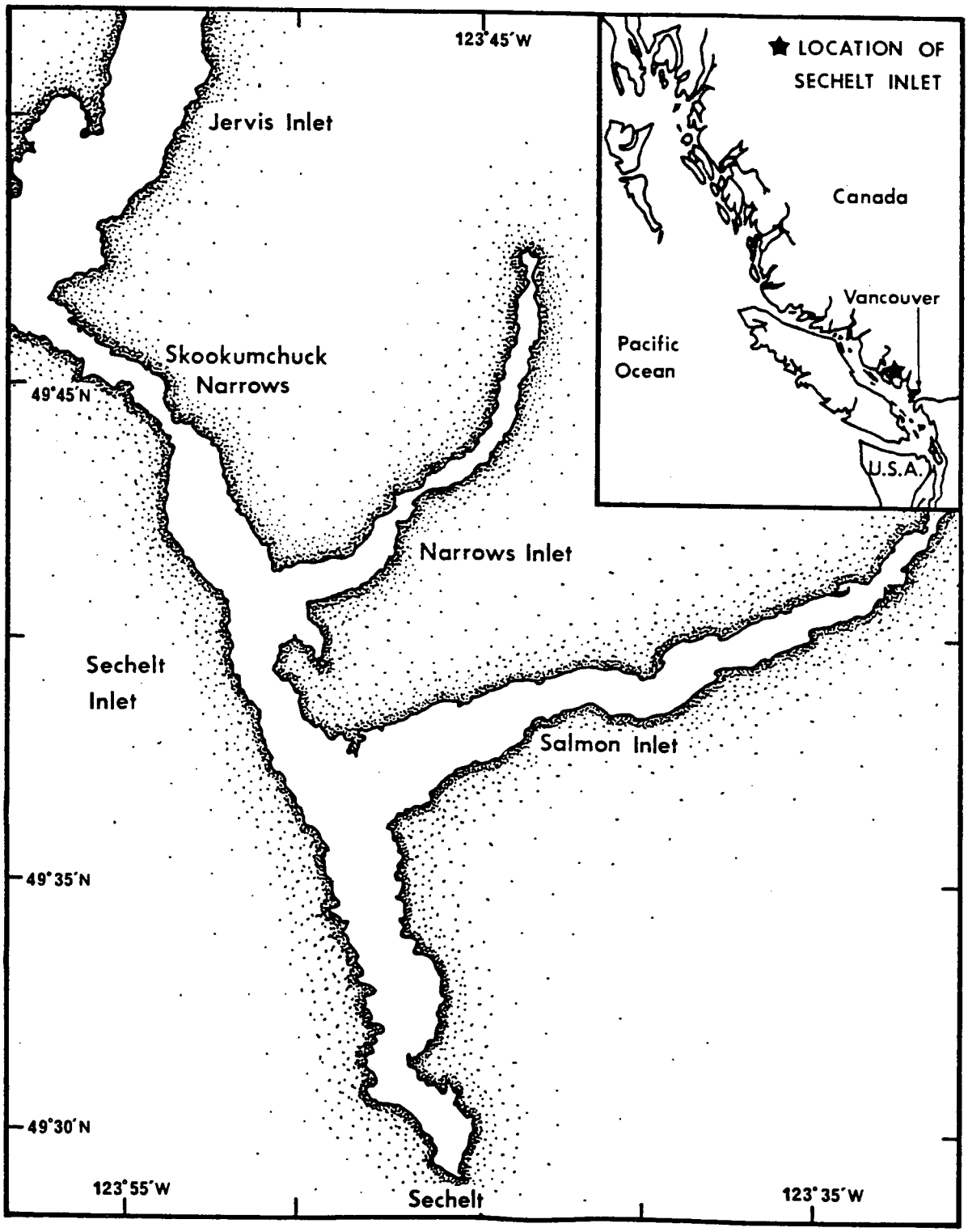

Figure 1.1: Location of study site, Sechelt Inlet, British Columbia

1963). Downstream of the sill the "free" turbulent jet spreads out and expands as the surrounding water is entrained into it. The jet also "hugs" the bottom topography of the sill and descends into the inlet until the intruding water mass reaches a depth with a similar density. This shallow-silled inlet experiences daily fluctuations in vertical profiles of temperature and dissolved oxygen as a result of internal waves generated at the sill entrance (Gormican, 1989). Nutriclines will be displaced vertically along with the density gradient.

Three distinct vertical layers exist in Sechelt Inlet (Figure 1.2) (Lazier, 1963). The surface layer (I) occupies the top 5 m and consists of low salinity and seasonally high temperature water due to precipitation, river runoff and solar heating. At the head of Narrows Inlet, layer I may freeze during the winter months. The intermediate layer (II) is influenced by the tidal jet and occupies a depth interval between about 5 and 65 metres. The deepest layer (III) of Sechelt Inlet usually lies below the layer of tidal influence and is characterized by uniform temperature and salinity. The continual oxidation of organic matter and the low frequency of flushing renders this "remnant" water low in oxygen. Oxygen levels lower than 7 $mg \cdot L^{-1}$ in the "remnant" water of Sechelt, observed by Lazier (1963) and Smethie (1987), may cause distress to farmed salmonids if the bottom water is pushed up to the surface waters (Weston, 1989). At intervals of one to several years the tidal jet may be sufficiently dense to penetrate into layer III and replace all or part of it.

Narrows Inlet is 14 km long, 85 m deep and contains a shallow sill (14 m) located 5.3 km along its length which partially separates this region from Sechelt Inlet. The shallow basin that extends past the shallow sill at Tzoonie Narrows is approximately 8.4 km long and 0.8 km wide and has a maximum depth of 85 m. The estuarine circulation proposed by Lazier (1963) for the main inlet system pertains to this region also. The low salinity runoff layer occupies the top 5 to 10 m while the intermediate layer is about 50 m deep. The deep layer spans the bottom 10 to 20 m, and forms the stagnant remnant water.

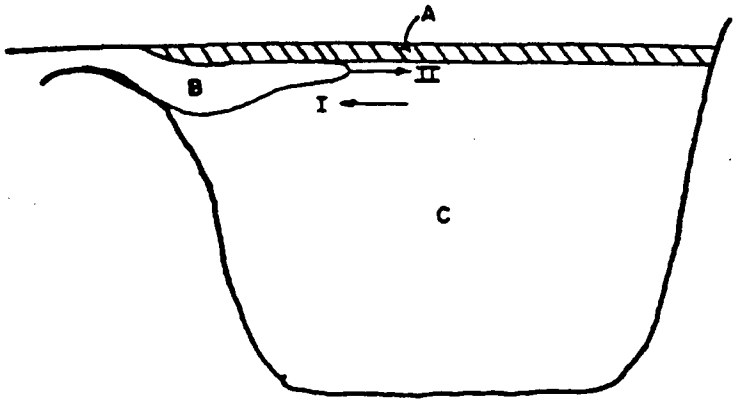

Figure 1.2: Two-layer circulation pattern of Sechelt Inlet during flood tide. A = freshwater surface layer, B = flood water, C = indigenous water, I = outflow, II = up-inlet flow (Lazier, 1963).

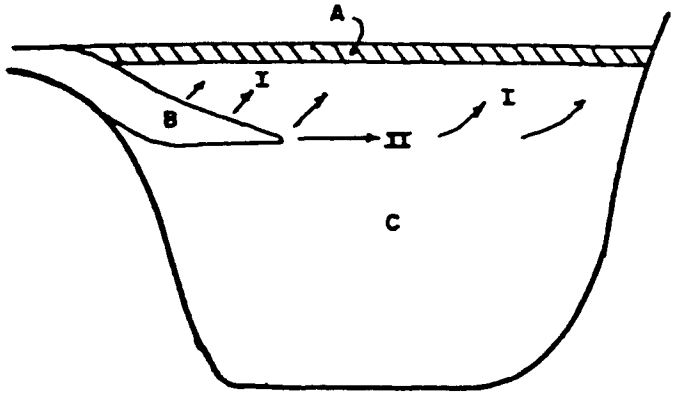

Figure 1.3: Two-layer circulation pattern of Sechelt Inlet during the sinking of flood tide water and consequent flushing of the indigenous inlet water (Lazier, 1963).

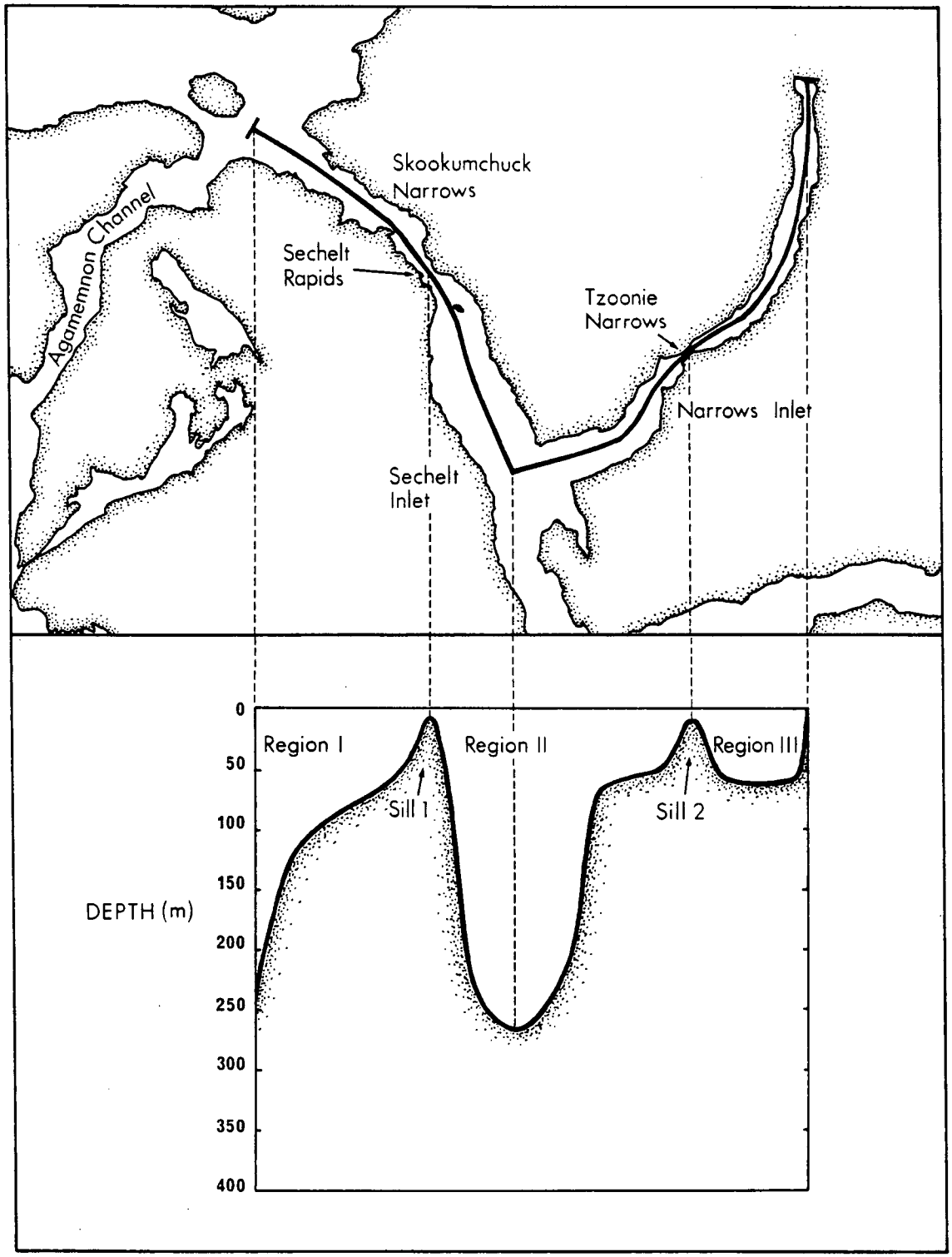

Figure 1.4: (A) Transect line through study site in Sechelt Inlet, British Columbia. (B) The presence of two sills in the cross-section of the transect line separates the study site into three regions (I, II, and III).

Narrows Inlet experiences prolonged periods of stratification due to substantial river input, the protection of the sill and the high altitude of the bordering mountains.

Figure 1.4 shows a cross-section of the transect line through the area in the Sechelt inlet system examined in this thesis. The two sills, located at Skookumchuck Narrows and Tzoonie Narrows, separate the area of interest into three distinct regions (I, II, and III). The succession of the phytoplankton communities found in these three regions between June and September will be discussed in Chapter Two. The phytoplankton community found in the water-sediment interface samples collected from each region is discussed in Chapter Three. A comparison of the planktonic and benthic phytoplankton communities will be made in the general discussion.

CHAPTER TWO: Phytoplankton community succession and the distribution of potentially harmful phytoplankton in three regions in Sechelt Inlet, British Columbia

2.1: INTRODUCTION

Succession involves the directional or progressive change in the dynamics of a community towards a stable state. Margalef (1963) compares the precise adjustment of a community of organisms to their environment as a succession proceeds to the maturing of an organism or to the evolution of a species. For example, the succession that takes place on a marine substrate involves a progression of species in the order of bacteria, diatoms, seaweeds, barnacles, sponges, and then mussels. The community continues to become more heterogeneous and complex as the number of niches increases through the introduction of parasites, symbionts, and animal forms.

Changing physical (light, temperature), chemical (nutrient, toxins), and biological (competition, grazers) variables within a given water mass influence changes in the species composition of a phytoplankton population (Smayda, 1980). An r and K continuum can be used to characterize the phytoplankton species that occur in the early and late stages of an ecological succession (Guillard and Kilham, 1977). R-selected (smaller diatoms) species generally have small body size, exhibit high growth rates with little intra- or inter-specific competition, prevail under unpredictable hydrographic conditions, and end up in catastrophic mortality due to nutrient depletion (Pianka, 1970, Guillard and Kilham, 1977). This type of phytoplankton dominates the early stages of a succession or during a spring bloom. K-selected species (larger flagellates and some diatoms) have larger body sizes, slower growth rates with more intense interspecies competition, predominate in constant or predictable conditions, and delegate a higher proportion of metabolic reserves for non-reproductive processes (e.g. toxin production). K-selected species dominate the latter stages of a succession.

Margalef (1967) postulated four stages of a phytoplankton succession that proceed in association with the stratification of hydrographic conditions. In temperate coastal regions the first stage is mainly represented by diatoms such as *Skeletonema costatum*, *Thalassiosira nordenskioeldii*, *Chaetoceros sociale*, *Ch. radicans*, *Ch. debile*, *Ch. affinis*, *Ch. compressum*, *Leptocylindrus danicus*, *Rhizosolenia delicatula*, *Asterionella* spp., *Thalassionema* spp., and *Nitzschia delicatissima* and small flagellates such as *Dictyocha speculum* that bloom in mixed nutrient-enriched waters (Margalef, 1967, Guillard and Kilham, 1977; Taylor and Pollingher, 1987). Typically, cell surface to volume ratios (≈ 1 $\mu m^2/\mu m^3$) and growth rates (> 1 division$\cdot day^{-1}$) are relatively high while the pigment index (chlorophyll-a/total pigment) ranges between 2.5 and 3.5. Phytoplankton population densities, reaching 100 to 1000 cells$\cdot ml^{-1}$, are regulated by nutrient input, dispersal and grazing. Appendages that are present are weakly-structured and cells are generally enveloped in excreted mucilaginous materials.

The second stage is dominated by medium-sized diatoms such as *Chaetoceros* spp. (linked in chains with long robust setae), *Bacteriastrum* spp., *Thalassiosira rotula*, *Schroderella*, *Eucampia zodiacus*, and *Rhizosolenia* spp. and some flagellates (Margalef, 1963, 1967; Guillard and Kilham, 1977). The cell surface to volume ratio ranges between 0.2 and 0.5 $\mu m^2/\mu m^3$ depending on the presence or absence of setae and a reduction in the pigment ratio is observed. Densities of phytoplankton populations in the second stage reach 20 to 200 cells$\cdot ml^{-1}$ with growth rates of one division every few days. The diversity of the community has increased relative to stage one and grazing tends to be an important factor during this stage.

Stage three represents a continuation of stage two except it is characterized by large cylindrical diatom genera such as *Bacteriastrum*, *Corethron*, *Nitzschia* and *Rhizosolenia* and flagellate genera such as *Prorocentrum*, *Dinophysis*, *Gonyaulax*, *Ceratium*, *Protoperidinium*, *Gymnodinium*, and *Gyrodinium* (Margalef, 1967; Guillard and Kilham, 1977). The cell surface to volume ratio is generally low and population densities are

around 10 cells•ml^{-1}. The diatom species present in this stage have adapted to grow slowly under poor nutrient conditions. The heterogeneous vertical profile associated with prolonged stratification allows for the vertical zonation of diatoms and flagellates causing an increase in diversity in a manner similar to the benthic succession.

Stage four may or may not follow stage three depending on the duration of the stratified conditions. During this stage the majority of diatoms form resting spores in response to the exhaustion of surface nutrients and sink rapidly from the upper water column (Guillard and Kilham, 1977). Only diatoms such as *Rhizosolenia*, *Chaetoceros*, or *Nitzschia delicatissima* persevere. Common dinoflagellates consist of *Ceratium*, *Dinophysis*, *Gonyaulax*, and *Oxytoxum* (Margalef, 1967). The cell surface to volume ratio of flagellates is lower than that of the last stage. The growth rates may be as low as one division per week and therefore may limit population densities to less than 10 cells•ml^{-1}. The large dinoflagellates, such as *Gymnodinium sanguineum* and *Protogonyaulax tamarensis*, are generally toxic (Taylor and Pollingher, 1987) and contain a higher proportion of carotene pigments and passive materials in the exterior coverings such as lists, keels, and horns (Margalef, 1967). The proportion of zooplankton increases causing an increase in diversity in total plankton. However, diversity decreases dramatically in the event of a toxic monospecific bloom or red tide (Taylor and Pollingher, 1987) which may develop if stratified conditions persist for several weeks (Margalef, 1958).

Differences in physical, chemical, and biological factors in contiguous waters may give rise to different regional successional patterns and dominance of phytoplankton species (Braarud, 1958). Some coastal regions may promote nutrient regeneration with prolonged stratified conditions, while nearby turbulent waters may not. Succession is predicted to proceed faster in the stratified region and delayed by the vertical mixing of phytoplankton cells in nearby mixed waters. In Sechelt Inlet, region III (Fig. 1.4) represents the former description while region I represents the latter description. It is

hypothesized that the tidal mixing that takes place in region I will slow down the rate of succession and favour the occurrence of stage one and two species, relative to that of region III. The advection of "seed" populations, comprised of stage one and two species, into the euphotic zone may also delay succession (Malone, 1977). A regional comparison of "seed" populations is discussed in Chapter three.

In the event of regional water admixture, changes in the species composition of the autochthonous population is influenced by the changing physical and chemical factors of the incoming water and also by the introduction of allochthonous phytoplankton species (biological factors) (Smayda, 1980). This type of change in species composition is referred to as a sequential change and is predicted to occur in regions I and II due to the strong erosion of the incoming tidal jet. True successional stages are hypothesized to occur in Region III since little tidal exchange takes place across the shallow sill at Tzoonie Narrows, minimizing the admixture of water. The extreme case of true marine succession, occurring where an isolated body of water remains uninfluenced by another, and of sequential changes, occurring where a body of water entirely displaces another, probably rarely happens (Smayda, 1977). The magnitude to which succession and sequential changes overlap varies depending on the season and the regional hydrographic characteristics. The extent and duration of succession or sequential changes will be discussed later in this chapter.

This chapter presents the successional stages of the groups and species of the phytoplankton communities found in regions I, II, and III (Fig. 1.4) between early June and late September in 1989. These stages are related to biological (nutrients, grazers) and physical (density) variables present at the time of sampling. The influence of allochthonous species (region I) and autochthonous species (region III) on the phytoplankton community in region II is examined. Also, a special focus is made towards the understanding of the occurrence and distributional patterns of harmful phytoplankton in the three regions in the Sechelt Inlet system.

2.2 METHODS

Phytoplankton and nutrient samples were taken from three stations (Fig. 2.0) located in regions I, II, and III (Fig. 1.4) in Sechelt Inlet between June and September, 1989. Bimonthly trips took place on the dates listed in Table 2.0 and sampling was performed from a 6.6 m departmental boat, the Tintannic. Compass bearings at each station were recorded and used in conjuction with triangulation methods to find the locations of the three stations and maintain the position of the boat on following field trips. The stations were sampled in order of one, two, and three, with station one sampled at the end of flood tide (Table 2.0). The sampling time spent at each station was one-half an hour.

TABLE 2.0: Maximum current speeds during the flood tide period at Skookumchuck Narrows (region I) in Sechelt Inlet before sampling at station one (Anon., 1989).

Sampling Date	Flood Tide Period (PST)	Maximum Current Speed (knots)
June 9	0825 - 0905	0.3
June 25	0820 - 1010	3.1
July 8	0715 - 0905	2.4
July 22	0540 - 0735	6.1
August 10	0930 - 1250	8.4
August 26	1100 - 1510	12.9
September 8	0815 - 1140	9.8
September 25	1115 - 1525	13.2

A Par ^{TM} bilge pump with a 2.5 cm diameter plastic hose was used to sample the top eighteen metres of the water column. The seawater flow through the hose was determined by recording the volume of seawater in the hose in a bucket and measuring the time period that the pump took to fill this volume. The flow rate of the pump

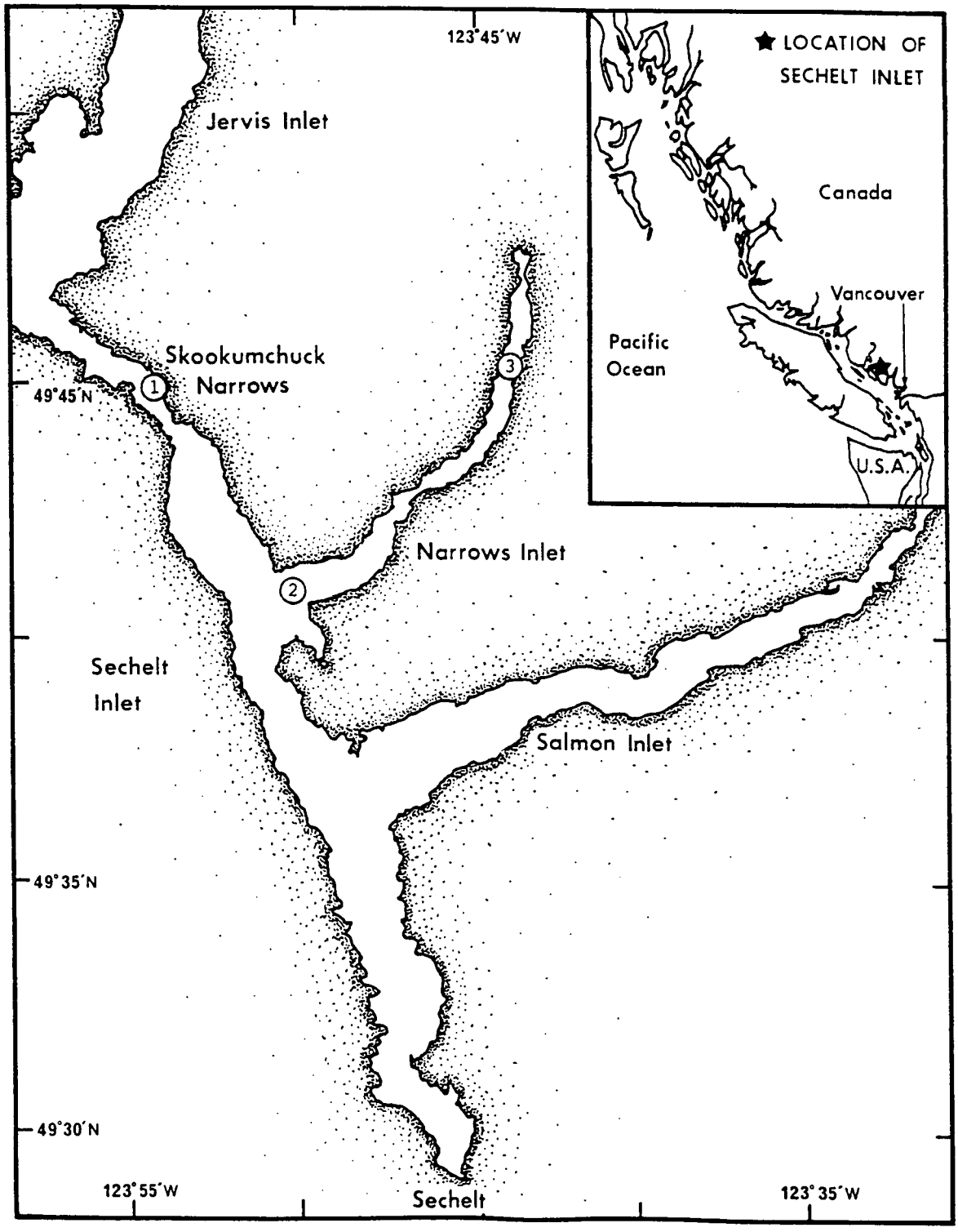

Figure 2.0: Location of the three plankton stations in Sechelt Inlet, British Columbia.

remained constant regardless of the depth sampled. Once the hose was at depth, the pump was turned on and the volume of the hose had cleared, seawater was collected in a bucket. An integrated water sample was collected by raising the hose three metres over a period of ten seconds. Then the volume of seawater in the hose was also collected in the bucket. This procedure was repeated five times to give six three metre depth intervals of the upper water column.

Seawater from each depth interval was collected in 125 ml jars and preserved with Lugol's solution for phytoplankton analysis. Seawater was also collected from each depth interval for nutrient analysis. One hundred ml of seawater was collected in a syringe and filtered through a precombusted 2.5 cm diameter Whatman GF/F filter contained in a Swinnex holder. The filtrate from each depth interval was collected in two 30 ml polypropylene bottles for nitrate and ammonium, and phosphate analysis. To reduce any enzymatic breakdown and bacterial activity during the sampling trips, the filters, kept for chlorophyll analysis, and filtrates were kept on ice. All equipment used in nutrient and chlorophyll analysis was acid washed (10% HCl) and distilled water rinsed several times. The temperature was recorded after a thermometer was placed in a bucket containing a water sample collected from a specific three metre depth interval. Back at the laboratory an ENDECO ^{TM} refractometer was used to determine the salinities of seawater from the six depth intervals. Observations of Secchi disc depth, cloud condition, relative wind speed, wave height at the time of sampling were also recorded.

Phytoplankton species were identified and enumerated under an inverted microscope (Hasle, 1978). Preserved samples were resuspended in the 125 ml jars and ten ml were removed and allowed to settle for twenty-four hours in ten mls Leitz settling chambers. Phytoplankton were viewed under low (120 X), medium (192 X), and high power (480 X) depending on size and abundance.

Chlorophyll analysis was performed by placing filters into ten mls of 90 percent acetone:water solution, sonicating for ten minutes, and allowing extraction to take place

for twenty-four hours in a cold/dark refrigerator (5 °C). Fluorescence was then measured using a Turner Designs Model 10 ^{TM} fluorometer. Fluorescence values were then converted to chlorophyll ($\mu g \cdot L^{-1}$) (Parsons *et al*, 1984).

Nitrate and ammonium samples were analyzed on an Technicon Autoanalyzer ^{TM} Standards consisted of 5, 10, 20, and 30 μM NO_3 for nitrate analysis and 0.4, 0.8, 1.6, 2.4, and 3.2 μM NH_4 for ammonium analysis. A baseline of three percent NaCl was used. Frozen ammonium samples prior to analysis result in ammonium concentrations with a high variability. Therefore, the ammonium values must be observed with some skeptism. Phosphate samples were analyzed according to Parsons *et al.* (1984) on a Bausch and Laumb ^{TM} spectrophotometer.

Phytoplankton that fall into the stage one and stage two categories, proposed by Margalef (1967), generally occur in numbers significantly greater than those that fall into the stage three and stage four categories. Even though the large potentially toxic dinoflagellates of stage three and four may not reach the abundance that a stage one diatom (*e.g. Skeletonema costatum*) will, they can have a great impact on the rate of succession. The production of inhibitory metabolites by dinoflagellates may cause a shift in phytoplankton commumity by influencing zooplankton to selectively graze on other co-existing organisms (Stoecker *et al.*, 1981) or altogether inhibit the growth of grazers (Carlsson *et al.*, 1989) and co-existing phytoplankton (Metaxas and Lewis, 1991; Rijstenbil, 1989) altogether. If cell concentrations are used in a relative comparison of phytoplankton stages, then the occurrence and influence of stage three and four organisms on phytoplankton succession will be underestimated. Therefore, phytoplankton concentrations ($cells \cdot L^{-1}$) were converted to biomass ($\mu gC \cdot L^{-1}$) to remove any biases appearing towards the occurrence of high concentrations of stage one and stage two species. Conversion equations for biomass calculations were based on geometric figures and were similar to those outlined by Smayda (1978). The conversion equation for ciliate biomass was taken from Putt and Stoecker (1989).

2.3 RESULTS AND DISCUSSION

This section is divided into three parts: the physical and chemical observations (2.3.1), the succession of phytoplankton communities (2.3.2), and the distribution and abundance of harmful phytoplankton (2.3.3).

2.3.1 PHYSICAL AND CHEMICAL OBSERVATIONS

Physical Observations

The temperature and salinity in region I are fairly uniform over depth due to the tidal mixing experienced in Skookumchuck Narrows (Fig. 2.1). In region III stratification appears in June, which is early compared to the rest of the inlet, and persists through to September 25 (Fig. 2.3). Surface temperatures from June to September ranged between 11 and 13.5°C in region I, 12.5 to 16.5°C in region II, and 12.5 to 15.5°C in region III. The largest vertical temperature change over the top twenty metres was reached on August 10 in region III (4.5°C), on July 23 in region II (3.5°C), and on July 8 in region I (3°C). Surface temperatures were never observed to be above 17°C, whereas in the following summer surface temperatures rose to 23°C. Surface salinities in region III have been observed to reach salinities as low as 5 psu (Pond, unpublished data), however, the salinity in the surface waters in this study appears relatively higher due to the integration of a large three metre depth interval.

Fig. 2.3.5 shows the one percent light levels present in regions I, II, and III between June 9 and September 25. In general, the one percent light levels present in region I are deeper than those in region II and III. The one percent light levels in region II and III decrease and increase respectively in a similar pattern across the sampling trips. The penetration of light in region III is very shallow relative to that in region I and II and may result from the sediment loading of the riverine plumes or the dense subsurface phytoplankton blooms observed in region III.

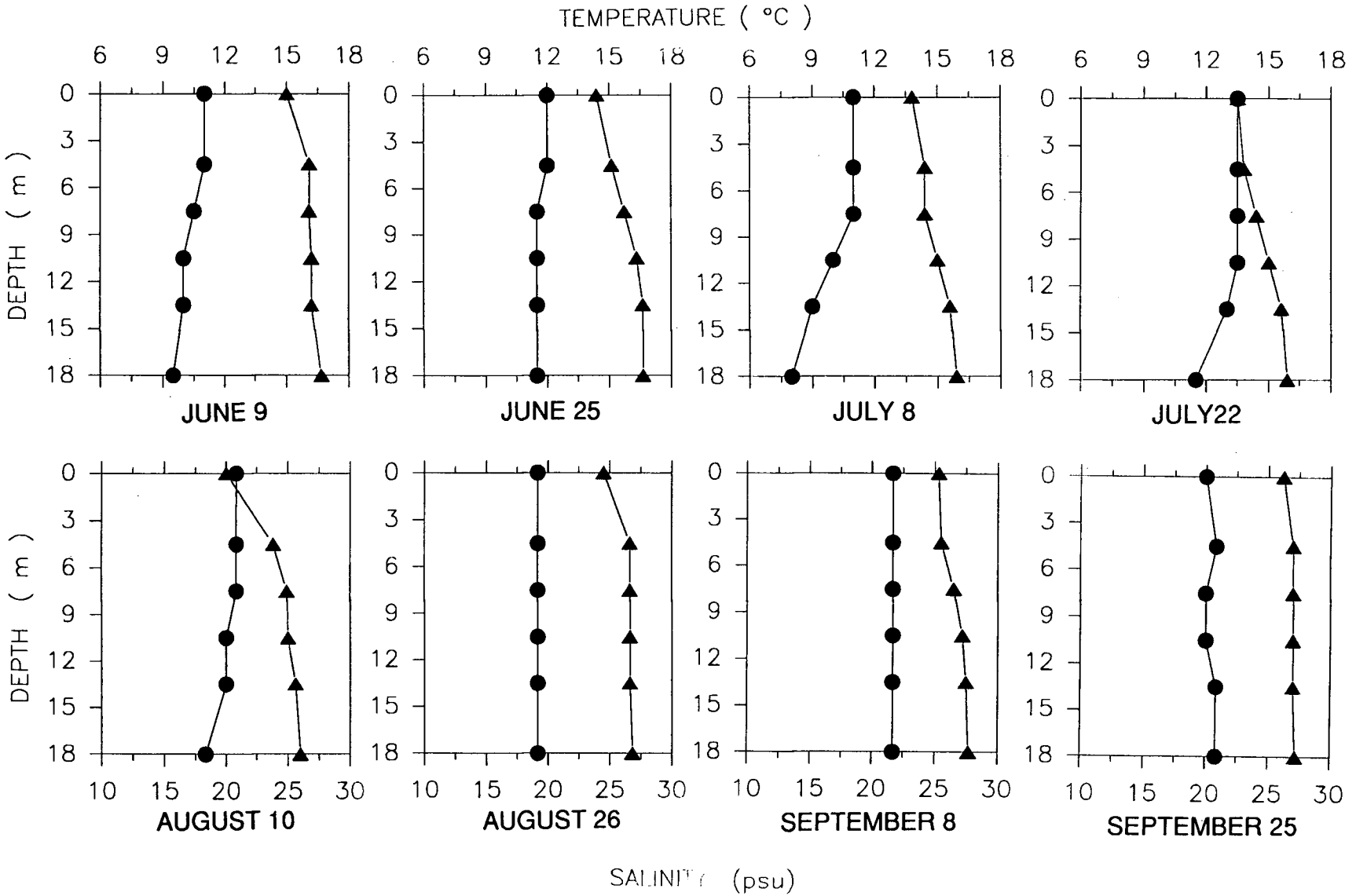

Figure 2.1: Temperature (°C) and salinity (psu) profiles for region I between June 9 and September 25. ▲ = salinity, ● = temperature.

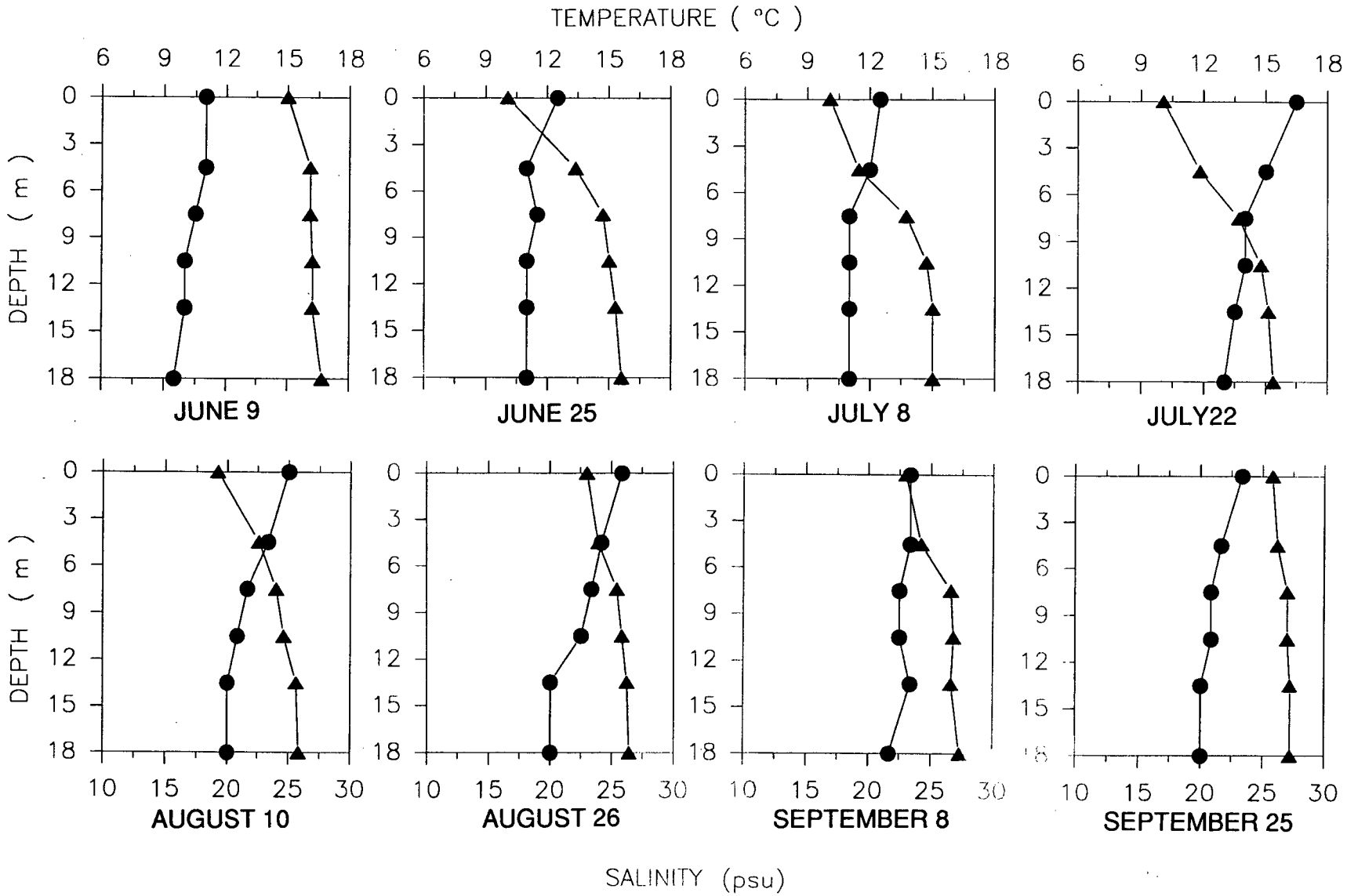

Figure 2.2: Temperature (°C) and salinity (psu) profiles for region II between June 9 and September 25. ▲ = salinity, ● = temperature.

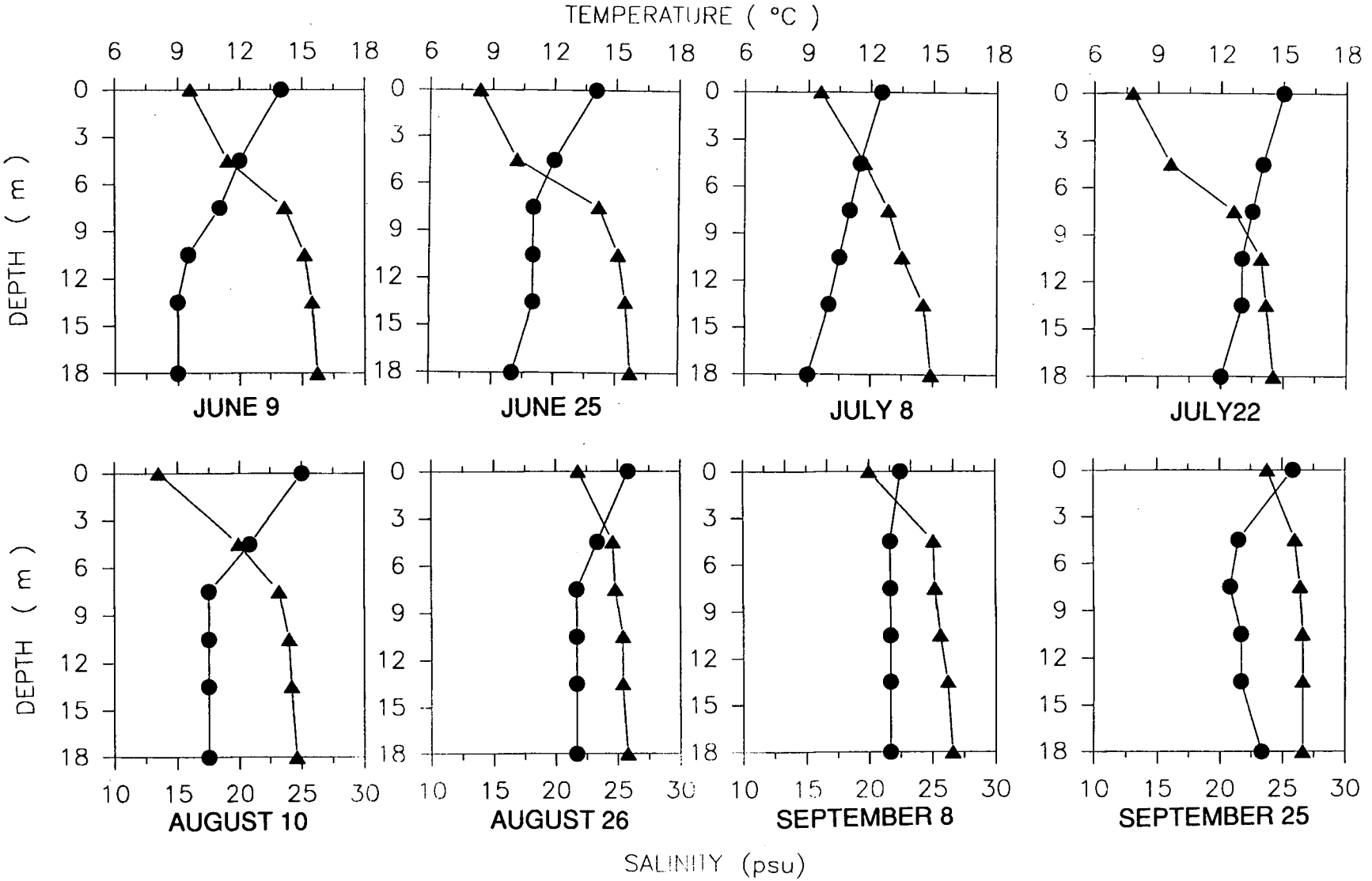

Figure 2.3: Temperature (°C) and salinity (psu) profiles for region III between June 9 and September 25. ▲ = salinity, ● = temperature.

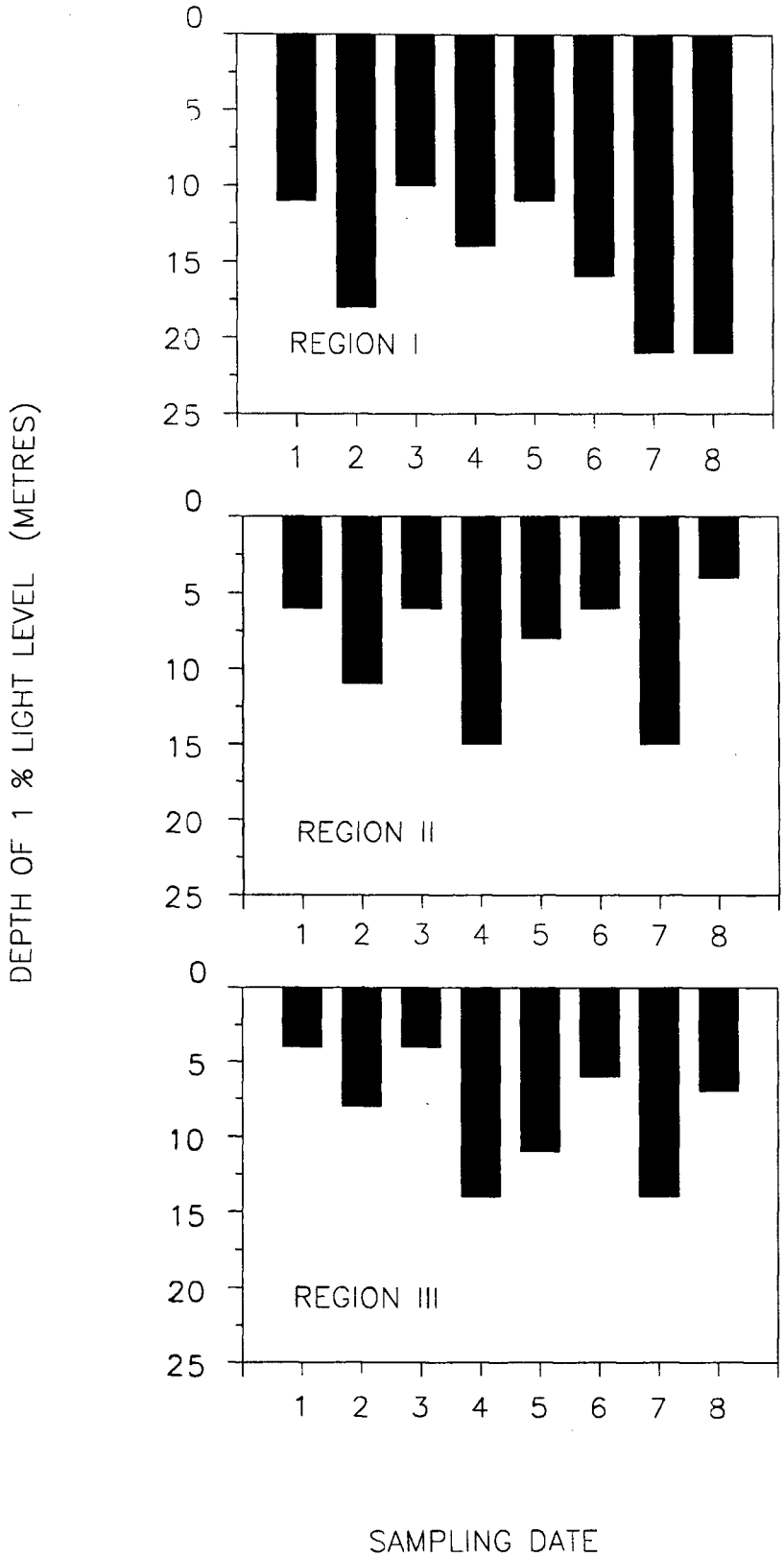

Figure 2.3.5: Depth of the 1 % light level in regions I, II, and III between June 9 and September 25. 1 = June 9, 2 = June 25, 3 = July 8, 4 = July 22, 5 = August 10, 6 = August 26, 7 = September 8, 8 = September 25.

Chemical Observations

The nitrate profiles of region I are very different from those in regions II and III (Fig. 2.4). The ammonium profiles show a difference between region I and III (Fig. 2.5). A nitrate or ammonium gradient did not exist in region I during the sampling period due to the strong tidal mixing that takes place at Sechelt Rapids located within Skookumchuck Narrows (Anonymous, 1989). A prolonged stratified period with strong nutriclines is shown in region III, while a shorter period of intermediate nutriclines can be seen in region II. The low surface concentrations of nitrate in regions II and III support previous observations that ammonium and nitrate exhibit sharp seasonal trends in coastal regions (Harrison *et al.*, 1987) (Fig. 2.4 and 2.5).

Nitrate (new production) often plays a more important role in nitrogen uptake by phytoplankton in the surface waters in the spring while ammonium (regenerated production) supports phytoplankton growth in the late summer when surface waters are stratified and nitrogen-depleted (Paasche and Kristiansen, 1982; Cochlan, 1986; Dortch and Postel, 1989, Wassmann, 1991). The nitrogen-replete waters of region I would likely support phytoplankton growth typifying stage one and stage two-type phytoplankton (spring bloom), while the phytoplankton growth in regions II and III would resemble stage three and stage four-type phytoplankton (summer bloom). Phytoplankton blooms that dominate in the spring and autumn lead to nutrient-depleted cells in the absence of a continual input of nitrate, while summer blooms supported by regenerated nitrogen or ammonium lead to more balanced growth (Sakshaug and Olsen, 1986). Even though the waters of region I are always nutrient replete, the amount of turbulence in region I may be inhibit the formation of large phytoplankton blooms since laboratory studies have shown that excess turbulence inhibits growth rates of flagellates (Thompson *et al.*, 1990) and causes cellular damage in diatoms such as *Chaetoceros curvicetum* and *Coscinodiscus concinnus* (Smayda, 1980).

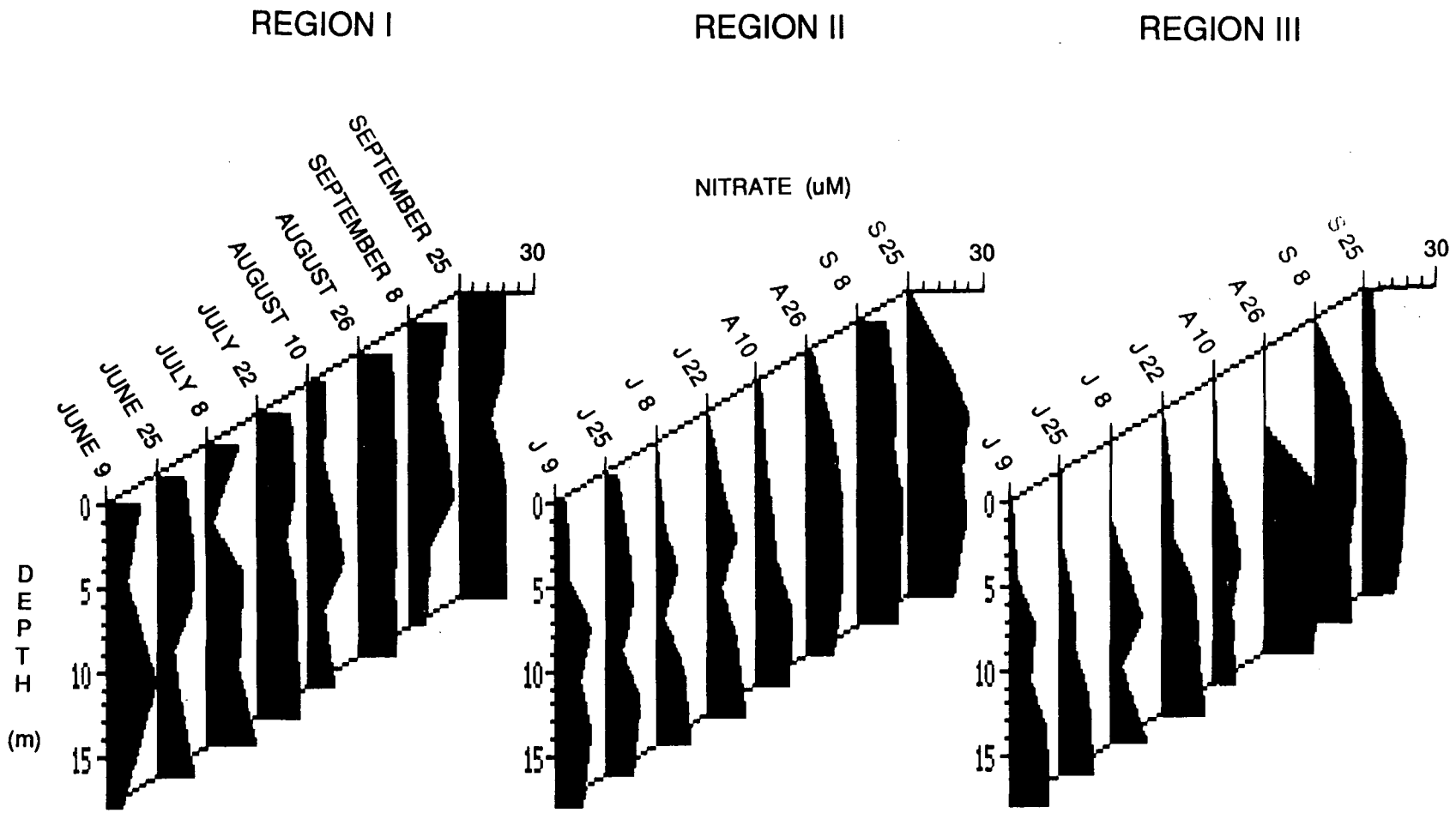

Figure 2.4: Nitrate (μM) profiles sampled between June 9 and September 25 in regions I, II, and III.

Table 2.1: Nitrate and ammonium concentrations (μM) at the 0 to 6 metre depth intervals between June and September in Regions I, II, and III. Values over 2 μM have one decimal place.

TIME	DEPTH INTERVAL	NITROGEN SOURCE	REGION I	REGION II	REGION III
JUNE 9	0-3m	NH_4	0.38	1.82	0.42
		NO_3	13.5	3.8	0.93
	0-6m	NH_4	1.66	1.28	3.1
		NO_3	8.4	5.5	2.9
JUNE 25	0-3m	NH_4	1.35	0.47	0.88
		NO_3	10.9	4.7	0.60
	0-6m	NH_4	0.47	0.75	0.23
		NO_3	13.9	8.6	0.60
JULY 8	0-3m	NH_4	0.48	0.45	0.54
		NO_3	11.7	0.00	0.00
	0-6m	NH_4	0.36	0.53	0.44
		NO_3	2.7	2.7	0.00
JULY 22	0-3m	NH_4	0.46	0.58	0.49
		NO_3	12.9	0.39	0.25
	0-6m	NH_4	0.36	2.3	0.67
		NO_3	15.0	6.3	3.5
AUG 10	0-3m	NH_4	1.28	0.46	0.35
		NO_3	6.7	1.23	0.17
	0-6m	NH_4	1.68	1.17	0.79
		NO_3	6.2	2.8	1.28
AUG 26	0-3m	NH_4	0.45	0.31	0.44
		NO_3	13.3	1.98	0.00
	0-6m	NH_4	0.43	0.44	0.49
		NO_3	14.1	0.53	0.34
SEPT 8	0-3m	NH_4	0.83	1.29	0.53
		NO_3	15.5	11.3	0.00
	0-6m	NH_4	2.1	0.65	1.29
		$N0_3$	11.1	14.5	13.9
SEPT 25	0-3m	NH_4	0.74	0.67	0.84
		NO_3	19.1	1.26	3.1
	0-6m	NH_4	1.65	0.99	1.41
		NO_3	18.2	16.6	4.2

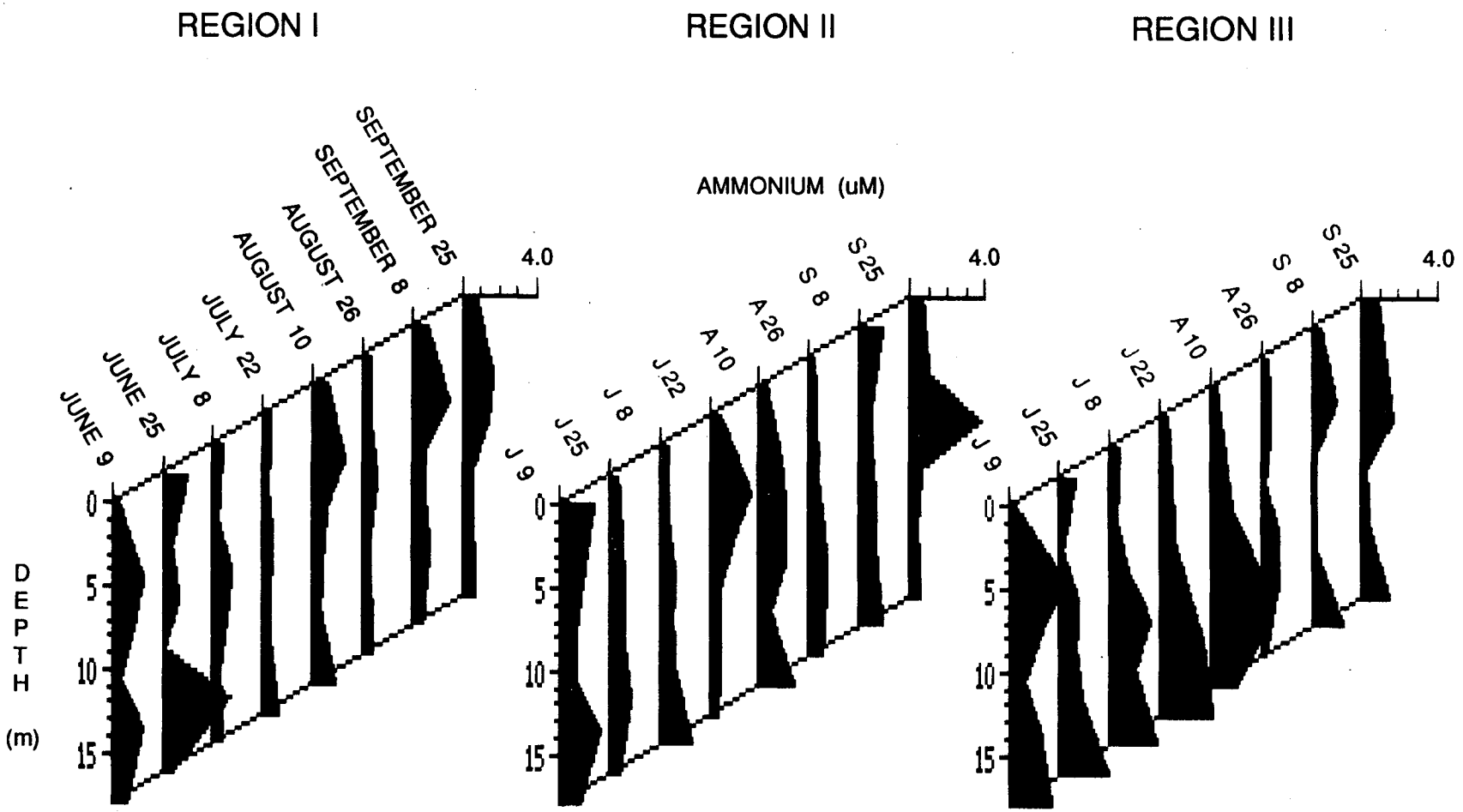

Figure 2.5: Ammonium (μM) profiles sampled between June 9 and September 25 in regions I, II, and III.

The surface waters (0-6 m) of region III appear to be nitrogen-depleted during the sampling trips between June 9 and September 9. If the ammonium concentrations were above 1 μM, ammonium should have been preferentially taken up by phytoplankton since this ammonium threshold concentration inhibits the uptake of nitrate in most phytoplankton (Dugdale and Goering, 1967; Eppley *et al.*, 1973; McCarthy *et al.*, 1977; Paasche and Kristiansen, 1982; Cochlan, 1989). However, ammonium remained below this inhibition threshold in the surface waters (0-6 m) of region III from June 9 to August 26. Nitrate may serve as an alternative source of nitrogen as it may be taken up simultaneously when ammonium concentrations are low (Dortch and Postel, 1989; Cochlan, 1989). In region III, the undetectable levels of nitrate observed at the surface depth intervals on July 8 (0-6 m), August 26 (0-3 m), and September 8 (0-3 m) (Table 2.1) imply that the phytoplankton in the surface waters are nitrogen-deficient. However, low surface nitrogen concentrations will not pose a problem for phytoplankton such as flagellates that are capable of controlling their position in the water column (Smayda, 1980; Taylor, 1987).

In region II, ammonium concentrations fell below 1 μM in the 0 to 3 metre depth interval from June 23 to August 26, and on September 25. Nitrate concentrations in this region fell to undetectable concentrations on July 8 and below 0.4 μM on July 22. In region I the nitrate concentrations were relatively high (> 2.65 μM) when ammonium concentration fell below 1 μM, implying that nitrogen deprivation did not occur in this region (Table 2.1).

Although it is clear that the concentrations of these two types of inorganic nitrogen are low, caution must be taken in concluding that phytoplankton are nitrogen limited, due to the possibility of rapid recycling (Dortch and Postel, 1989) and unmeasured organic nitrogen sources in this study (Antia *et al.*, 1991). If a pycnocline is located above the light compensation depth following a spring bloom, the surface waters will become nutrient-depleted (Skjoldal and Wassmann, 1986). In region I a pycnocline does not

develop over the sampling period in region I (Fig. 2.1 and Fig. 2.3.5). In region II a pycnocline does not seem to develop above the compensation depth or the one percent light level (Fig. 2.2 and Fig. 2.3.5). Nitrogen depleted surface waters may result from the development of the pycnocline above the compensation depth on June 25, July 22, August 10, and September 8 in region III. Nitrogen limited regions can be characterized by low uptake rates at the surface with a subsurface chlorophyll maximum in or above the nitricline (Harrison *et al.*, 1983; Cochlan, 1986; Dortch and Postel, 1989). The chlorophyll maxima (Fig. 2.9) in region III are located in or just above the nitriclines (Fig. 2.4) during the latter sampling trips on August 10, August 26, September 8, and September 25 indicating that this region is likely nitrogen-limited.

The uptake of nitrate and ammonium varies with species composition and light conditions (Cochlan, 1989; Dortch and Postel, 1989). Certain species avoid the highly irradiated nutrient-depleted surface waters since they may experience photochemical damage. The depth of the one percent light level fell above the nitracline and was situated in the nutrient-depleted surface interval (0 to 6 m) on June 9, July 8, and August 26 in region III and on July 8 in region II (Fig. 2.3.5), implying that phytoplankton above and below the nitracline are nitrogen-limited. Nitrogen deprivation in phytoplankton may reduce photosynthetic rates, increase the uptake systems for nitrogen compounds other than nitrate and decrease the activity of nitrogen-assimilatory enzymes and cause the loss of chlorophyll (Syrett, 1981). Although flagellates and some diatoms can control their position at the nutrient-rich depths, nitrogen uptake below the nitracline will still required a sufficient amount of light. Nitrate is found to be the most light dependent, while ammonium is found to be the least light dependent of the sources of nitrogen tested (Cochlan, 1989; Dortch and Postel, 1989). One adaptive response to nitrogen limitation suggested by Cochlan (1989) was that picoplankton decrease their light dependence of nitrogen uptake and maintain their position in the nitrogen-deficient surface waters to avoid the cost of migration.

Phosphate

Phosphate is thought to generally limit phytoplankton growth in fresh and brackish water (Sakshaug and Olsen, 1986), but not in marine environments because it is recycled quickly (Perry and Eppley, 1981). Phosphate concentrations fell between the range of 0 and 3 μM in regions I, II, and III (Fig. 2.6). This range of values does not differ from those found in Sechelt Inlet (Smethie, 1987; Taylor *et al.*, 1991), the Strait of Georgia (Harrison *et al.*, 1983), and Puget Sound (Rensel *et al.*, 1990). Phosphate concentrations tended to be lower in the surface waters of regions II and III than region I. Region III exhibited the strongest gradients of increasing phosphate concentration with depth. On July 8, both an increase in phosphate (Fig. 2.6) and chlorophyll was observed in region III (Fig. 2.9), but nitrate and ammonium levels remained low.

Nitrogen : Phosphate ratio

The N:P ratios over time and depth in regions I, II, and III are 8.68 ($r = 0.52$), 7.5 ($r = 0.70$), and 7.2 ($r = 0.76$) respectively (Fig. 2.7) and are lower than the average ratios (16:1) of plankton material (Redfield *et al.*, 1963). The Jervis Inlet system was found to have an average ratio of 11.7 and 11.1 in the upper 30 m of water in 1975 and 1976 respectively (Smethie, 1987). Denitrification was thought to be responsible for the decrease in combined nitrogen (ammonium and nitrate) relative to phosphate. The highest rates of denitrification observed in Narrows Inlet existed in the mid to late summer and were made possible due to a strong coupling between nitrification and denitrification. Narrows Inlet showed a small increase in phosphate concentration in the summer months (Smethie, 1987). Regeneration of phosphate was relatively low in the early summer (apparently due to the complexing of iron oxyhydroxophosphates) and higher in the mid summer.

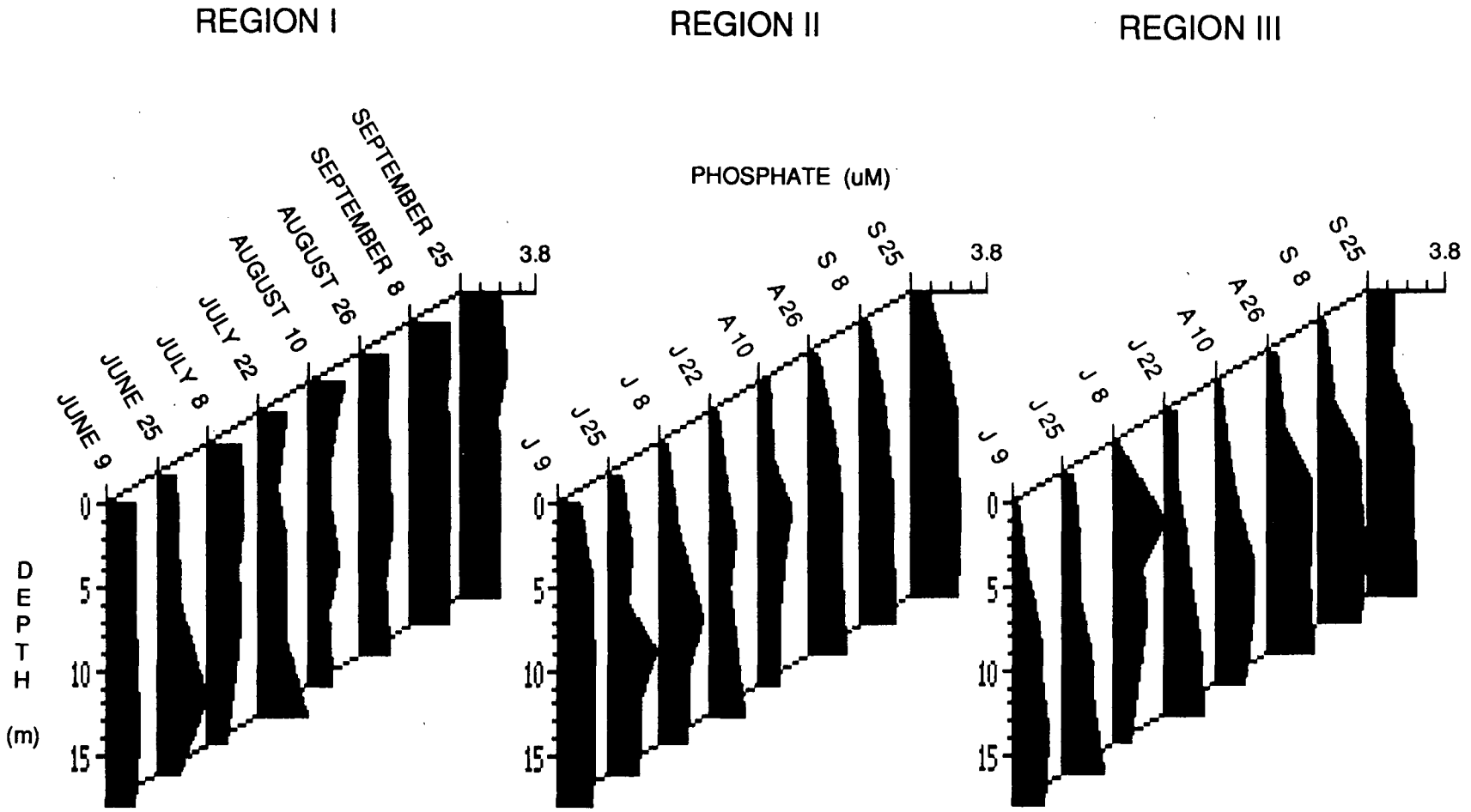

Figure 2.6: Phosphate (μM) profiles sampled between June 9 and September 25 in regions I, II, and III.

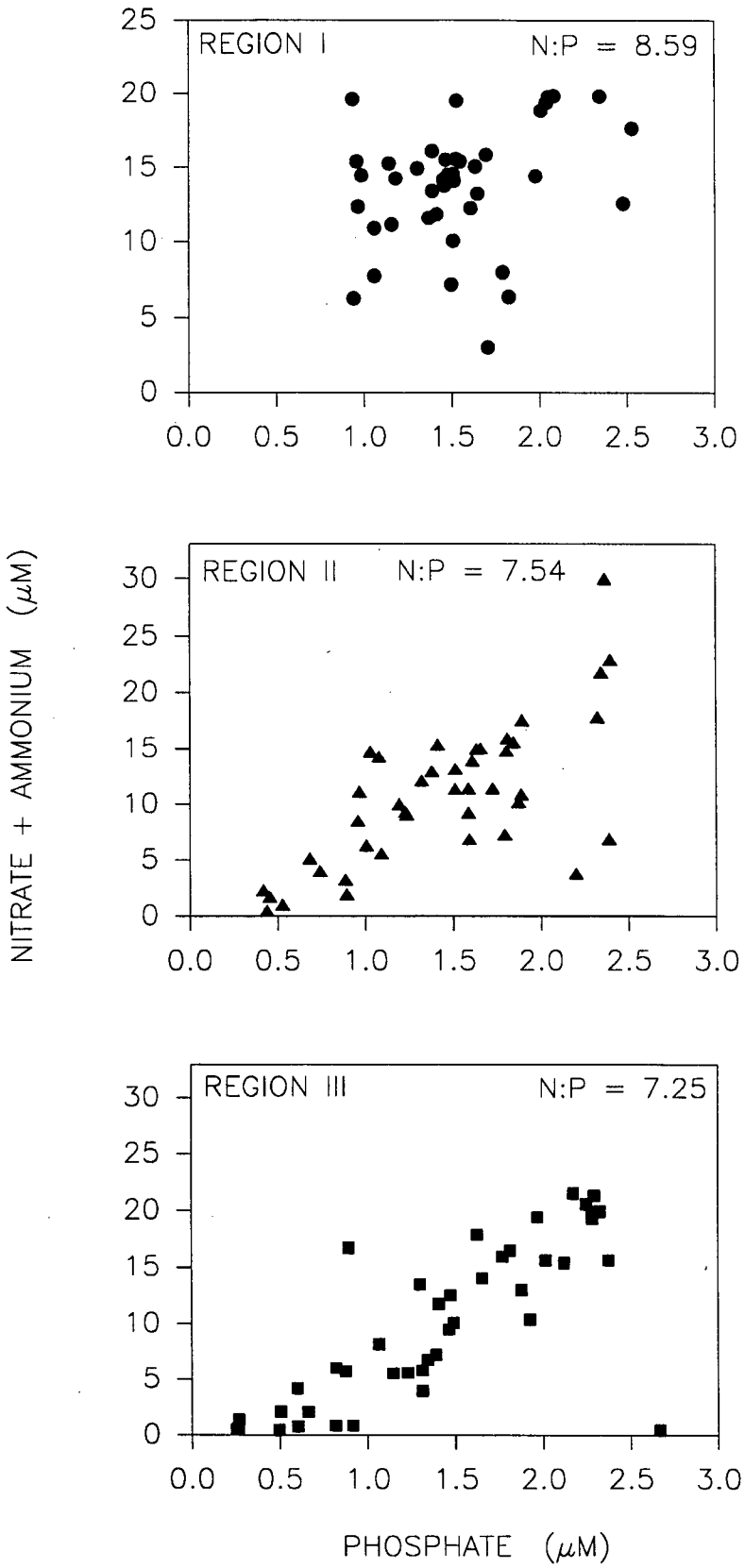

Figure 2.7: Total nitrogen (nitrate + ammonium) to phosphate ratios in regions I, II, and III.

The combination of low or infrequent pulses of freshwater run-off into Sechelt Inlet, regulated by B.C. Hydro, and sewage loading could lead to a nitrogen-deficient Inlet and explain the low nitrogen to phosphate ratio found here. The Sechelt Inlet system was considered by Pickard (1961) to have low freshwater drainage (110 $m^3 \cdot s^{-1}$) and thus a lower nitrate or new production supply. Sources of human input in the Sechelt Inlet system consist of two gravel quarries, several logging outfits, 11 fish farms, and 14 oyster leases (Black, 1989). Three fish farms, two logging outfits and one oyster lease exist in Narrows Inlet. Addition of sewage to an environment primarily shifts natural systems towards eutrophication (Sakshaug and Olsen, 1986). The low freshwater runoff and flushing rate of Sechelt Inlet do not provide a strong dilution factor for the system. A secondary effect of eutrophication may be nitrogen limitation since some nitrogenous compounds have lower solubility properties relative to phosphate compounds. Ryther and Dunstan (1971) noted phosphate supplies in coastal waters with sewage input and little freshwater run-off exceed the phosphate demands of phytoplankton. In sewage discharges or polluted areas, phosphate is found in larger amounts relative to nitrate (Ryther and Dunstan, 1971; Parsons *et al.*, 1977; D'Elia et al., 1986) and phosphate levels will exceed the demands of phytoplankton. N:P ratios have been known to drop below 5:1 during low-flow, late summer season in the eutrophied Patuxent River estuary (D'Elia *et al.*, 1986).

Although a low nitrogen to phosphate ratio is considered indicative of nitrogen-limited waters, other factors must be considered. Dissolved organic nitrogen has been shown to possibly link the organismal N:P ratio to ambient N:P concentrations (Antia *et al.*, 1991). In a region where the euphotic zone was nitrogen-depleted for months, biochemical factors proved that phytoplankton were not completely nitrogen-deficient. Nutrient uptake rates or internal stores of phytoplankton may be in a ratio of 16:1 although the ambient waters contain a low N:P ratio (Smethie, 1987). Other factors such as nitrogen uptake rates, turn-over times and storage capacities of phytoplankton need to

be investigated before nitrogen-deficiency can be declared. The type of phytoplankton species found in region II and III, where surface nitrogen concentrations periodically fall below the "limiting" level, are typically stage two and three flagellates (e.g.) and stage

2.3.2: THE SUCCESSION OF PHYTOPLANKTON COMMUNITIES

Regional differences in the succession of phytoplankton groups

The strong tidal exchange that takes place in region I offers conditions conducive for sequential changes in phytoplankton species as opposed to successional changes since the incoming flood waters displace the body of water present on the ebb tide. The progressive changes of phytoplankton species in region III would be hypothesized to represent a true succession since admixture of another water mass is minimized due the shallow sill at Tzoonie Narrows. Freshwater phytoplankton are largely responsible for any allochthonous interference with the successional pathway of species found in region III. However, if freshwater species do not reproduce and survive in this region they are considered to be sterile introductions (Smayda, 1980). Region II is thought to represent a mixture of region I and III and is considered a "transition" or "friction" zone.

Fig. 2.8 reveals that large fluctuations take place in the progression of phytoplankton groups over the sampling period in region I, while fluctuations are only intermediate in region II, and subtle in region III. This difference suggests that the density and nutrient conditions transported into region I are subject to considerable changes while the indigenous body of water in region III, protected by the presence of a shallow sill and higher altitude bordering mountains, probably does not have such changes. In general, region I is characterized by a higher proportion of small, fast-growing, non-motile cells such as diatoms that readily recolonize during strong tidal episodic mixing events (r-selected), while region III is characterized by a higher proportion of large, motile, slow-growing phytoplankton such as flagellates that persist in stable stratified waters (K-selected).

Since the flushing time of the resident water of Sechelt Inlet may have a period of over three years (Lazier, 1963) no dilution factor exists for the phytoplankton community in Region II. The diatom and dinoflagellate biomass in region I and II, however, decrease and increase in a similar pattern between June and September (Fig. 2.8), implying that

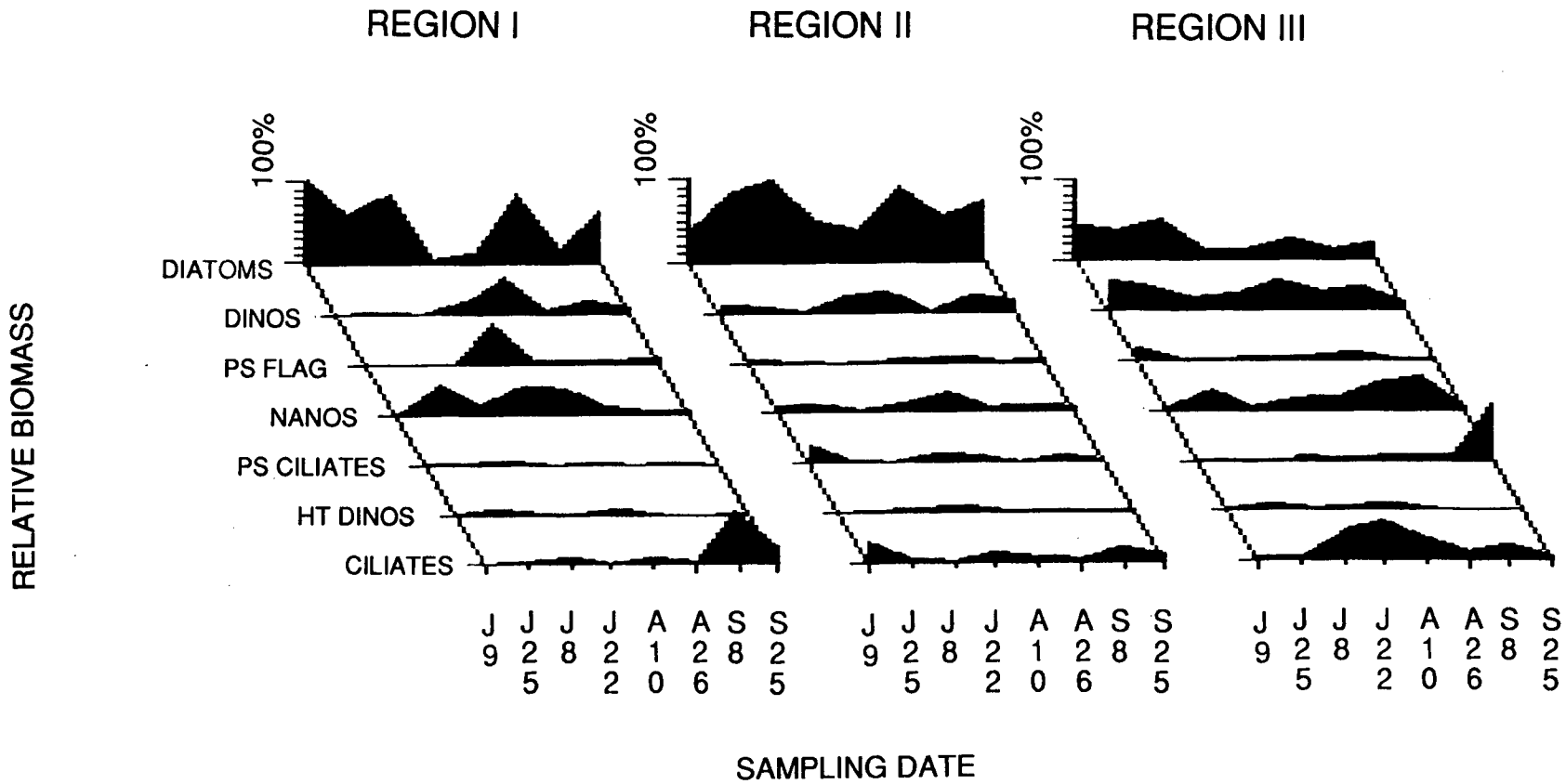

Figure 2.8: Changes in relative biomass per station of the different planktonic groups found in regions I, II, and III between June 9 and September 25. DINOS = dinoflagellates, PS FLAG = photosynthetic flagellates, NANOS = nanoflagellates, PS CILIATES = *Mesodinium rubrum*, HT DINOS = heterotrophic dinoflagellates, J9 = June 9, J25 = June 25, J8 = July 8, J22 = July 22, A10 = August 10, A26 = August 26, S8 = September 8, S25 = September 25. Numerical values are given in Table 2.2.

Table 2.2: Biomass ($\mu gC \cdot L^{-1}$) of the plankton groups found in regions I, II, and III between June and September in 1989. (DIAT = diatoms, DINO = dinoflagellates, PS FLAG = photosynthetic flagellates, PS CIL = *Mesodinium rubrum*, NANO = nanoflagellates, H DINO = heterotrophic dinoflagellates, CILIAT = other ciliates). Biomass values for each depth interval in Appendix 1.

GROUPS	REGION I		REGION II		REGION III	
June 9	$\mu gC \cdot L^{-1}$	% OF TOTAL	$\mu gC \cdot L^{-1}$	% OF TOTAL	$\mu gC \cdot L^{-1}$	% OF TOTAL
DIAT	1333.0	93.2	417.6	6.4	294.4	38.7
DINO	9.4	0.6	104.4	9.1	244.1	32.1
PS FLAG	11.1	0.8	44.6	3.9	108.9	14.3
PS CI	16.7	1.2	218.6	19.1	7.6	1.0
NANO	20.8	1.5	89.6	7.8	34.9	4.6
H DINO	11.1	0.8	7.0	0.6	31.8	4.2
CILIAT	27.5	1.9	264.9	23.1	38.9	5.1
TOTAL	1429.6		1146.7		760.6	
June 25						
DIAT	440.8	54.5	2351.9	75.5	340.1	34.1
DINO	16.1	2.0	191.5	6.1	268.7	26.9
PS FLAG	1.7	0.2	9.4	0.3	18.8	1.9
PS CIL	18.8	2.3	89.4	2.9	6.9	0.7
NANO	255.6	31.6	260.9	8.4	220.5	22.1
H DINO	45.1	5.6	53.7	1.7	89.1	8.9
CILIAT	30.8	3.8	158.3	5.1	53.4	5.4
TOTAL	808.9		3115.1		997.5	
July 8						
DIAT	484.9	75.2	2921.4	89.1	647.1	44.5
DINO	9.8	1.5	78.2	2.4	193.3	13.3
PS FLAG	2.0	0.3	0.0	0.0	28.6	2.0
PS CIL	22.2	3.4	18.4	0.6	30.6	2.1
NANO	68.8	10.7	91.9	2.8	47.1	3.2
H DINO	3.5	0.5	119.0	3.6	39.4	2.7
CILIAT	53.9	8.4	50.3	1.5	469.3	32.2
TOTAL	645.1		3279.2		1455.4	
July 22						
DIAT	25.8	6.8	449.2	44.5	108.5	12.4
DINO	58.3	15.3	188.4	18.7	157.1	17.9
PS FLAG	169.8	44.7	1.8	0.2	43.9	5.0
PS CIL	0.0	0.1	104.7	10.4	24.9	2.8
NANO	110.6	29.1	95.1	9.4	126.8	14.4
H DINO	8.0	2.1	63.1	6.2	40.9	4.7
CILIAT	7.4	1.9	107.1	10.6	375.0	42.8
TOTAL	379.9		1009.4		877.1	

Table 2.2 cont'd: Biomass ($\mu gC \cdot L^{-1}$) of the plankton groups found in regions I, II, and III between June and September in 1989. (DIAT = diatoms, DINO = dinoflagellates, PS FLAG = photosynthetic flagellates, PS CIL = *Mesodinium rubrum*, NANO = nanoflagellates, H DINO = heterotrophic dinoflagellates, CILIAT = ciliates). Biomass values for each depth interval in Appendix 1.

GROUPS	REGION I		REGION II		REGION III	
August 10	$\mu gC \cdot L^{-1}$	% OF TOTAL	$\mu gC \cdot L^{-1}$	% OF TOTAL	$\mu gC \cdot L^{-1}$	% OF TOTAL
DIAT	78.6	13.6	780.1	35.1	118.4	11.6
DINO	232.5	40.3	501.6	22.7	333.9	32.7
PS FLAG	33.7	5.9	71.8	3.2	51.4	5.1
PS CIL	4.2	0.7	156.3	7.0	36.1	3.5
NANO	154.3	26.8	505.1	22.7	153.2	15.0
H DINO	29.1	5.1	52.7	2.4	81.2	7.9
CILIAT	43.9	7.6	153.1	6.9	246.8	24.2
TOTAL	576.3		2220.7		1021.0	
August 26						
DIAT	657.8	75.2	2523.5	80.8	186.8	24.5
DINO	40.3	4.6	81.5	2.6	153.7	20.2
PS FLAG	45.8	5.3	202.6	6.5	66.6	8.7
PS CIL	1.4	0.2	6.7	0.2	52.8	7.0
NANO	89.4	10.2	149.5	4.8	220.8	29.0
H DINO	1.2	0.1	56.7	1.8	3.0	0.4
CILIAT	38.5	4.4	104.3	3.3	77.6	10.2
TOTAL	874.4		3124.8		761.3	
September 8						
DIAT	79.3	16.5	304.4	47.9	55.6	11.8
DINO	75.1	15.6	115.2	18.1	124.7	26.5
PS FLAG	21.1	4.4	9.7	1.5	11.9	2.5
PS CIL	9.7	2.0	43.2	6.8	27.8	5.9
NANO	16.9	3.5	56.5	8.9	168.9	35.9
H DINO	0.5	0.1	11.2	1.8	0.2	0.1
CILIAT	278.2	57.9	95.5	15.0	81.7	17.3
TOTAL	480.8		635.7		470.8	
September 25						
DIAT	468.9	57.9	671.9	65.8	156.0	19.4
DINO	70.9	8.7	144.9	14.2	81.1	10.1
PS FLAG	59.4	7.3	26.6	2.6	10.5	1.3
PS CIL	0.0	0.2	21.5	2.1	479.4	59.7
NANO	29.1	3.4	44.8	4.4	32.3	4.0
H DINO	15.6	2.0	15.5	1.5	4.3	0.6
CILIAT	166.3	20.5	96.5	9.4	39.2	4.9
TOTAL	810.2		1021.7		802.8	

the phytoplankton groups in region I may influence the compostion of those in region II. The strong turbulent incoming tidal jet which reaches maximal current speeds of 17 knots across the sill (Anon. 1989) would likely transport a substantial amount of phytoplankton into the inlet. The dominant phytoplankton groups present in region II may serve as an indicator for the allochthonous (region I) or autochthonous (region III) source of phytoplankton and the hydrographic conditions present.

The transport of phytoplankton across Tzoonie Narrows at low concentrations is possible and may serve as an "inoculum" for the development of flagellate blooms in region II. The tidal current speeds across Tzoonie Narrows are twenty-five percent of those across Skookumchuck Narrows (Anon. 1989). Because the incoming water hugs the bottom of the sill, the export of water from region III is restricted to the top few metres (Lazier, 1963). Flagellates must migrate into the nutrient-depleted surface waters of region III in order to be transported across the eleven metre sill at Tzoonie Narrows. In region II a flagellate bloom will be favoured only if the hydrographic conditions remain stratified and are not largely influenced by faster-growing diatoms transported in from region I. A series of events are required to "seed" and support a flagellate bloom in region II and therefore close monitoring is required to predict the timing of such an event. Lower concentrations of *Heterocapsa triquestra* (June 9) and *Prorocentrum minimum* (August 26) in region II may have resulted from the transport of organisms from region III where high surface concentrations of these organisms were found (Sutherland and Taylor, 1990).

In all three regions, a reciprocal codominance between the dinoflagellate and diatom biomass can be observed (Fig. 2.8). The dominance of the dinoflagellate or diatom group over one another will serve as an indicator for the cycle or stage of succession. Periods of minor turbulence will cause minor irregularities in the typical seasonal succession, creating smaller successional repetitions or cycles. Perturbations may slow down the velocity of succession by lengthening stage one or reverse the direction of latter stages.

reverse the direction of latter stages. The replenishment and depletion of nutrients and the associated sharp rise and fall of the diatom biomass signifies the start and end of the successional stages recognized by Margalef (1967). Sharp increases in diatom biomass on July 8 and August 26 in region I and II indicates the interruptions in the natural progression by episodic mixing events. Smaller increases in diatom biomass were also observed in region III relative to those in the other regions on these sampling dates.

Regional differences in vertical distributions of three phytoplankton groups: dinoflagellates, photosynthetic flagellates, and diatoms

Both spatial and temporal heterogeneity influence phytoplankton community structure (Margalef, 1958, 1963, 1967; Smayda, 1980) as demonstrated by the vertical distributions of chlorophyll (Fig. 2.9) and of phytoplankton groups (Figs. 2.10, 2.11, 2.12, and 2.13). The vertical profiles shown in Figs. 2.9, 2.10, 2.11, 2.12, and 2.13 reveal that the differences that exist between regions appear to be stronger that those that exist temporally, between June and September. The turbulent waters of region I create a fairly uniform vertical distribution of chlorophyll (Fig. 2.9). In region III chlorophyll maxima are located in subsurface waters in or above the nutricline (Fig. 2.4) throughout most of the sampling period. The chlorophyll gradients in region II are not as pronounced as region III.

Flagellates commonly form thin surface layers in stratified waters (Anderson *et al.*, 1985). Flagellates are phototactic and undergo daily migration patterns to the surface for photosynthesis and to depth to access nutrients located below the depleted surface waters (Raven and Richardson, 1984; Wada *et al.*, 1985; Anderson *et al.*, 1985; Cullen *et al.*, 1985; Tyler, 1985). However, density gradients (Tyler and Seliger, 1981), light intensity (Heaney and Talling, 1980), and nutrients (Cullen and Horrigan, 1981) control the extent to which vertical migration takes place. Avoidance of strongly illuminated nutrient-depleted surface waters by phytoplankton will minimize photochemical damage. *Heterocapsa niei* is known to migrate to a position just above the nitracline (Cullen *et al*,

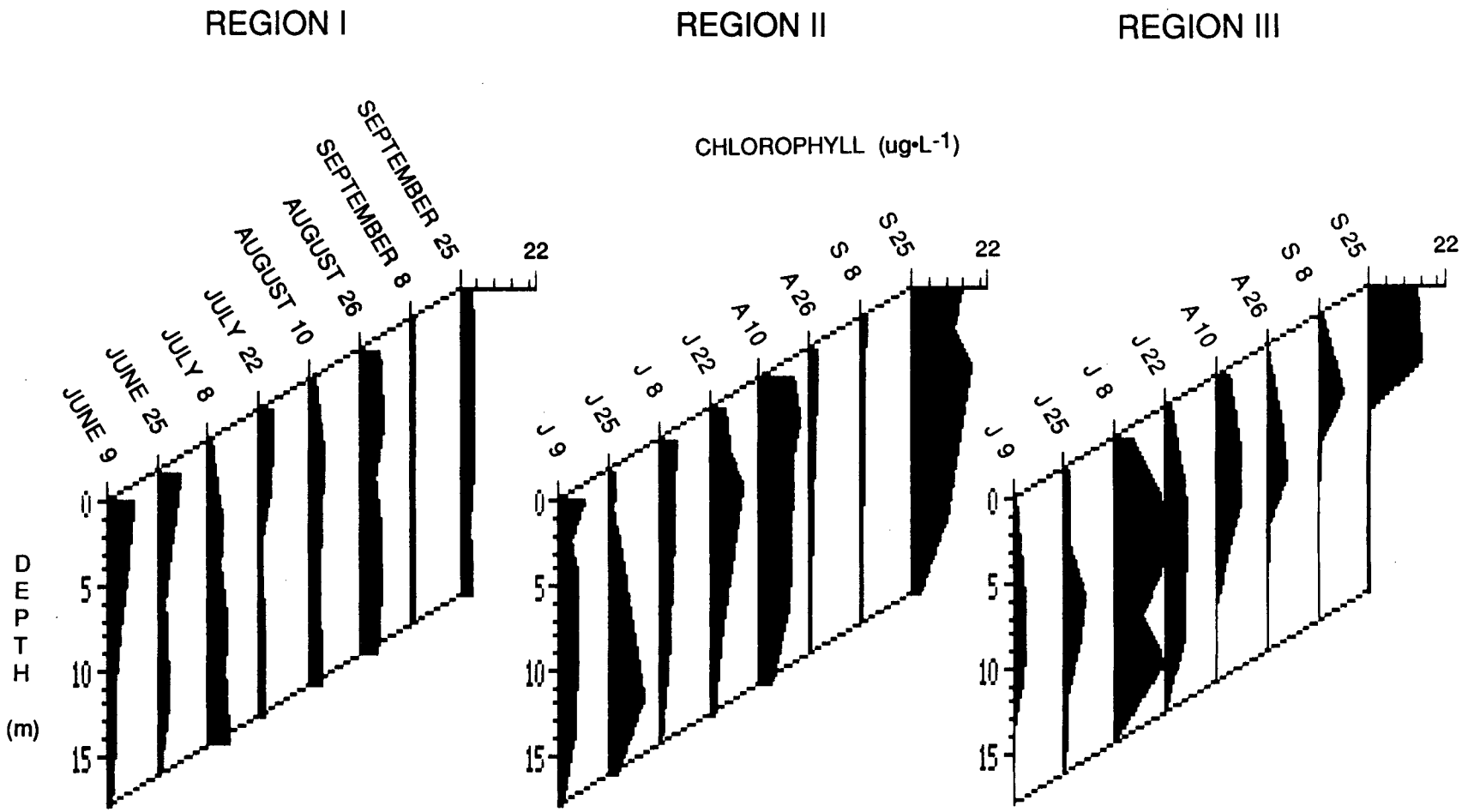

Figure 2.9: Chlorophyll ($\mu g \cdot L^{-1}$) profiles of regions I, II, and III between June 9 and September 25.

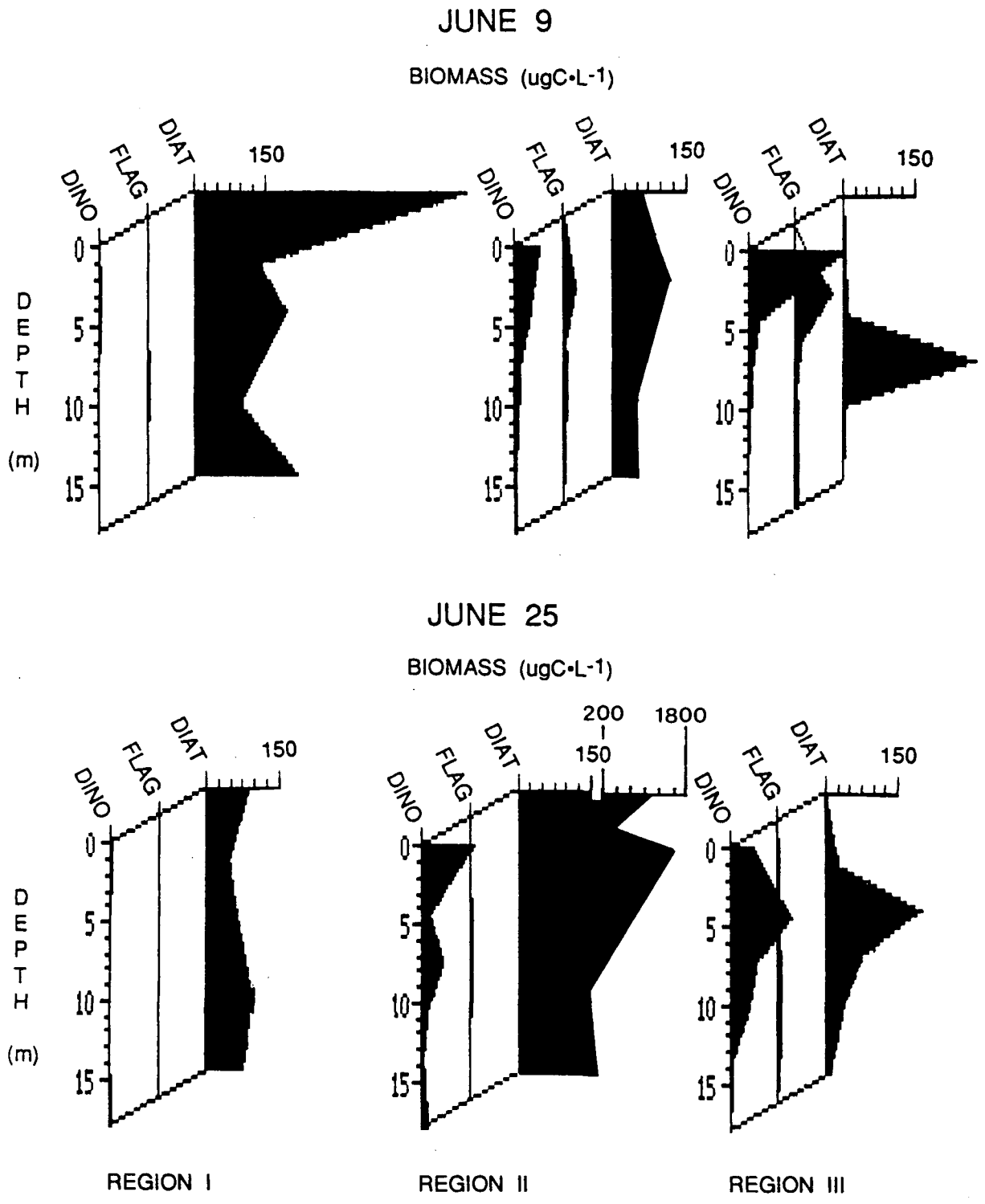

Figure 2.10: Vertical profiles of the biomass ($\mu gC \cdot L^{-1}$) of dinoflagellates (DINO), other photosynthetic flagellates (FLAG), and diatoms (DIAT) on June 9 and June 25 in regions I, II, and III.

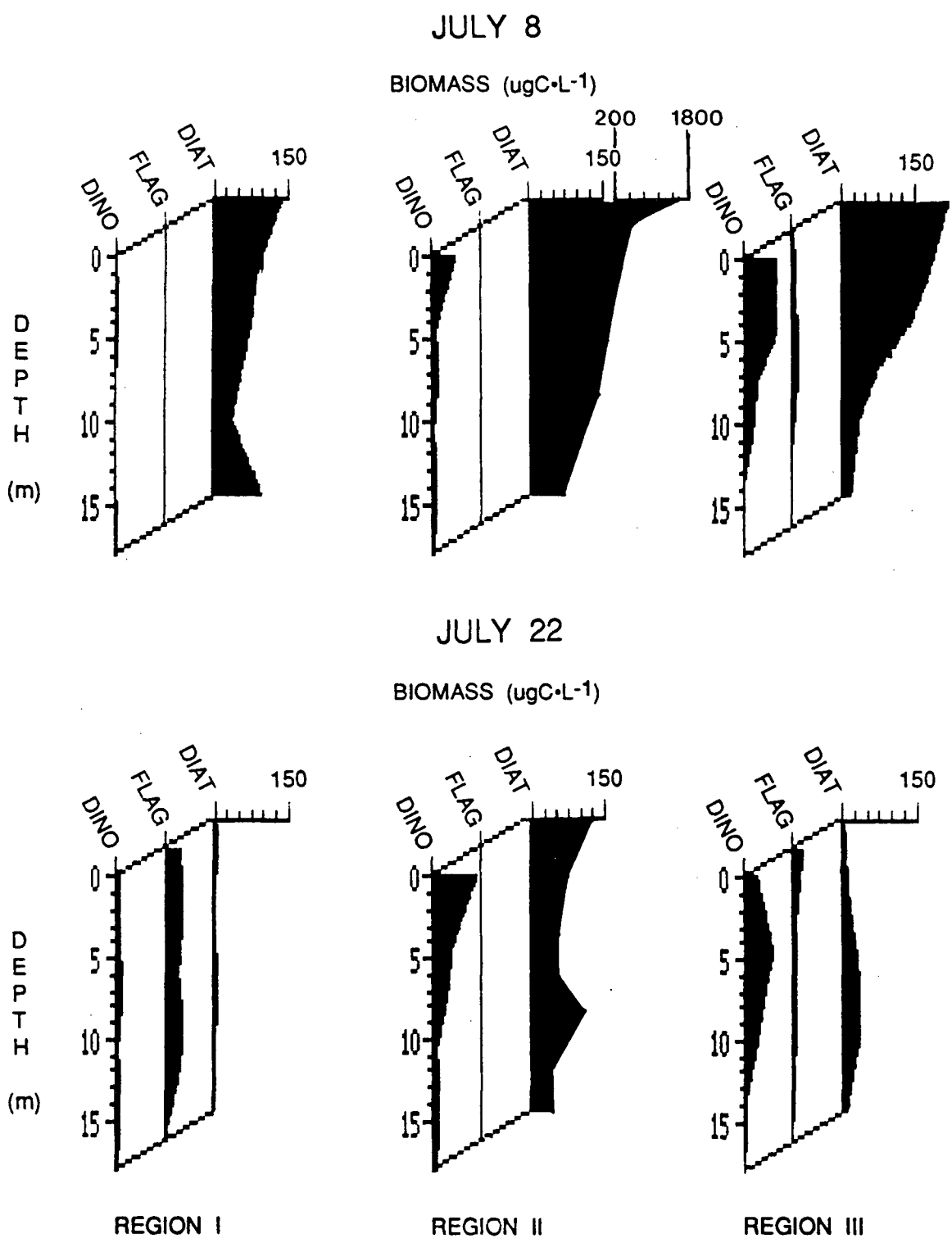

Figure 2.11: Vertical profiles of the biomass ($\mu gC \cdot L^{-1}$) of dinoflagellates (DINO), other photosynthetic flagellates (FLAG), and diatoms (DIAT) on July 8 and July 22 in regions I, II, and III.

1985). In region III the flagellate maxima were found in the the surface waters (Fig. 2.10, 2.11, 2.12, and 2.13). The dinoflagellate maxima were found below the 0-3 metre depth interval on June 25, July 23, August 26, and September 9. The photosynthetic flagellate maxima were generally found in the 3-6 metre depth interval. Dinoflagellates present in highly irradiated, nutrient-depleted surface waters may produce mycosporine-like amino acids to serve as a protection filter to UV radiation (Carreto *et al.*, 1990). This adaptive response will allow dinoflagellates to migrate into surface waters and be transported across Tzoonie Narrows into region II. In region III, On June 9, July 8, August 10, and September 25, the dinoflagellate maxima were found in the 0-3 metre depth interval. A subsurface maximum may still exist below the top one or two metres but remain undetected because an average over the top three metres is sampled. The isolated two-layer estuarine flow in region III may act as a "phytoplankton trap" concentrating flagellates and giving rise to the higher biomass found in this region. Avoidance of the surface depth interval (0-3 m) by flagellates was not observed in regions I and II.

The diatom maxima were found in the cooler waters below the well developed thermocline on June 9 and 25, July 23, and August 10 in Region III (Fig. 2.3, 2.10, 2.11, and 2.13). The growth and survival of the non-motile diatoms in this stratified region is dependent on low sinking rates, which in turn is dependent on cell size, shape, chemical composition or age of the population (Malone, 1980; Walsby and Reynolds, 1980). On July 8, August 26, September 9 and 26, both the flagellate and diatom layer were situated above the thermocline/nutricline. This vertical displacement of the diatom layer into surface waters during the latter trips may be due to small scale resuspension or due to the persistence of certain species with specific adaptations for such "oceanic" conditions. Diatoms exhibiting greater physiological adaptations for sun tolerance, nutrient uptake (luxury consumption), or the production of certain enzymes to allow differential nutritional capability (Smayda, 1980) will have the greatest survival success under

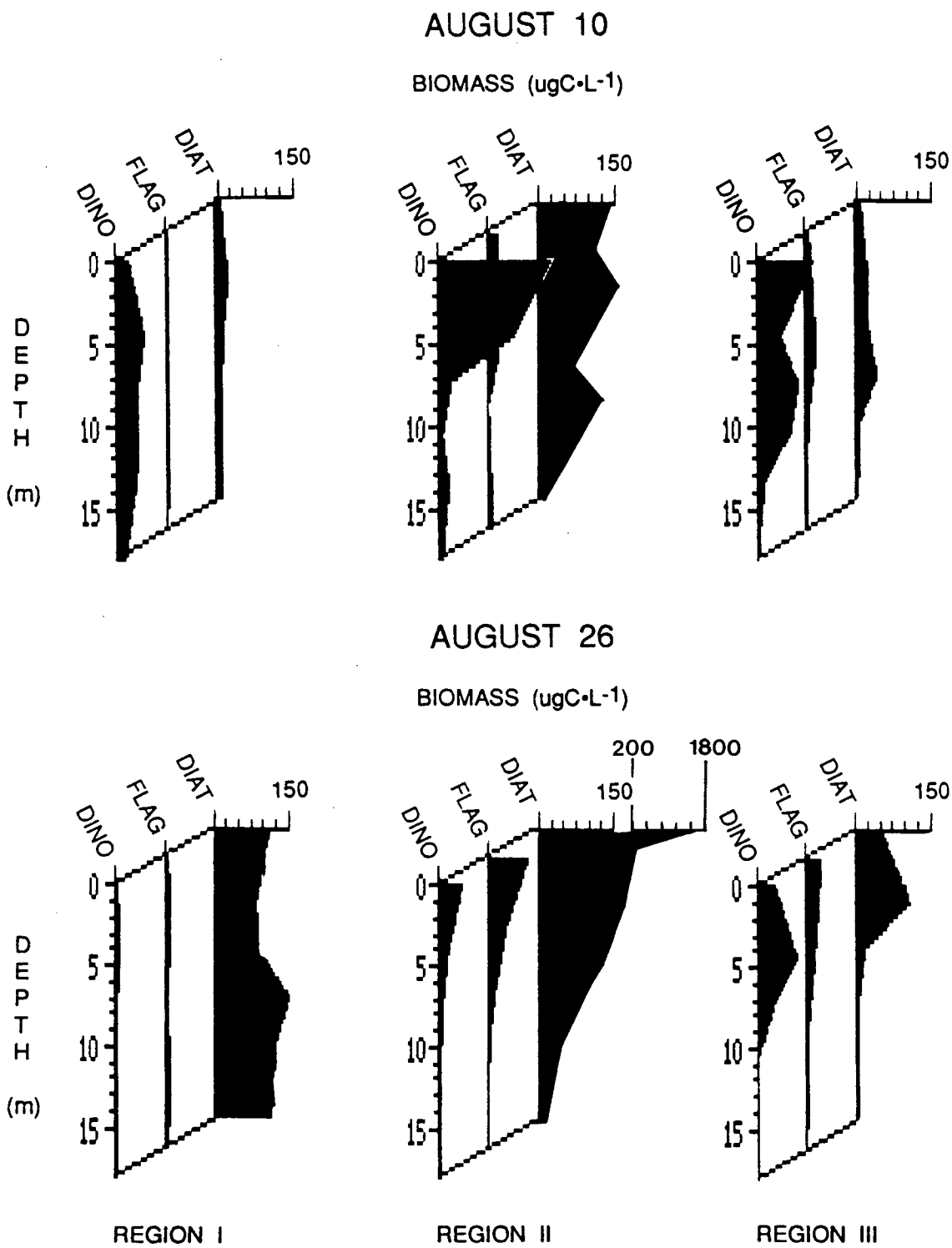

Figure 2.12: Vertical profiles of the biomass ($\mu gC \cdot L^{-1}$) of dinoflagellates (DINO), other photosynthetic flagellates (FLAG), and diatoms (DIAT) on August 10 and August 26 in regions I, II, and III.

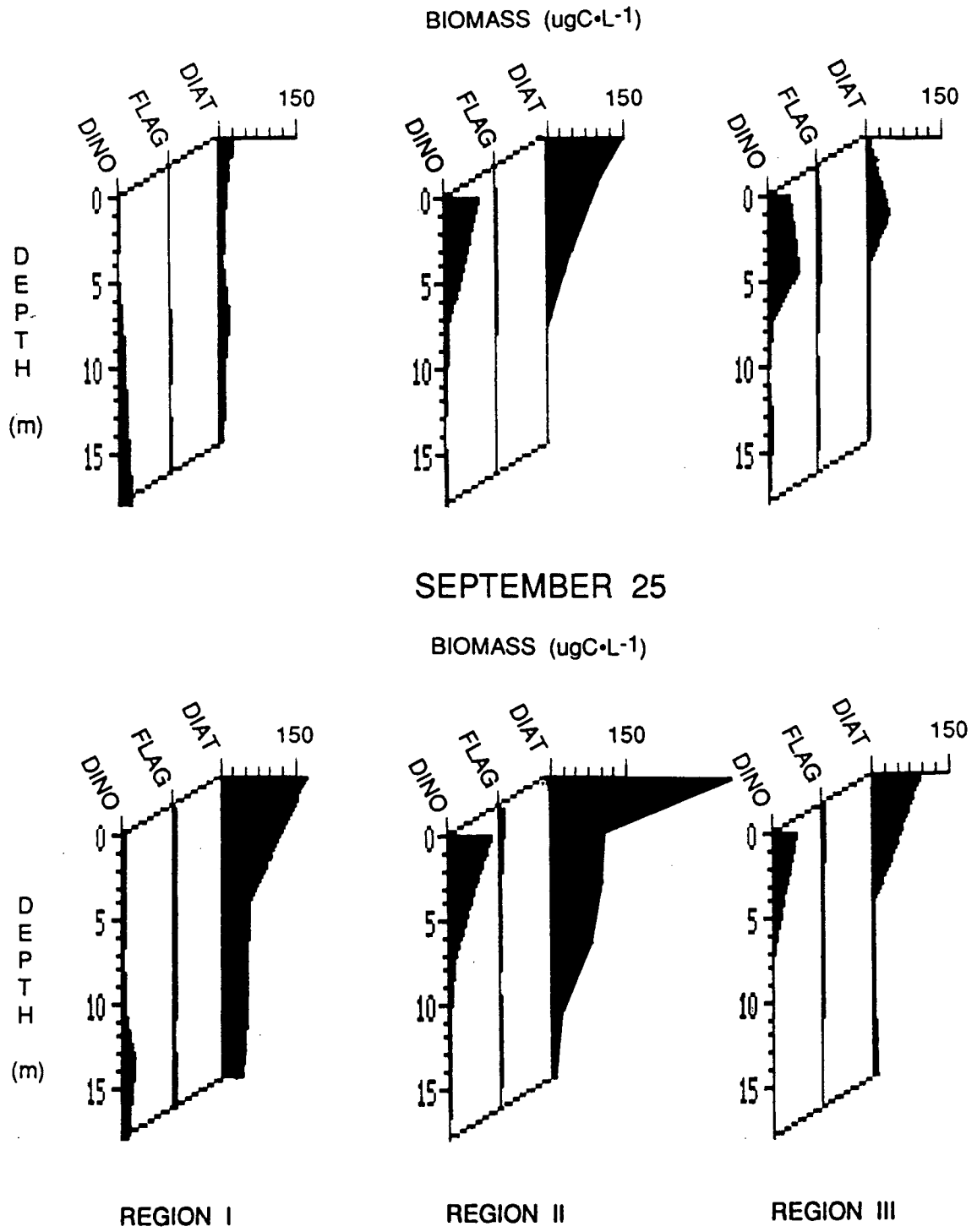

Figure 2.13: Vertical profiles of the biomass ($\mu gC \cdot L^{-1}$) groups, dinoflagellates (DINO), other photosynthetic flagellates (FLAG), and diatoms (DIAT) on September 8 and September 25 in regions I, II, and III.

layering of the diatom biomass in region III provides evidence towards the hypothesis that diatoms can control their bouyancy physiologically.

The vertical profiles of diatom biomass in region II remain fairly uniform over the sampling period. Perturbations due to wind-mixing events (July 8) may have induced resuspension of the diatoms causing increases in diatom biomass in the surface waters. Subsurface diatom maxima below the 0-3 metre depth interval were not evident in regions I and II. An investigation into the change in species composition over the sampling period will be discussed later.

Phytoplankton species succession

Each phytoplankton genus/species in the top ninety percent of the biomass per sampling date and region was assigned a successional stage-type characterized by Margalef (1967). The relative percentage of each successional stage-type in each region is shown in Fig. 2.14. Figs. 2.15, 2.16, and 2.17 shows the relative biomass of phytoplankton genus or species found in regions I, II, and III between June and September.

In region I the progressive increase of stage three phytoplankton and decrease of stage one phytoplankton in region I provides evidence in support of the temporal succession outlined by Margalef (1963; 1967). The gradual change and overlap of dominant stage-types is typical of a succession. The dominant organisms of a community involved in a terrestrial succession are known to replace other dominant organisms gradually (Ricklefs, 1973). In succession the replacement of entire communities is very rare. Since region I is sampled after flood tide its composition must reflect the phytoplankton development in the surrounding waters of the Jervis Inlet system and the northern Strait of Georgia. Therefore, the predicted sequential changes or displacement

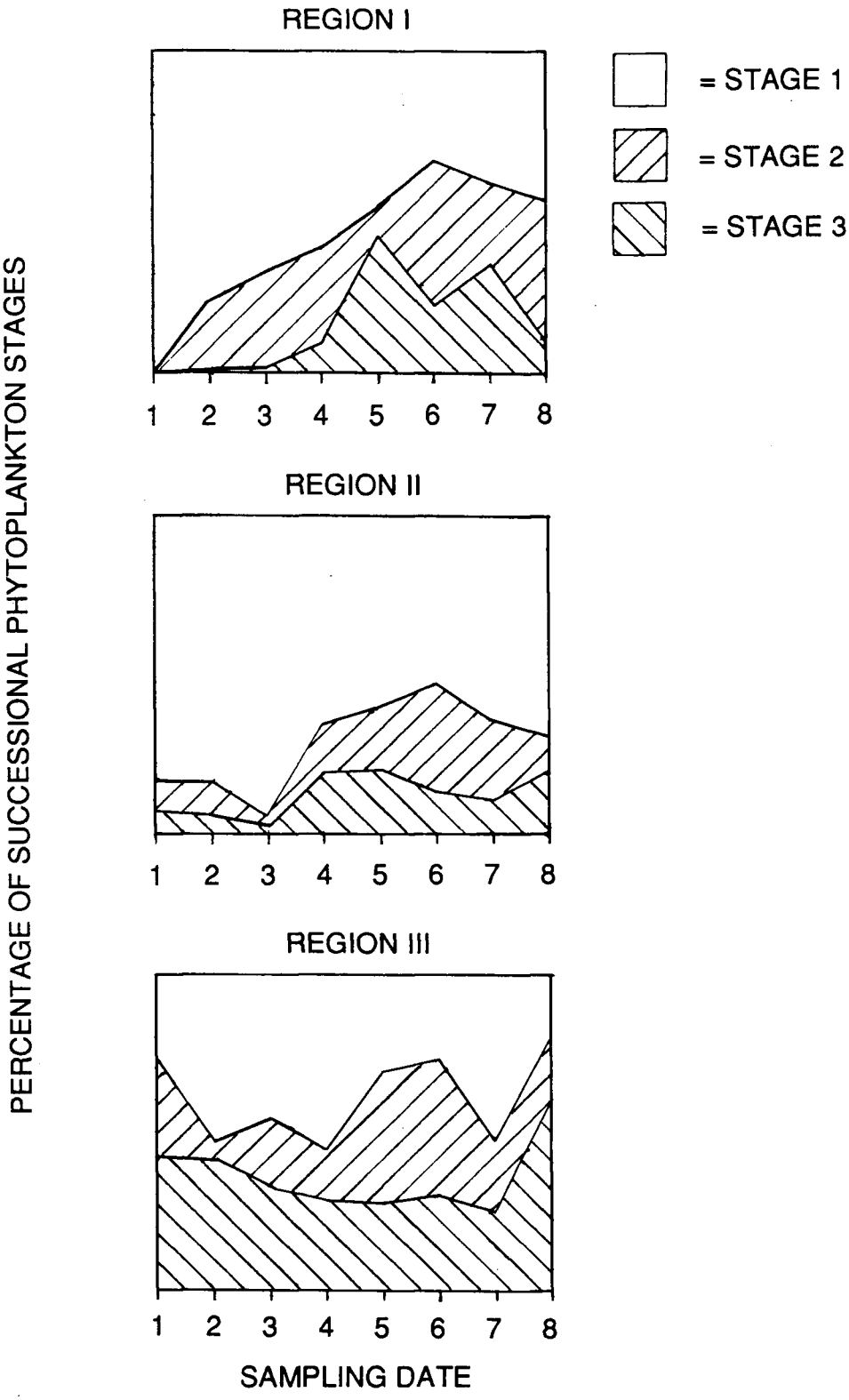

Figure 2.14: Relative percent of successional stages of phytoplankton species present between June 9 and September 25 in regions I, II, and III. 1 = June 9, 2 = June 25, 3 = July 8, 4 = July 22, 5 = August 10, 6 = August 26, 7 = September 8, 8 = September 25.

present. Other marine phytoplankton with low salinity tolerances may thrive in region III and add to the number of species that can exist in this region.

An increase in species richness of a phytoplankton community may also serve as an indicator for the latter stages of a succession (Margalef, 1963; Smayda, 1980). For example, the vertical heterogeneity that exists in region III allows the flagellate population to occupy the surface layer while the diatom population occupies a deeper layer below the thermocline or nutricline (Figs. 2.10, 2.11, 2.12, 2.13). Fig. 2.14 reveals that the biomass consists of 40% stage three phytoplankton.

A decrease in species richness may result from a lack of stratification (Smayda, 1980) or the presence of growth-inhibiting ectocrine substances (Taylor, 1987). For example, winds greater than 12 knots may have caused a breakdown of stratified conditions on July 8 and August 26 in region II. Also, in region I, *Heterosigma akashiwo* and *Dictyocha speculum* may have promoted the absence of diatoms from the top 80 % of the phytoplankton biomass on July 22 (Fig. 2.17). *H. akashiwo* is known to form monospecific blooms at high concentrations (pers. comm. F.J.R. Taylor) and has been shown to inhibit the presence of *Skeletonema costatum* from the water column in Narragansett Bay (Pratt, 1966).

Diatom succession

The diatom succession in region I consists of *Thalassiosira nordenskioeldii*, *Skeletonema costatum* (June 9), *Coscinodiscus radiatus*, *Cylindrotheca closterium*, *Chaetoceros compressum*, *Ch. concavicorne* (June 25 and July 8) *Corethron criophilum* (August 10), *S. costatum*, *T. rotula* (August 26), *C. radiatus*, *Ch. laciniosum*, *Ch. convolutum*, *Ch. compressum* (September 25) between June and September (Fig. 2.15).

The diatom succession in region II consists of *Skeletonema costatum*, *Chaetoceros debile*, *Ch. sociale* (June 9), *S. costatum*, *Thalassiosira nordenskioeldii*, *Ch. compressum*, *Ch. sociale*, *Ch. debile*, *T. rotula* (June 25 and July 8), *T. nordenskioeldii*, *Corethron criophilum*, *Ch. gracile*, *Cylindrotheca closterium*, *Rhizosolenia fragilissima*, (July 22 and August 10), *S. costatum*, *T. rotula* (August 26 and September 8), and *Ch. laciniosum*, *Ch. convolutum*, *Ch. compressum*, *R. setigera* (September 25) (Fig. 2.16).

The diatom succession in region III consists of *Chaetoceros decipiens* (June 9), *Skeletonema costatum*, *Pleurosigma* sp. (June 25), *Coscinodiscus radiatus*, *Pleurosigma* sp., *Cylindrotheca closterium* (July 8), *Thalassiosira rotula*, *T. nordenskioeldii* (July 22 and August 10), *S. costatum*, *T. nordenskioeldii* (September 9), *Navicula wawrickae*, and *Rhizosolenia setigera* (September 25) (Fig. 2.17).

Flagellate succession

The flagellate succession in region I starts on July 22 since flagellates were absent in the top sixty percent of the biomass on June 9, July 25 and July 8. The succession proceeded as *Heterosigma akashiwo*, *Dictyocha speculum*, and *Chrysochromulina* spp. (July 22), *Goniodoma pseudogonyaulax* sp., *Chrysochromulina* spp., cryptomonads, *Protoceratium reticulatum* (August 10 and 26), *Scrippsiella* spp., *H. akashiwo*, *G. pseudogonyaulax* (September 9), and *Protogonyaulax catanella* on September 25 (Fig. 2.15).

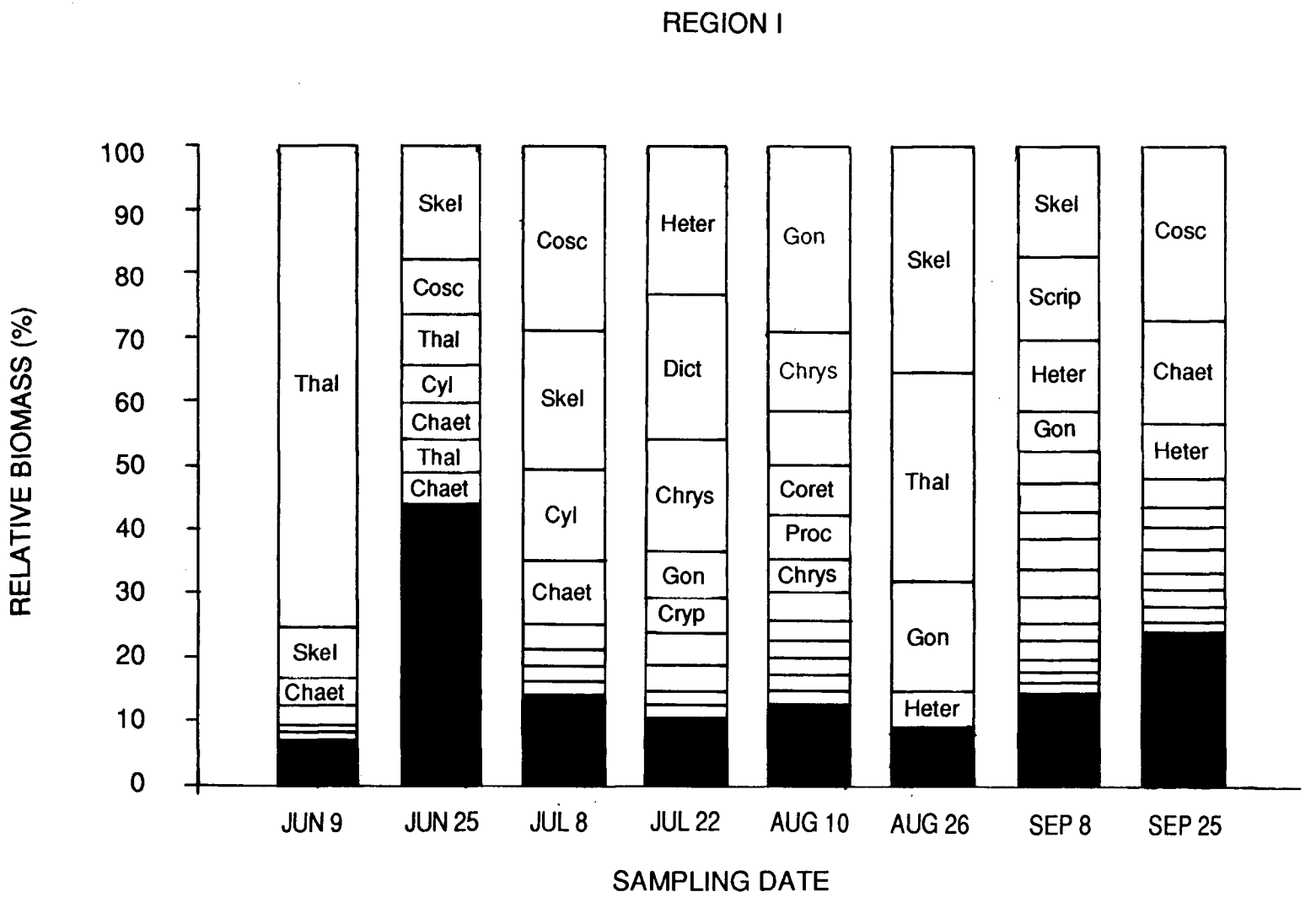

Figure 2.15: Relative biomass of phytoplankton genus or species found in region I between June 9 and September 25 in 1989. Black area = other phytoplankton species < 2 $\mu gC \cdot L^{-1}$ of total phytoplankton biomass.

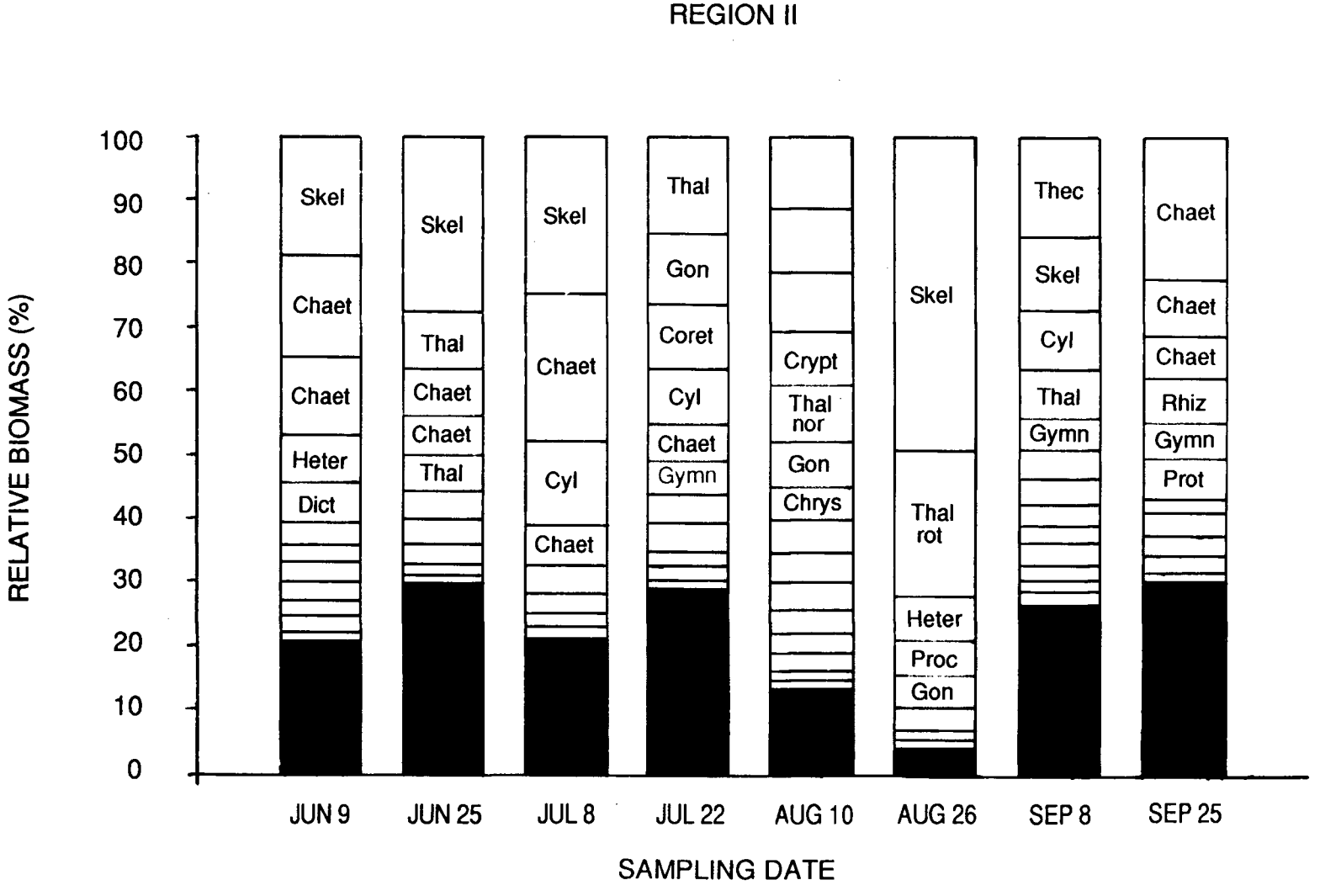

Figure 2.16: Relative biomass of phytoplankton genus of species found in region II between June 9 and September 25 in 1989. Black area = other phytoplankton species < 2 $\mu gC \cdot L^{-1}$ of total phytoplankton biomass.

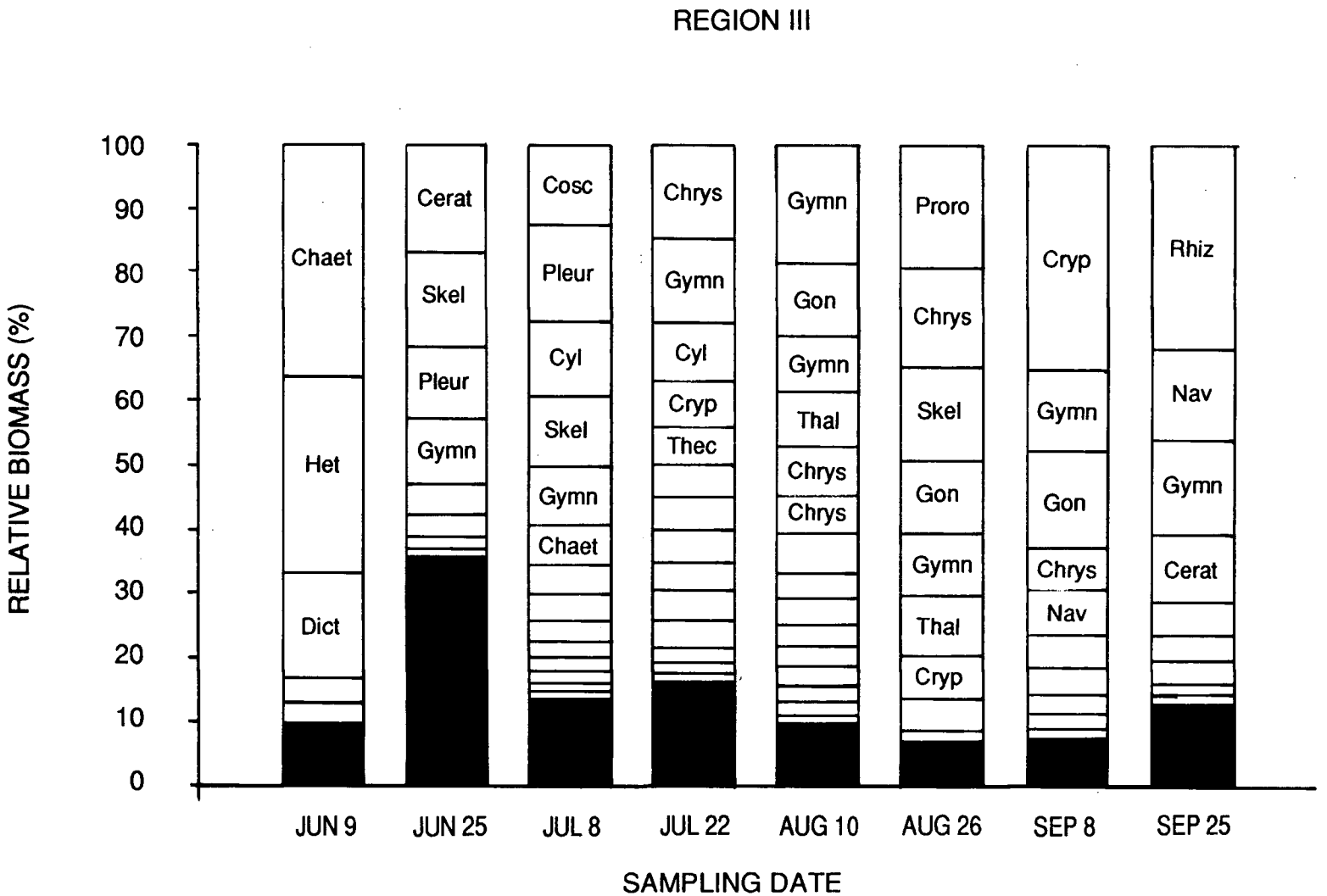

Figure 2.17: Relative biomass of phytoplankton genus or species found in region III between June 9 and September 25 in 1989. Black area = other phytoplankton species < 2 $\mu gC \cdot L^{-1}$ of total phytoplankton biomass.

The flagellate succession in region II consists of *Heterocapsa triquestra*, *Dictyocha speculum* (June 9), *Goniodoma pseudogonyaulax* (July 22), *Protoceratium reticulatum*, cryptomonads, *Goniodoma pseudogonyaulax* (August 10), *Heterosigma akashiwo* (August 26), unidentified thecate dinoflagellate (September 9), and *Protogonyaulax catanella* (Fig. 2.16).

The flagellate succession found in region III consists of *Heterocapsa triquestra*, *Dictyocha speculum* (June 9), *Ceratium longipes*, *Gymnodinium sanguimium*, (June 25 and July 8), *Chrysochromulina* spp., cryptomonads, unidentified thecate dinoflagellates (July 22), *Gymnodinium* spp. *Goniodoma pseudogonyaulax* (August 10), *Prorocentrum minimum*, *Chrysochromulina* spp. (September 9), and Gymnodinoids (September 25) (Fig. 2.17).

Since the northern Strait of Georgia (NSG) surrounds the entrance to the Jervis Inlet system and hence Sechelt Inlet phytoplankton observed in the NSG by Haigh (in press, 1991) may provide a source for the phytoplankton community in Sechelt Inlet. The phytoplankton succession observed Haigh (1988) in the northern Strait of Georgia (NSG) in 1986 consisted of nanoflagellates (Cryptomonads) and small-sized diatoms (*Leptocylindrus minimus* and *Skeletonema costatum*) in March and April, *Heterosigma akashiwo*, cryptomonads and gymnodinoids in June, *Chaetoceros compressum*, *Ch. debile*, *Skeletonema costatum*, *Rhizosolenia fragilissima*, and *Ch. sociale* at a subsurface maxima and nanoflagellates at the surface in August, and then finally *Rhizosolenia setigera* and cryptomonads in September. *Ch. compressum*, *Ch. debile*, and *S. costatum* appear to be dominant in both the NSG and region I of this study between June and August. *R. setigera* and cryptomonads are dominant in September in both the NSG and region III of this study. Because these phytoplankton species and groups are not dominant in region I and II, it is not likely that the NSG served as a source for the phytoplankton composition of region III.

In region I, *Thalassiosira nordenskioeldii* is the dominant (77%) phytoplankton species of the biomass on June 9 and disappears as a dominant phytoplankton for the remainder of the sampling period (Fig. 2.15). *T. nordenskioeldii* is considered to be stenothermal as it exhibits a preference for low *in situ* temperatures and has an optimal growth temperature of 10 - 15°C (Smayda, 1980). Growth rates of this species declines above this optimal range. Surface temperatures remained below 12°C in regions I (Fig. 2.1) and II (Fig. 2.2) until July 23 when they rose to 14.5°C. A steady increase in surface temperatures may be responsible for the disappearance of *T. nordenskioeldii* from the temporal succession. *T. nordenskioeldii* did not predominate in region III (Fig. 2.17) where surface temperatures reached 14°C as early as June 9. In the Strait of Georgia, *T. nordenskioeldii* has been observed to lead the spring diatom succession followed by *Skeletonema costatum*, and then *Chaetoceros* spp. (Harrison *et al.*, 1983).

Skeletonema costatum is considered to be eurythermal as it is capable of growth between 0 and 30°C. This species is thought to replace *Thalassiosira nordenskioeldii* in dominance when growth conditions improve during the spring time (Guillard and Kilham, 1977). *S. costatum* has the highest relative biomass in region I on June 25, August 26, and September 9 and in region II on June 9 and 25, July 8, and August 26. The similarity between the relative biomass of *S. costatum* in regions I and II appears to indicate the sampling dates that the biomass in region I had the most influence on the biomass in region II.

In region III the diatoms that have a high biomass are those with a large size and generally cylindrical shape compared to those in the other regions (Fig. 2.17). For example, *Rhizosolenia setigera* and *Navicula wawrickae* made up the top 47 % of the phytoplankton biomass on September 25. The retention of these large cells in the euphotic zone and the formation of a distinct horizontal layer in this stratified region is unusual since large cells have faster sinking rates than small cells (Walsby and Reynolds, 1980). Nitrogen replete cells have slower sinking rates than nitrogen deplete cells

(Smayda, 1970). A decrease in surface to volume ratio may decrease the nutrient-depleted zone around a cell or increase the sinking rate and move the cell deeper into a nutrient rich layer (Smayda, 1970; Malone, 1980). Also, the lower nutrient requirements per unit time and growth rates (Smayda, 1970; Guillard and Kilham, 1977) associated with these stage three type diatoms (Margalef, 1958) will facilitate higher sinking rates (Smayda, 1970) and influence *R. setigera* and *N. wawrickae* to sink to the nitracline. The fall diatom bloom in region III differs from that of Region I and II and the remaining Sechelt Inlet system (Taylor et al., 1991). Stage one and two type diatoms such as *Skeletonema costatum* and *Chaetoceros* spp. each exhibit a biomass below 1 $mgC \cdot L^{-1}$. Species composition and size-selectivity of grazers may also be responsible for the near absence of smaller diatoms found in region III on September 25.

Chaetoceros decipiens has the highest relative biomass (38%) on June 9 in region III (Fig. 2.17). In the Aegean Sea, Ignatiades (1969) found that *Ch. decipiens*, *Hemiaulus* sp. and *Rhizosolenia* sp. were the only species that remained in the phytoplankton after the spring diatom bloom. Although the spring bloom was not sampled during this study in Sechelt Inlet, it had probably taken place by June 9. These species are considered "oceanic" species and must have adaptive strategies to remain in stratified nutrient-depleted waters.

Pleurosigma sp. is a large-sized diatom that rated the third highest relative biomass (11%) on June 25 and the second highest (15%) on July 8 (Fig. 2.17). The formation of a distinct horizontal layer exhibited by this benthic diatom signifies that it must have some buoyancy adaptations for a planktonic existance. *Pleurosigma* sp. reached a mean concentration of 33,000 $cells \cdot L^{-1}$ over a 15 metre depth in a relatively shallow, southern region (117 m) of Sechelt Inlet (Porpoise Bay) on August 29, 1990. Southerly winds may have enhanced the estuarine surface flow and an upwelling event may have caused the benthic cells to be resuspended. Resuspension in region III may have also delivered *Pleurosigma* sp. to the euphotic zone.

Heterotroph succession

Oligotrichs, *Protoperidinium pallidum* and *P. conicum*, and tinitinnids appear to be the dominant heterotrophs in region I and II and III (Fig. 2.18, 2.19, and 2.20). *Laboea*, *Protoperidinium depressum* and rotifers are also dominant in region III. Region II contains the largest number of heterotrophs in the top ninety percent of the biomass.

In region III, the top ninety percent of the heterotroph biomass seems to be dominated by fewer genera or species than in region I and II. The presence of potentially toxic flagellates, such as *Dictyocha speculum*, *Prorocentrum minimum*, *Heterosigma akashiwo*, and *Gymnodinium sanguinium* may have caused an exclusion response in certain heterotrophs. The presence of larger zooplankton not sampled in this study, may also affect the presence or absence of microzooplankton sampled in this study. In region III the avoidance of the ebbing surface layers by larger zooplankton will lead to the retention of these organisms and an increase in grazing pressures in this region. The combination of an increase in grazing pressure and potential selectivity of prey may contribute to the reduced number of heterotrophs in the top ninety percent of the total heterotroph biomass in region III.

Species richness

The numbers and species of phytoplankton is expected to be greater in the "transition" zone or along the boundary of admixing bodies of water containing different phytoplankton communities (Margalef, 1958). Figs. 2.16 and 2.17 reveal that regions II and III have a higher number of phytoplankton species in the top ninety percent of the biomass relative to that of region I. A higher relative richness in species may be encountered in region III due to the mixture of freshwater and saltwater. *Cyclotella* sp. was the only freshwater species to contribute to an increase in the number of species

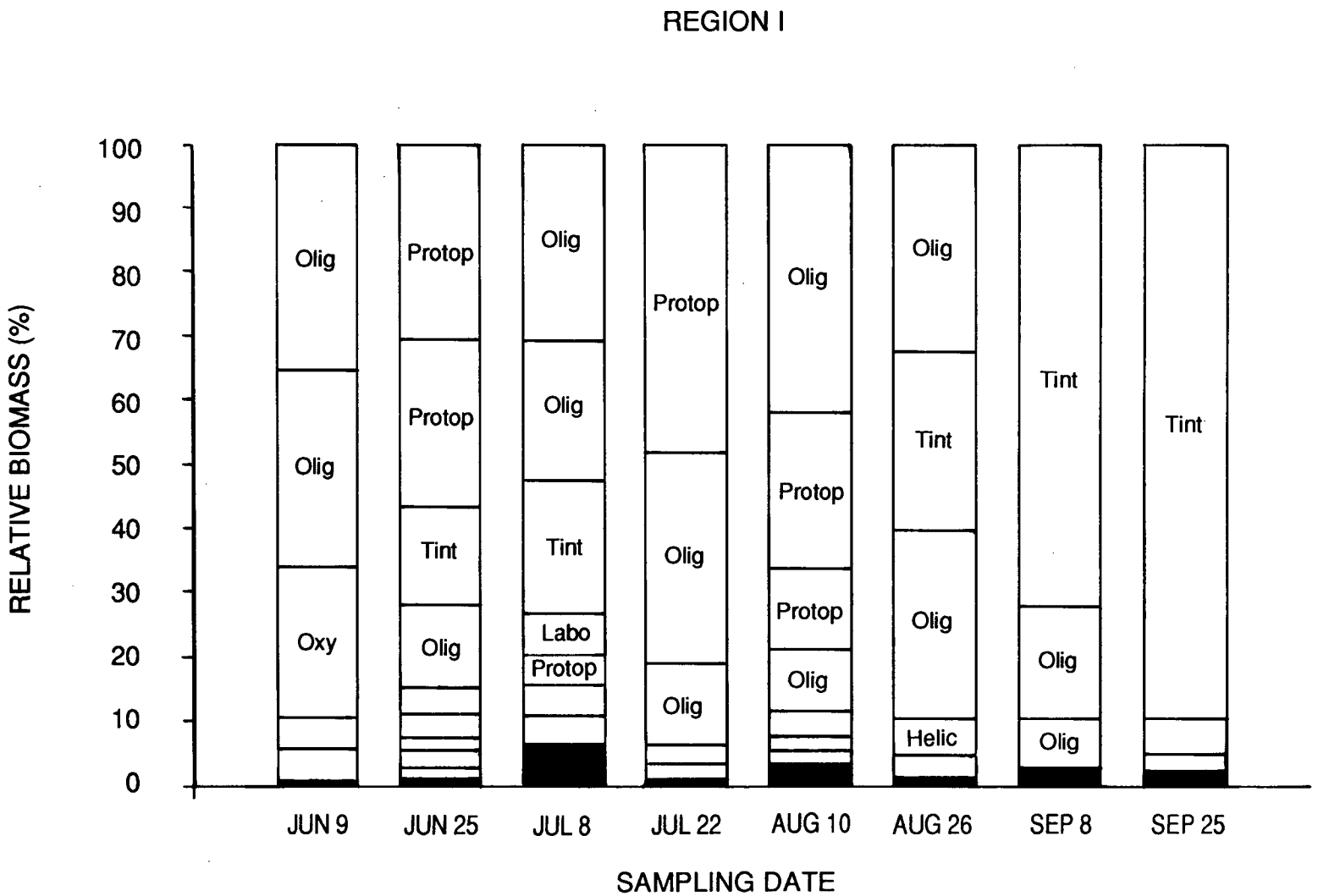

Figure 2.18: Relative biomass of heterotrophs found in region I between June 9 and September 25 in 1989. Black area = other heterotrophs < 2 $\mu gC \cdot L^{-1}$ of total heterotroph biomass.

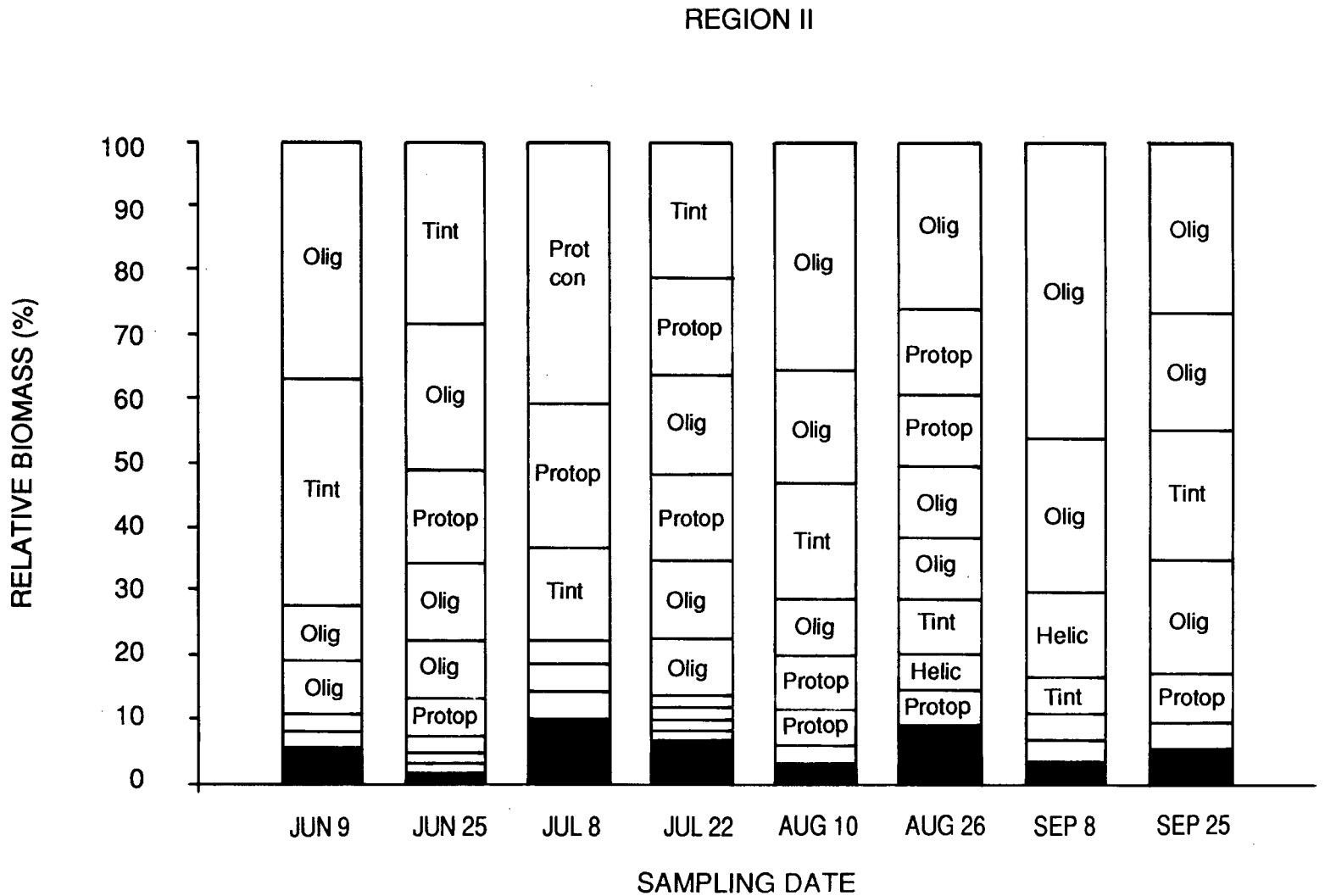

Figure 2.19: Relative biomass of heterotrophs found in region II between June 9 and September 25 in 1989. Black area = other heterotrophs < 2 $\mu gC \cdot L^{-1}$ of total heterotroph biomass.

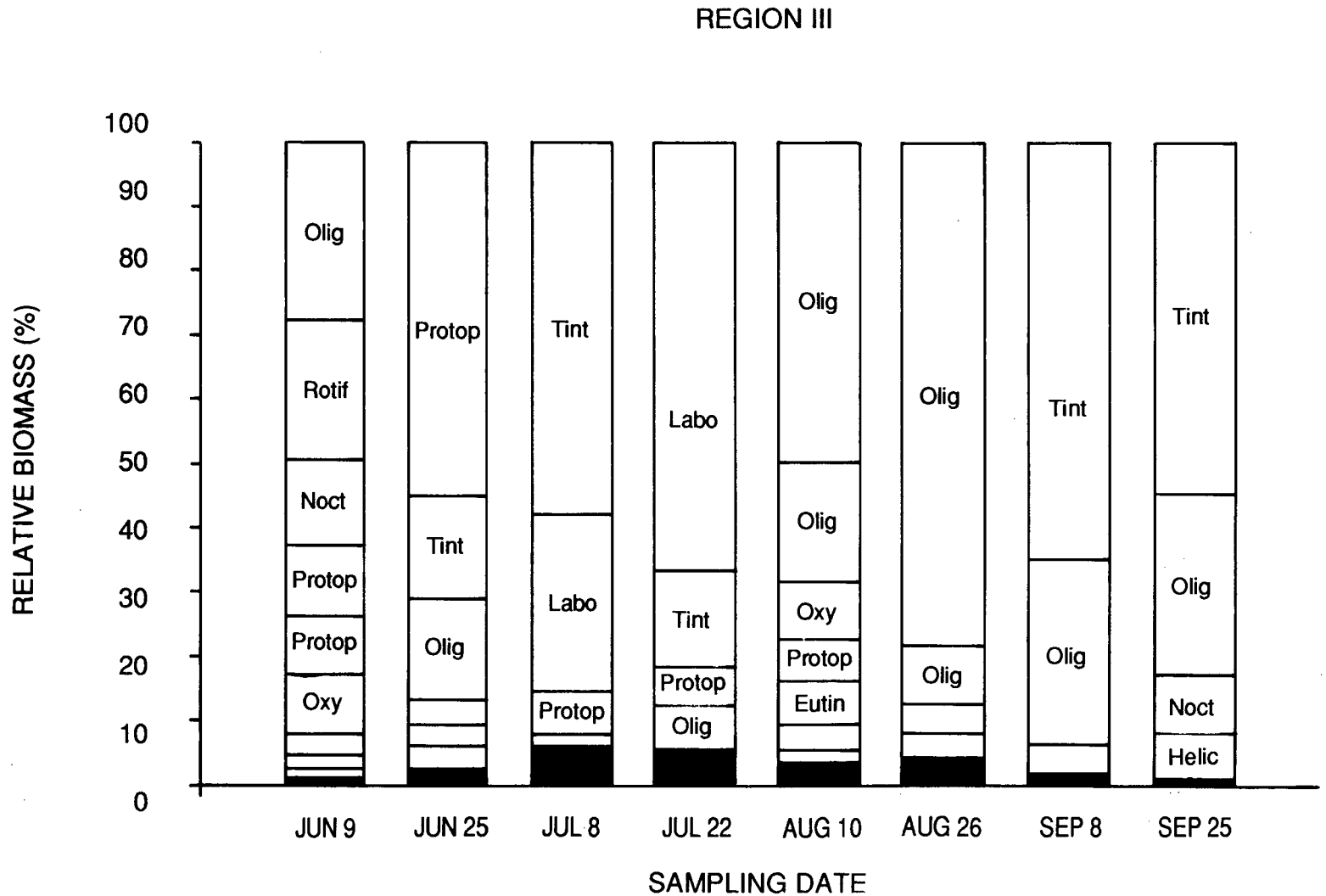

Figure 2.20: Relative biomass of heterotrophs found in region III between June 9 and September 25 in 1989. Black area = other heterotrophs < 2 $\mu gC \cdot L^{-1}$ of total heterotroph biomass.

present. Other marine phytoplankton with low salinity tolerances may thrive in region III and add to the number of species that can exist in this region.

An increase in species richness of a phytoplankton community may also serve as an indicator for the latter stages of a succession (Margalef, 1963; Smayda, 1980). For example, the vertical heterogeneity that exists in region III allows the flagellate population to occupy the surface layer while the diatom population occupies a deeper layer below the thermocline or nutricline (Figs. 2.10, 2.11, 2.12, 2.13). Fig. 2.14 reveals that the biomass consists of 40% stage three phytoplankton.

A decrease in species richness may result from a lack of stratification (Smayda, 1980) or the presence of growth-inhibiting ectocrine substances (Taylor, 1987). For example, winds greater than 12 knots may have caused a breakdown of stratified conditions on July 8 and August 26 in region II. Also, in region I, *Heterosigma akashiwo* and *Dictyocha speculum* may have promoted the absence of diatoms from the top 80 % of the phytoplankton biomass on July 22 (Fig. 2.17). *H. akashiwo* is known to form monospecific blooms at high concentrations (pers. comm. F.J.R. Taylor) and has been shown to inhibit the presence of *Skeletonema costatum* from the water column in Narragansett Bay (Pratt, 1966).

2.3.3 DISTRIBUTION AND ABUNDANCE OF HARMFUL PHYTOPLANKTON

The temperature, salinity (physical), and nutrient (chemical) profiles reveal a strong spatial heterogeneity between regions I, II, and III. This knowledge of water column stability and nutrient availability allow for the prediction of the occurrence of harmful diatoms or dinoflagellates in these regions according to Margalef's scheme (Fig. 1.0; 1978). The contour plots to be discussed shortly reveal the "hot" spots for the presence of *Heterosigma akashiwo*, *Protogonyaulax catenella* and *P. tamarensis*, *Prorocentrum minimum*, *Dinophysis fortii* and *D. acuminata*, *Chaetoceros convolutum* and *Ch. concavicorne*, and *Nitzschia pungens* (Fig. 2.21, 2.22, 2.23, 2.24, 2.25, and 2.26)

2.3.3.1 HARMFUL FLAGELLATES

Heterosigma akashiwo

As the number of fish farms in British Columbia increased from eight in 1985 to 130 in 1988 (Castledine and Marsh, 1988), the risk of heavy losses of farmed fish due to *Heterosigma akashiwo* (Gaines and Taylor, 1986), *Chaetoceros convolutum* and *Chaetoceros concavicorne* (Bell, 1961), and potentially *Dictyocha speculum* (Erard-Le Denn and Ryckaert, 1990) increased. For example, in 1986, a *Heterosigma akashiwo* bloom in Sechelt Inlet was responsible for the death of more than 100,000 salmon and trout and the loss of 2.5 million dollars (Insurance and B.C. Ministry of Agriculture and Fisheries data). In 1989, a *H. akashiwo* bloom took place in the Jervis Inlet system and wiped out five fish farms, resulting in a loss of 350 tonnes of salmonids (Brooks, 1989). A pilot study performed by Taylor et al. (1991) revealed that *H. akashiwo* reached its highest concentrations in Narrows Inlet in 1988. Research discussed in this thesis was designed to investigate factors promoting the excystment and distribution of this fish-killing phytoplankton species. However, in 1989 *H. akashiwo* reached its highest concentrations in Jervis Inlet (outside Sechelt Inlet). As a result this investigation was

expanded to encompass the dynamics of the entire phytoplankton populations found in regions I, II and III.

Chattonella antiqua, a close relative of *Heterosigma akashiwo*, contains a fatty acid that is involved in the first step of a fish kill by destroying the surface cells of fish gills (Okaichi, 1985). *C. antiqua* causes a decrease in the number of mucous cells on gill primary lamellae, thereby reducing the mucous coat on the gill, altering ion transport in gill filaments and resulting in edema and inhibited gas exchange (Toyoshima *et al.*, 1987). Biochemical analysis of *C. antiqua* and *H. akashiwo* reveals that both phytoplankton species have a large percentage of similar fatty acids (Nichols, 1987). Consequently, the cause of fish death induced by *H. akashiwo* may be similar to that cause by *C. antiqua.*

In 1988 *Heterosigma akashiwo* reached its highest concentrations (36,000 cells•L^{-1}) in the surface depth interval of (0-3m) in July in the outer part of Narrows Inlet relative to five other stations located in other regions in Salmon and Sechelt Inlets (Taylor *et al.*, 1991). *H. akashiwo* forms a benthic stage which consists of encapsulated masses of non-motile cells whose excystment success increases above temperatures of 9.5°C (Tomas, 1978; Yamochi, 1987, 1989). Narrows Inlet was predicted to favour the excystment of benthic cells and growth of vegetative cells of *H. akashiwo*. Temperature profiles from Lazier (1963) and Pond (unpublished data) reveal that bottom temperatures in regions II and III exceed this critical excystment temperature. The two-layer estuarine flow in region III was thought to trap diurnally migrating vegetative cells avoiding the low salinity surface layers and allow sinking benthic forms to accumulate at the water-sediment interface layer forming a "seed bed". This aspect will be discussed further in Chapter three. Taylor *et al.* (1991) found that the highest concentrations of *H. akashiwo* took place at the entrance (station 1) and the shallower regions (outer Narrows and near the town of Sechelt) over a three year study.

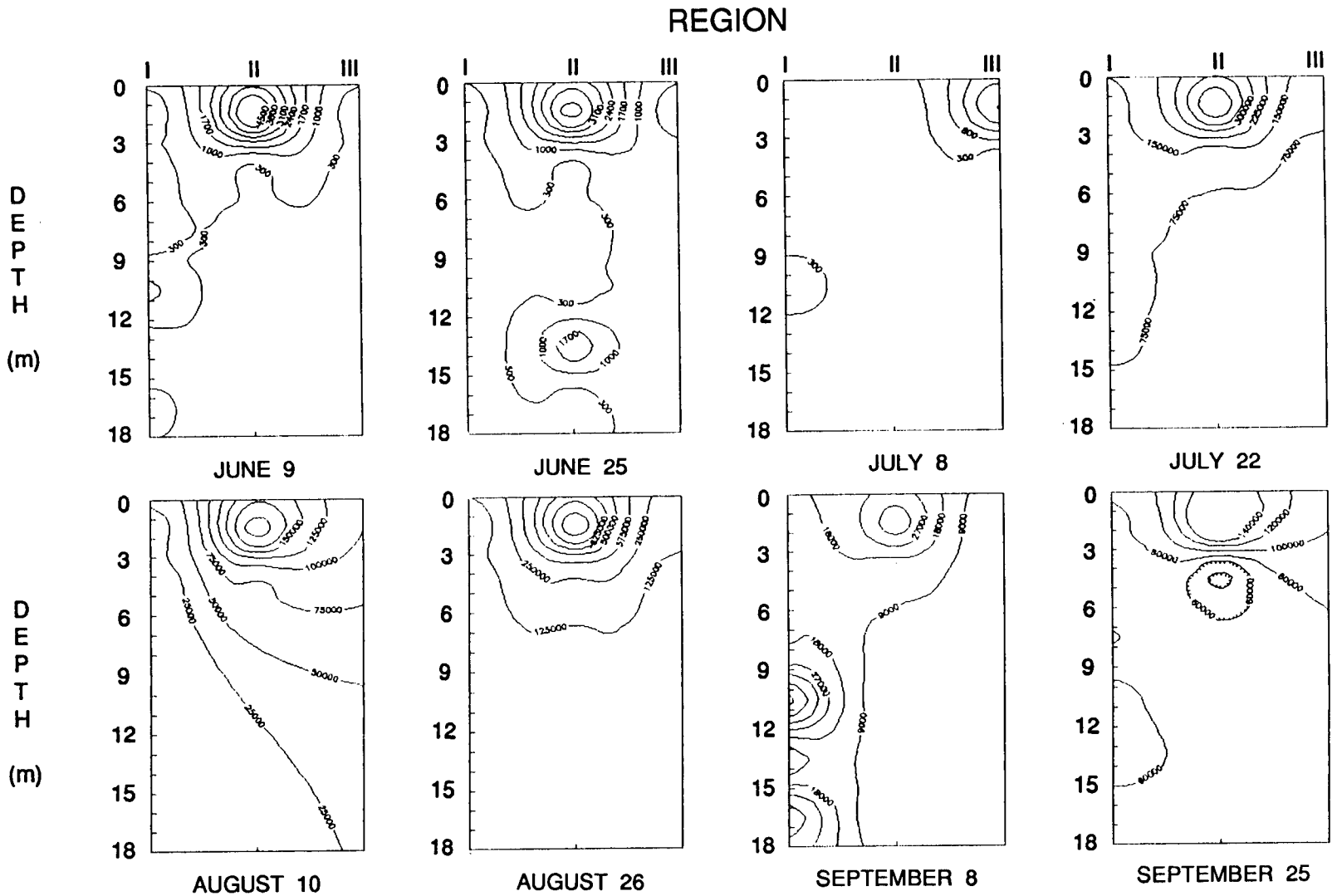

Figure 2.21: The distribution of *Heterosigma akashiwo* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

The calm, thermally stratified summer conditions of region II and III were predicted to favour the growth of *Heterosigma akashiwo* since optimal growth of this chloromonad takes place at 20°C over a wide salinity range of 5 to 35 psu (Tomas, 1978). The highest surface temperatures observed during the 1989 sampling trips were 16.5°C in region II and 17°C in region III.

The ecological advantage of diel migration allows a flagellate to maintain its position in the upper water column and accumulate near the surface during daylight hours. At night *Heterosigma akashiwo* is known to cross strong salinity gradients while undergoing vertical migration at speeds of 1.0 to 1.3 metre•hour^{-1} to nutrient-replete depths of 12 metres (Hatano *et al.*, 1983; Yamochi and Abe, 1984; Wada *et al.*, 1985). The stratified conditions in region III did not promote the same surface cell densities of *H. akashiwo*. The highest cell densities reached in this region were 100,000 cells•L^{-1} on August 10 (Fig. 2.21).

The numbers of *Heterosigma akashiwo* present in region I increased between June 9 (< 300 cells•L^{-1}) and August 26 (90,000 cells•L^{-1}). An increase in concentrations of *H. akashiwo* was also seen in region II during the same time period, suggesting that blooms of *H. akashiwo* in Sechelt Inlet may arise from the allochthonous source waters of region I. The highest numbers of *Heterosigma akashiwo* were reached in region II in the surface waters (Fig. 2.21). The wind speed recorded for July 8 was greater than ten knots and may have diluted the surface accumulation of this organism through wind-mixing turbulence. The highest cell numbers were greater than 875,000 cells•L^{-1} in region II on August 26.

A bloom of *Heterosigma akashiwo* was responsible for the loss of 350 tonnes of salmon (Brooks, 1989) farmed in Agamemnon Channel on September 6, 7, and 8. Winds and tidal forces appeared to keep the bloom on the northern edge of the channel that runs east-west. Fish farms on the southern edge of the channel did not experience the losses of those on the northern edge. The southeast border of Agamemnon Channel joins the

mouth of Skookumchuck Narrows (Region I). It was feared that the tidal exchange that takes place at Sechelt Rapids (Region I) located in the Narrows would draw the bloom into Sechelt Inlet. *H. akashiwo* was present at 20,000 cells•L^{-1} in region I during flood tide. However, the cell counts in Region II and III on this sampling date were the lowest they had been since July 8. A bloom of *H. akashiwo* did not develope inside Sechelt Inlet following the bloom that took place in Agamemnon Channel. The concentrations increased on the September 25 sampling trip to 150,000 cells•L^{-1} in region II.

Protogonyaulax catenella* and *Protogonyaulax tamarensis

Protogonyaulax catenella and *P. tamarenis* are responsible for producing saxitoxin which is accumulated in shellfish and causes Paralytic Shellfish Poisoning (PSP) if contaminated shellfish are consumed (Gaines and Taylor, 1986). Symptoms initially consist of tingling or burning on lips spreading to fingers, toes, arms, and legs and finally may end up in respiratory paralysis and consequent death.

Protogonyaulax catenella and *P. tamarensis* appeared on July 8 and 22, August 10, and September 25 (Fig. 2.22). Cell concentrations remained below 375 cells•L^{-1} on July 8 and 22 and on August 10, while cell concentrations reached 20,000 cells•L^{-1} on September 25. *P. catenella* and *P. tamarensis* was absent from Region III and present in region I only on August 1. Taylor *et al.*, (1991) found that one population of *P. catenella* and *P. tamarensis* was introduced through Skookumchuck Narrows (Region I) and another formed in the Porpoise Bay Region at the other end of Sechelt Inlet.

Prorocentrum minimum

Prorocentrum minimum first appeared in region III on June 25 with maximum cell concentrations of 21,000 cells•L^{-1} at the 6-12 metre depth interval (Fig. 2.23). Maximum cell concentrations then progressed from 5000 cells•L^{-1} on July 8, 40,000 cells•L^{-1} on July 22, 75,000 cells•L^{-1} on August 10, peaked at 100,000 cells•L^{-1} on August 26, and

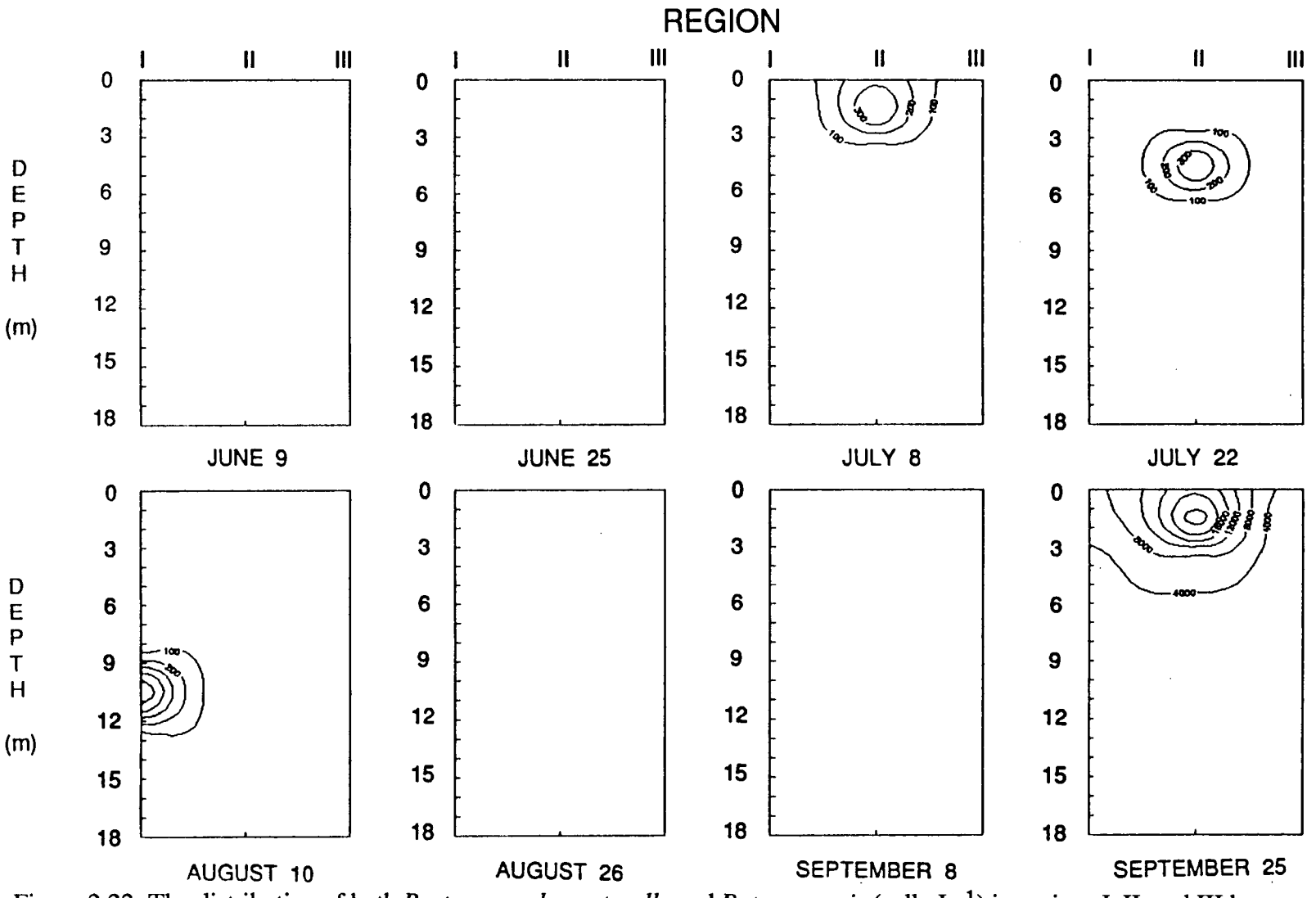

Figure 2.22: The distribution of both *Protogonyaulax catenella* and *P. tamarensis* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

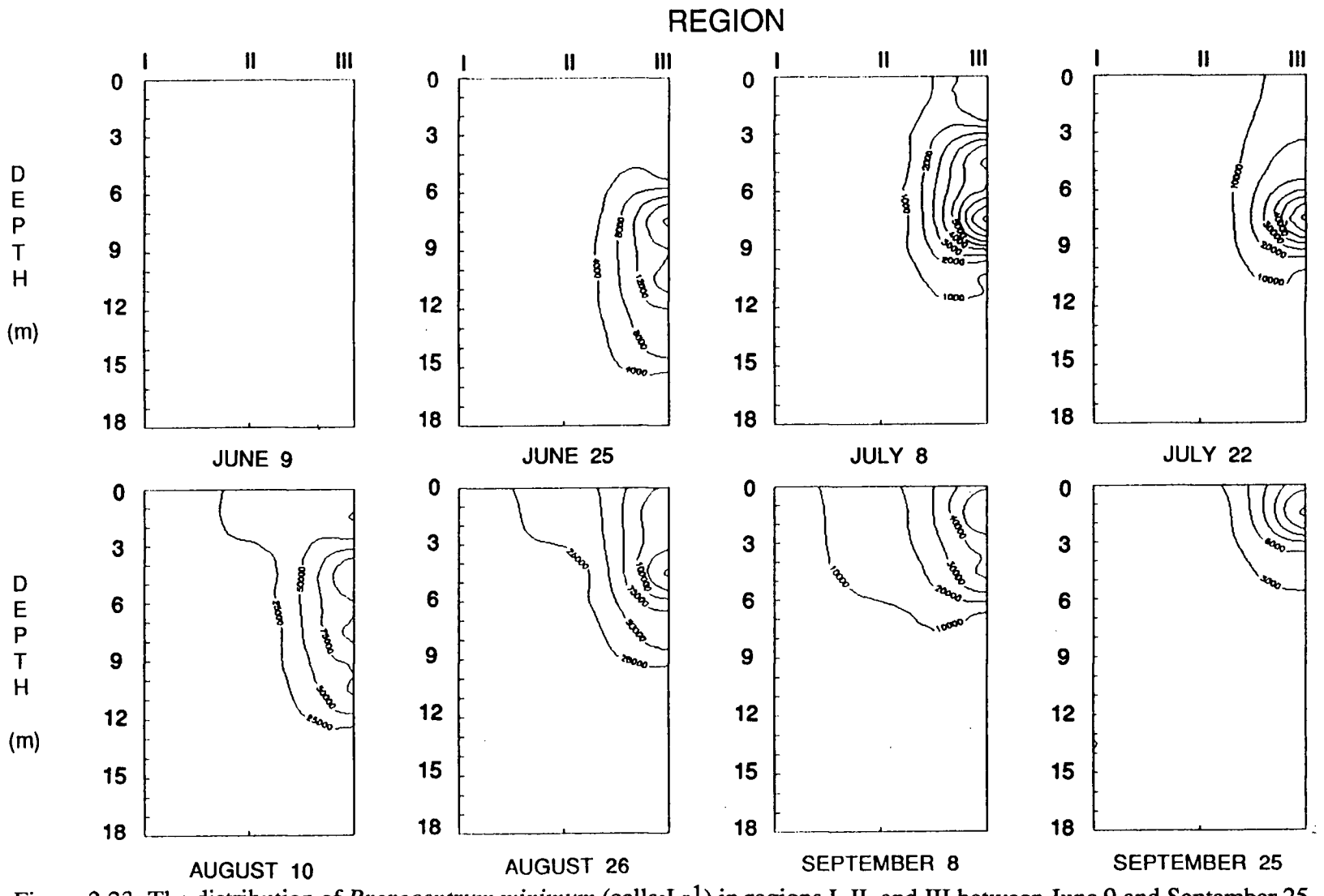

Figure 2.23: The distribution of *Prorocentrum minimum* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

decreased to 40,000 cells•L^{-1} on September 8, and finally 6000 cells•L^{-1} on September 25. The maximum cell counts were found at the 6-9 metre depth interval from July 8 to 23, the 3-9 metre depth interval on August 10, the 3-6 m depth interval on August 26, and then remained at the 0-3 m depth interval on the two sampling trips in September. An avoidance of the nutrient-deplete surface layers in July and August and then the migration into the nutrient-replete surface layers of *P. minimum* may be due to the photochemical damage experienced under low-nutrient/high-light conditions.

Prorocentrum minimum may have been transported in the surface waters from region III to region II on an ebb tide. *P. minimum* appears in the 0-3 m depth interval only in region II on August 10, August 26, and September 8. This "inoculum" of *P. minimum* may serve as an autochthonous source for toxic dinoflagellate blooms in Sechelt Inlet. Other flagellates such as *Heterocapsa triquetra* exhibit similar transporation and distributional patterns as *P. minimum.*

Dinophysis fortii* and *D. acuminata

Okadaic acid is produced by *Dinophysis fortii* and *D. acuminata*, accumulated in shellfish, and responsible for symptoms such as nausea, vomiting, and diarrhea or Diarrheic Shellfish Poisoning (DSP). Shellfish toxicity has been observed when cell concentrations of *D. fortii* are as low as 200 cells•L^{-1} (Taylor *et al.*, 1991) (Fig. 2.24). *D. fortii* formed a subsurface maximum at the 6-12 metre depth interval in region III on June 9 and 25 and July 8. On June 25, *D. fortii* (400 cells•L^{-1}) was present in the source waters of region I. In August and early September, cell counts decreased to 200 cells•L^{-1} relative to July 22. On September 25, cell concentrations rose to 800 cells•L^{-1} in region II with low concentrations present in Region I.

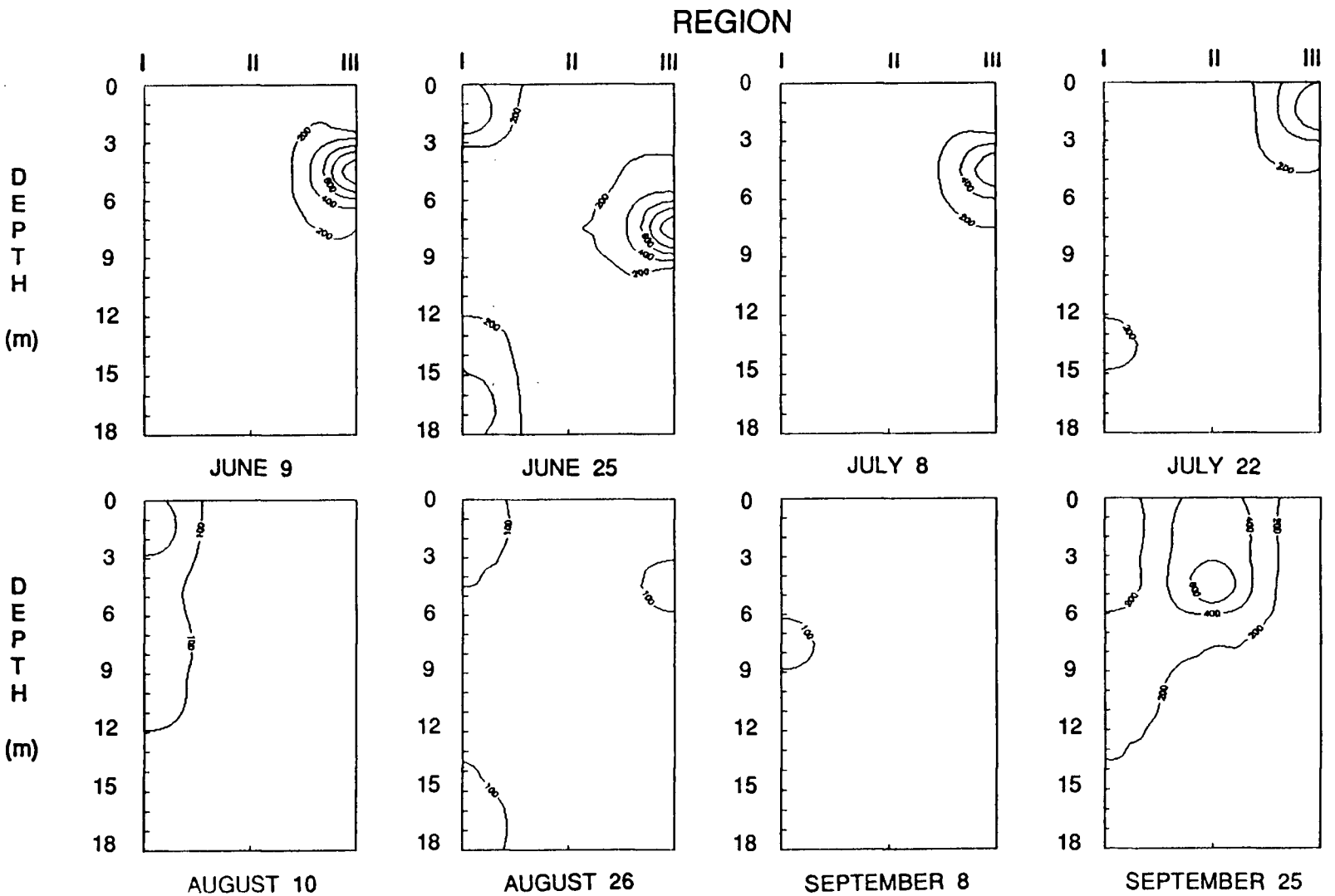

Figure 2.24: The distribution of both *Dinophysis fortii* and *D. acuminata* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

2.3.3.2 HARMFUL DIATOMS

Chaetoceros convolutum and Chaetoceros concavicorne

Bell (1961) examined the gills of lingcod exposed to a bloom of *Chaetoceros convolutum* and found barbed setae embedded in the gill tissues of the dying fish. Concentrations of *Ch. convolutum* of roughly 1000 cells•L^{-1} were observed to cause extensive damage to gills of salmon reared on a Nanaimo experimental fish farm in 1974 (Kennedy *et al.*, 1976). In 1975, it was noted that injury inflicted by *Ch. convolutum* frequently served as a point of entry for the bacterium *Vibrio anguillarum* and increased mortality rates. During a 1977 *Ch. convolutum* bloom with surface concentrations of 8000 cells•L^{-1}, losses of farmed sockeye salmon reached sixty percent (Brett *et al.*, 1978). Smolts are reported to be more susceptible to damage by this diatom than older salmon, although the reason for this increased susceptibility is unknown (Caine, 1988).

The barbed spines of *Chaetoceros convolutum* cause much physical damage to the epithelial gill tissue of farmed fish. If the barbs are directed towards the surface of the gill, they will act as an anchor and ensure the setae remains implanted despite the counter circulation current produced by the gills of the fish. Capillaries ruptured by the penetration of these barbed spines will decrease blood flow in the gills, preventing circulation of oxygenated blood to the rest of the body (Hicks, 1988). Entrapped setae may stimulate secretion of a protective heavy mucus over the gills preventing the absorption of oxygen from water to blood.

Concentrations of *Chaetoceros convolutum* on June 9 remained below the fish-killing concentration of 5000 cells•L^{-1} reported by Bell *et al.* (1974). The surface water between 0-3 m and 6-9 m in region II contained cell concentrations of 3800 cells•L^{-1} (Figure 2.25). The concentrations of this species in region I and III were lower relative to II, with region I having a slightly higher number than region III.

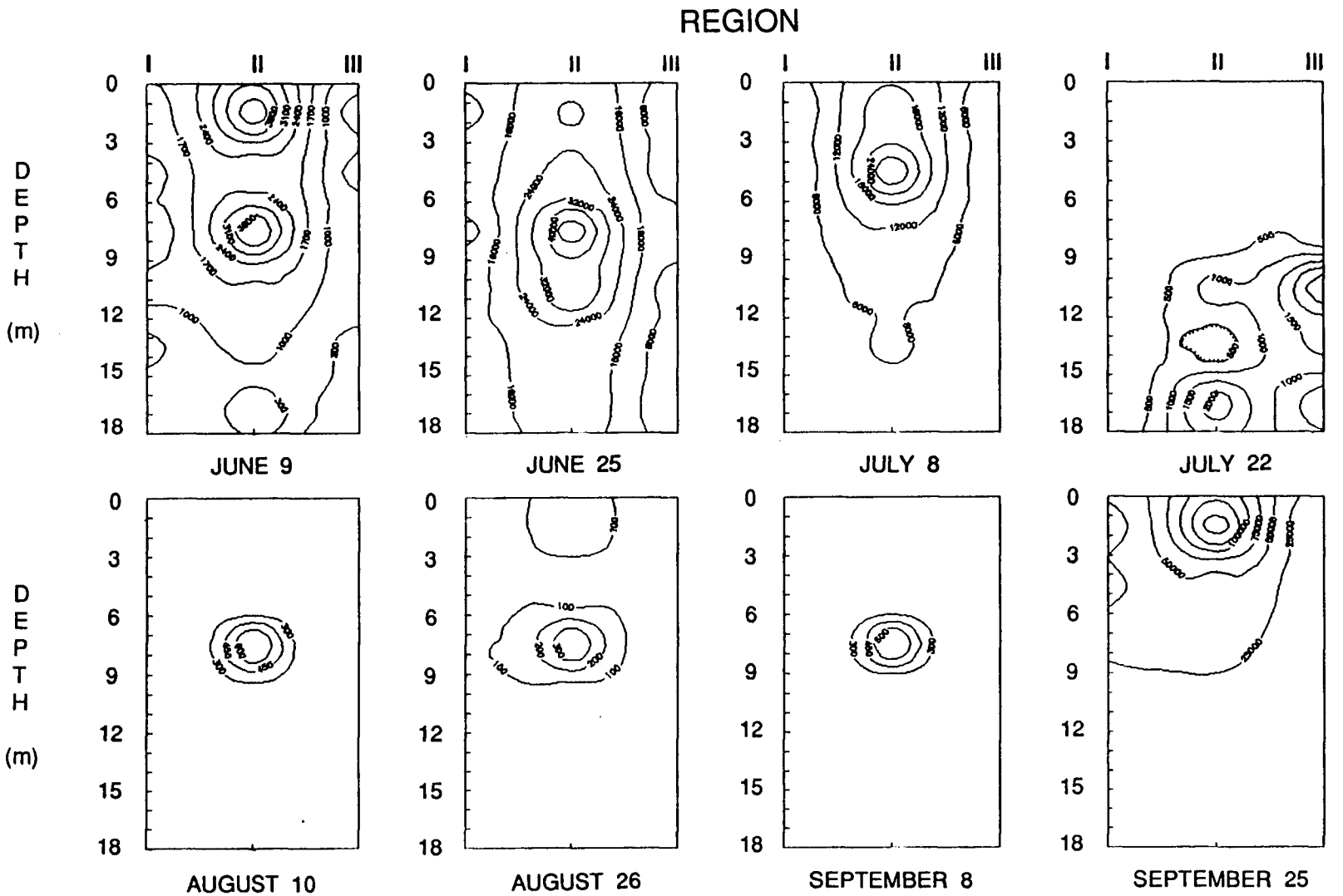

Figure 2.25: The distribution of both *Chaetoceros convolutum* and *Ch. concavicorne* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

In region II and III, subsurface maxima of *Chaetoceros convolutum* at the 6-9 m were observed on June 25 as cell counts reached a lethal 48,000 cells•L^{-1} and 8602 cells•L^{-1} respectively. In region I, *Ch. convolutum* was distributed uniformly over the top eighteen metres with an average cell concentration of 11,000 cells•L^{-1}. The high concentrations found in region II probably resulted from the transportation of *Ch. convolutum* across sill 1 and subsequent accelerated growth.

High winds (> 10 knots) on July 8 were probably responsible for breakdown of a density gradient and the resuspension of the subsurface maxima (25,300 cells•L^{-1}) of *Chaetoceros convolutum* found at the 3-6 m depth interval in region II. Cell concentrations in regions I and III were less than 5000 cells•L^{-1}. The stratified conditions on July 22 was associated with a deep subsurface maxima below the 6-9 m depth interval in regions II and III. The low cell concentrations ranging between 300 to 1700 cells•L^{-1} maintained at the deeper depths reflects the percentage of the population capable of resisting sinking pressures. An absence of *Chaetoceros convolutum* in region I is striking and may be due to an inhibition by the dominance of *Heterosigma akashiwo* (Fig. 2.21 and 2.25). Pratt (1966) found a reciprocal codominance between the occurrence of *Skeletonema costatum* and *Heterosigma akashiwo* in Narragansett Bay. Another potentially toxic phytoplankton species dominating in region I was *Dictyocha speculum*.

A subsurface concentration of *Chaetoceros convolutum* below 500 cells•L^{-1} persisted at the 6-9 m depth interval during the sampling trips on August 10, August 26, and September 8. On September 25 the highest cell concentrations of the sampling period were observed in the surface 0-3 m depth interval in region II. This species also occurred in high conentration during late September and early October in 1989 (Taylor *et al.*, 1991). The surface temperature in region II was 14°C. Gatzke (1988) reported that maximal growth rates of *Chaetoceros convolutum* were observed at 14 °C under low light level conditions. The persistence of the near surface maxima, the allochthonous transport of cell concentrations between 25,000 and 50,000 cells•L^{-1} from region I

(September 25), and the competitive strategy of high growth rates under autumn low-light levels are thought to contribute to the fall bloom in region II.

Nitzschia pungens

Amnesic Shellfish Poisoning (ASP) is caused by the human consumption of mussels that have accumulated high concentrations domoic acid produced by *Nitzschia pungens* (Todd, 1980). An outbreak of ASP was reported in Prince Edward Island in the autumn of 1987 where people experienced symptoms such as intestinal distress and brain damage.

Nitzschia pungens did not appear in all three regions until June 25 (Fig. 2.26). At this time cell concentrations ranging from 15,000 to 20,000 cells•L^{-1} were distributed over the top 12 metres in region II. Cell concentrations below 5000 cells•L^{-1} were observed in the source waters of region I.

On July 8 *Nitzschia pungens* reached its highest concentration (100,000 cells•L^{-1}) between 0-3 m. In region III cell concentrations of *Nitzschia pungens* had increased five to ten fold relative to the previous sampling trip. The wind-mixing event experienced on July 8 did not appear to resuspend the subsurface maximum of *N. pungens* in the protected region III.

The distribution of *Nitzschia pungens* for the remainder of the sampling period is very similar to that of *Chaetoceros convolutum*. On July 22 a population (< 2500 cells•L^{-1}) of *N. pungens* was found at depths below the 12 metre depth interval in regions II and III. *N. pungens* was not present in region I and may have been inhibited by the presence of *Heterosigma akashiwo*. A surface population persisted throughout the remaining sampling trips and was located at the depth interval (0-3 m) above the depth interval (3-6 m) that *C. convolutum* was observed to persist. Low cell concentrations (< 1000 cells•L^{-1}) were observed in the source waters of region I and may have contributed to the small

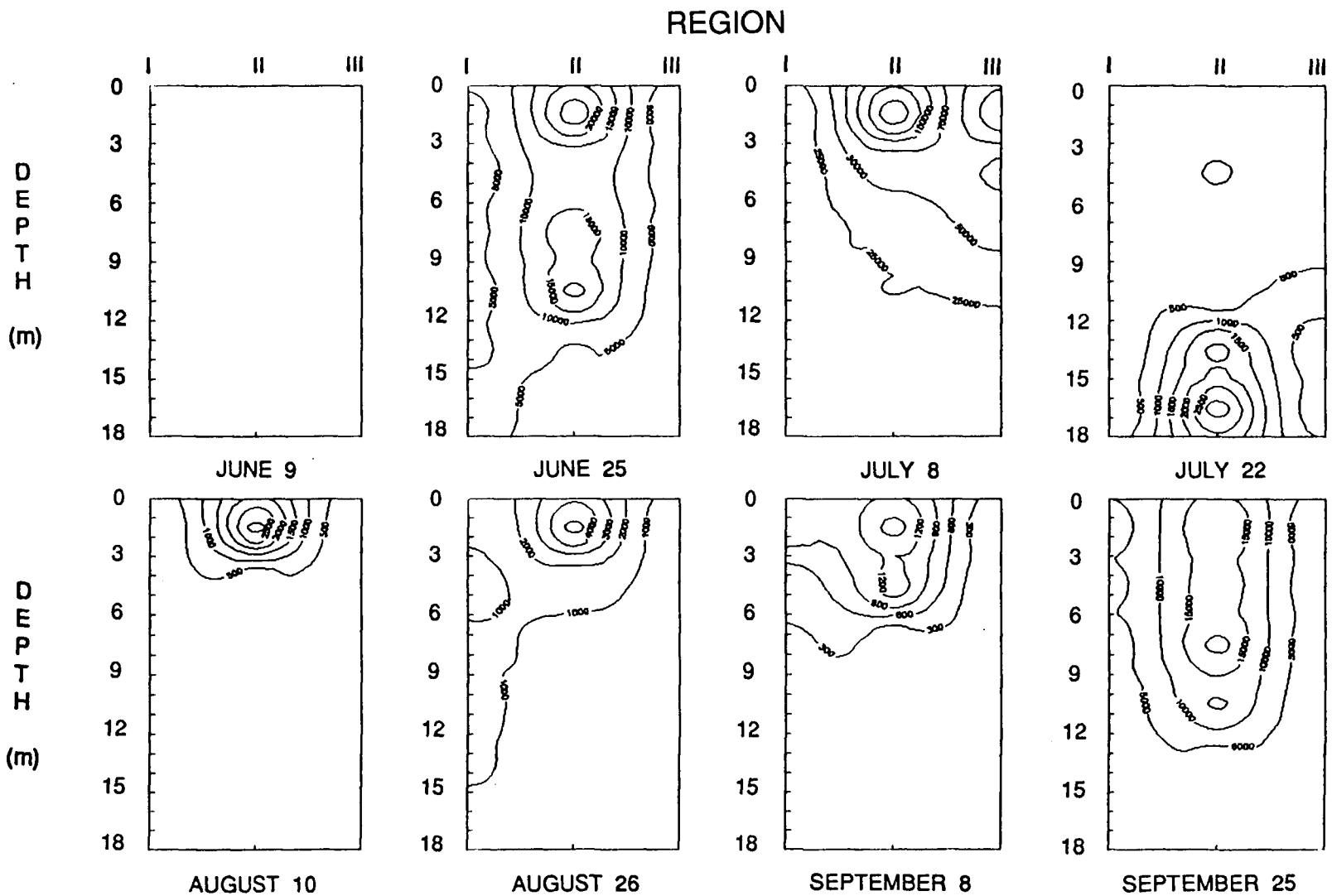

Figure 2.26: The distribution of *Nitzschia pungens* (cells•L^{-1}) in regions I, II, and III between June 9 and September 25 in 1989.

increase in the surface population in region II. On September 25 cell counts increased to 15,000 cells•L^{-1} and ranged over the top 12 metres.

CHAPTER THREE: A comparison of phytoplankton communities present at the water-sediment interfaces of regions I, II, and III: Implications for the "seed bed" theory.

3.1: INTRODUCTION

Many laboratory and field studies reveal that flagellate cysts form in association with conditions such as nutrient deficiency (Watanabe, 1982; Anderson, 1985; Nakamura, 1990), induction of sexual reproduction (Tyler, 1982; Anderson, 1984), decreasing light intensity, photoperiod, and temperature (Von Stosch and Drebes, 1964), and oxygen depletion and pH decrease (Marasovic, 1989). The termination of a phytoplankton bloom or the autumn period following the stratified summer months offers stressful conditions conducive to encystment. A mandatory resting period of four weeks to six months, depending on the species, is required for subsequent excystment (Endo, 1984; Binder, 1987; Anderson and Keafer, 1987; Imai and Itoh, 1986; Matsuoka, 1989; Yamochi, 1989). Excystment in some flagellates has been shown to be controlled by an endogenous circannual clock (Wall and Dale, 1969; Anderson and Keafer, 1987). The synchronization of seasonal excystment with periods of favourable growth conditions, such as oxygen repletion, increases in temperature, light intensity, and photoperiod has great ecological significance for the reestablishment and survival of a motile population (Anderson and Keafer, 1987; Costas, 1990).

The formation of resting stages in diatoms is also induced by the seasonal onset of nutrient-depleted surface waters (Davis *et al.*, 1980; Von Stosch, 1979; French and Hargraves, 1985), cold temperatures (French and Hargraves, 1985), lower light levels, and shorter photoperiods (Von Stosch, 1979). Hargraves and French (1983) have suggested that resting spore formation may also be a mechanism to avoid damage caused by photo-oxidative effects and metabolic imbalance in the presence of highly irradiated, nutrient-depleted surface waters. Germination of diatom resting spores in favourable conditions also requires a mandatory resting period consisting of darkness and cold temperatures (Davis *et al.*, 1980; Drebe, 1977; Von Stosch, 1979).

The circulation patterns and slow flushing rates of many fjords provide the conditions necessary for the accumulation of phytoplankton resting stages and consequent "seed bed" formation. Estuaries and fjords may act as "phytoplankton traps" as well as "sediment traps" due to the two-layer estuarine circulation patterns. Phytoplankton settle in the deeper regions of estuaries and fjords where finer sediment can be found (Dale, 1976; Lewis, 1985; Anderson and Keafer, 1985). Since resting cysts and spores have faster sinking rates than vegetative cells (Davis *et al.*, 1980; Hargraves and French, 1983; Anderson, 1985; Lewis, 1985), they will separate from the vegetative population and increase their probability of becoming "trapped".

Deep water renewal in temperate shallow-silled fjords may take place in the winter, spring, or summer (Lazier, 1963; Dale, 1976; Smethie, 1987). The period between flushing allows the resting stages of phytoplankton to "overwinter" or remain dormant for the mandatory, cold, dark period required for excystment or germination. Deep water renewal may act as a resuspension mechanism and introduce resting spores to shallower depths of higher light levels and optimal germination conditions. Also, the intrusion of highly oxygenated, nutrient-replete water to the water-sediment interface of deep fjords may provide conditions conducive for excystment or germination of non-resuspended resting stages. The synchronization of deep water renewal with the circannual rhythm of flagellate excystment and presence of optimal growth conditions will play an important role in the initiation and reoccurrence of phytoplankton blooms.

In Sechelt Inlet deep water replacement events may take place in region II or III, while daily tidal flushing takes place in region I. Isolated studies looking at deep water renewal in Sechelt Inlet between 1957 and 1964 (UBC Dept. Oceanography data reports; Lazier, 1963), 1975 and 1976 (Smethie, 1987), and 1990 and 1991 (Pond, unpublished data) reveal that deep water renewal may not take place during a specific year or on the other hand it may take place several times throughout year. The frequency of deep water

renewal and probable resuspension of sedimented phytoplankton will influence the direction or rate of the phytoplankton succession developing in the overlying waters.

The deep water that makes up the third layer of region III may become hypoxic or anoxic after flushing events take place. Anoxic periods are associated with the production of ammonium and H_2S (Smethie, 1987) and the decomposition of organics and as a result may cause the loss of viability in sedimented phytoplankton and their resting stages, as shown for *Leptocylindrus danicus* (Davis *et al.*, 1980). The anoxic state of the bottom water may act as a filter by reducing the types of sedimentated phytoplankton available to initiate blooms following a resuspension event. Those phytoplankton species able to maintain a meroplanktonic existence by not losing their ability to germinate after "overwintering" in anoxic benthic conditions may influence the spring (diatom) or summer (flagellate) blooms inside region III proceeding a resuspension event. These phytoplankton blooms of autochthonous origin may differ considerably from those blooms existing in contiguous waters outside the fjord.

The retention role of phytoplankton species that form resting spores in a confined area of prolonged adverse conditions (region III) was proposed by French and Hargraves (1980). Evidence to support this idea was found in a few investigations where *Chaetoceros* resting spores have been shown to contribute significantly to many marine sediments (Calvert, 1966; DeVries and Schrader, 1981; Roeloffs, 1983; Sancetta, 1989). Roeloffs (1983) found that *Chaetoceros* spp. are represented almost entirely by resting spores found in the fjordic sediments of British Columbia. The repeated occurrence of the vegetative cells of *Chaetoceros radicans*, *Ch. vanheurckii*, *Ch. debile* and *Ch. didymus* in the inner region of Saanich Inlet, B.C. and of their resting spores in cores in the centre of this fjord favours the idea that these spores serve to "re-seed" this region. Walsh (in Davis *et al.*, 1980) suggested that resting spores were responsible for the high production that took place in a region where chlorophyll-a containing material was resupended following a storm. Resting spore formation plays an important role in the life cycle of the

diatom and is often a missed event in field sampling (Davis *et al.*, 1980). More emphasis on the comparison of benthic and pelagic populations of phytoplankton should reveal persuasive evidence for the "reseeding" theory.

Phytoplankton blooms may be "reseeded" by both resting stages or temporary flagellate cysts that remain suspended in the water column (Matsuoka *et al.*, 1989) for short periods or that settle in both deep and shallow areas. Generally, temporary cysts do not undergo any internal morphological changes and form through asexual reproduction during unfavourable conditions. Germination conditions such as light and oxygen are optimal in the shallow areas relative to the deeper areas, however, phytoplankton act as fine silt particles and tend to accumulate in the deeper regions of fjords (Dale, 1976).

Resting spores could fulfill different roles in the life cycle of diatoms such as the retention of a certain species in an area during adverse conditions (long-term mechanism), the endurance of nutrient deficient periods inside zooplankton guts (short-term mechanism involved in downward transport), or the dispersal of species through transportation via the guts of herbivores to an environment of favourable growth conditions (French and Hargraves, 1980).

In this chapter the sedimented phytoplankton community observed in the water-sediment interface samples collected from region I, II, and III were compared and discussed. A vegetative population was cultured from each core sample to investigate the potential influence the sedimented phytoplankton may have in intiating spring or summer blooms in overlying waters.

3.2: METHODS

Water-sediment interface samples were collected from regions I, II, and III in the Sechelt Inlet area on February 19 and 20, 1990 (Fig. 3.1). A Pedersen Corer TM was used to collect core samples from regions II and III, while a Shippex Grab TM was used in region I due to the scoured rock bottom. The top two centimeters of the water-sediment interface were collected and stored temporarily in a dark cool place on the ship.

Water-sediment samples were stored in the dark and cold (5-6°C), below flagellate excystment temperature, back at the laboratory. A Canadian Standard Sieve Series TM was used to determine the relative amount of each sediment size class found in the core samples collected from each region. A large amount of region I sediment did not pass through the largest mesh size of 425 mm. Therefore, a 1000 mm mesh was use on the sediment not passing through the 425 mm mesh. A serial dilution technique was used to quantitatively survey any fragile "naked" flagellates present in the core samples that may be suppressed by high concentrations of phytoplankton species with fast growth rates or by herbivore grazing. All the equipment used in the serial dilution-culture technique (Throndsen, 1978) was soaked for 24 hours in a ten percent 1N HCl solution, rinsed with distilled water three times, and finally autoclaved for twenty minutes in a Standard Laboratory Castle TM autoclave at twenty psi.

Three ml of sediment from region I were added to a 25 x 150 mm glass test tube containing 27 ml of HESNW medium (Harrison *et al.*, 1980). A subsample was drawn from this suspended sediment solution using a 60 cc disposable syringe (Fig. 3.2). Three mls of this subsample was added to a set of three replicate test-tubes, each containing 27 mls of autoclaved HESNW medium. The remaining subsample except for the last three mls was expelled from the syringe. Twenty-seven mls of HESNW medium was then drawn into the syringe to produce a 10:1 dilution. This new dilution was suspended and three mls was added to a new set of replicate test tubes containing 27 ml of HESNW medium. Three mls of this 10:1 dilution was retained in the syringe. The above procedure

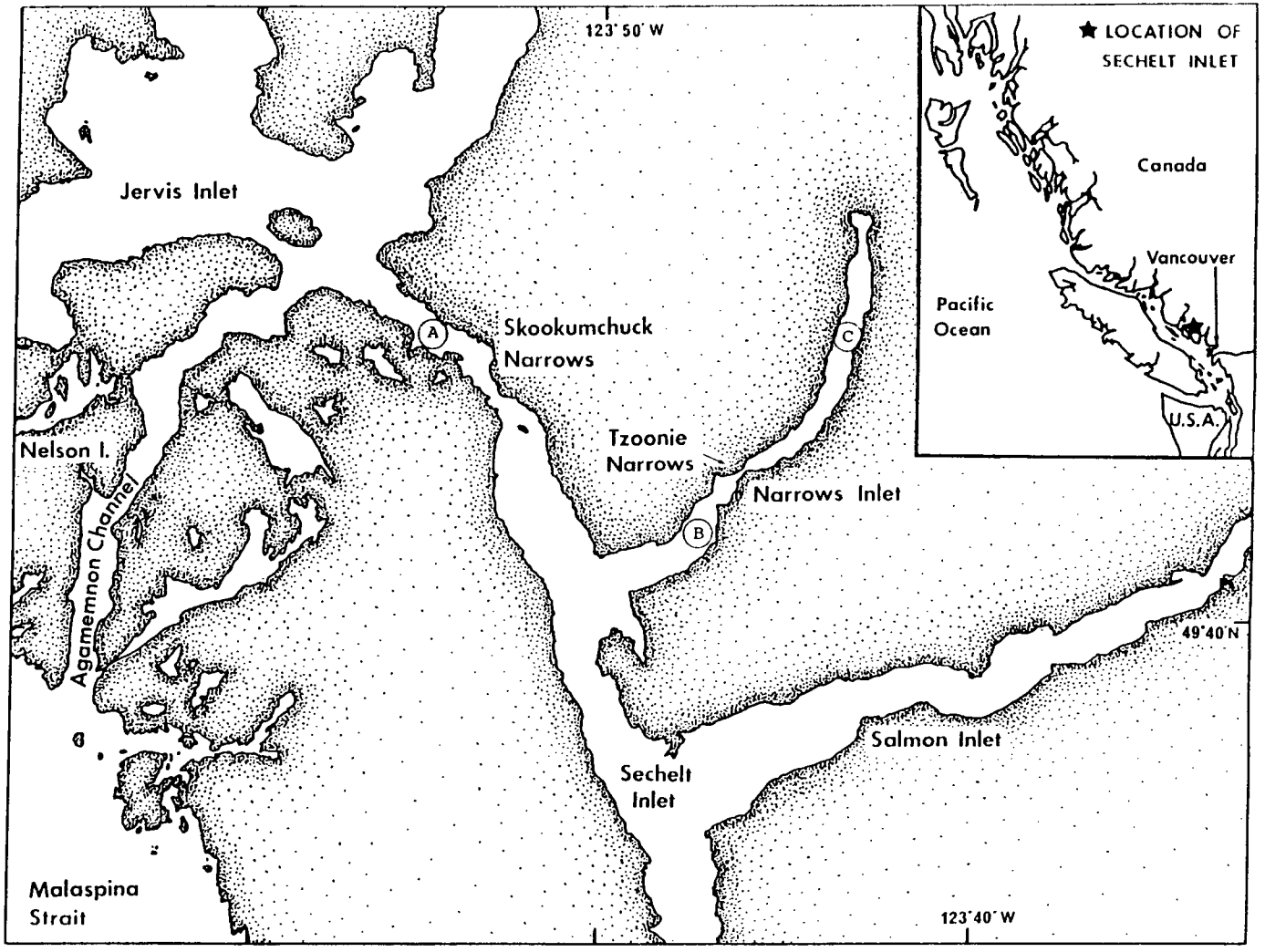

Figure 3.1: Location of the three core stations in Sechelt Inlet, British Columbia.
A = region I, B = region II, C = region III.

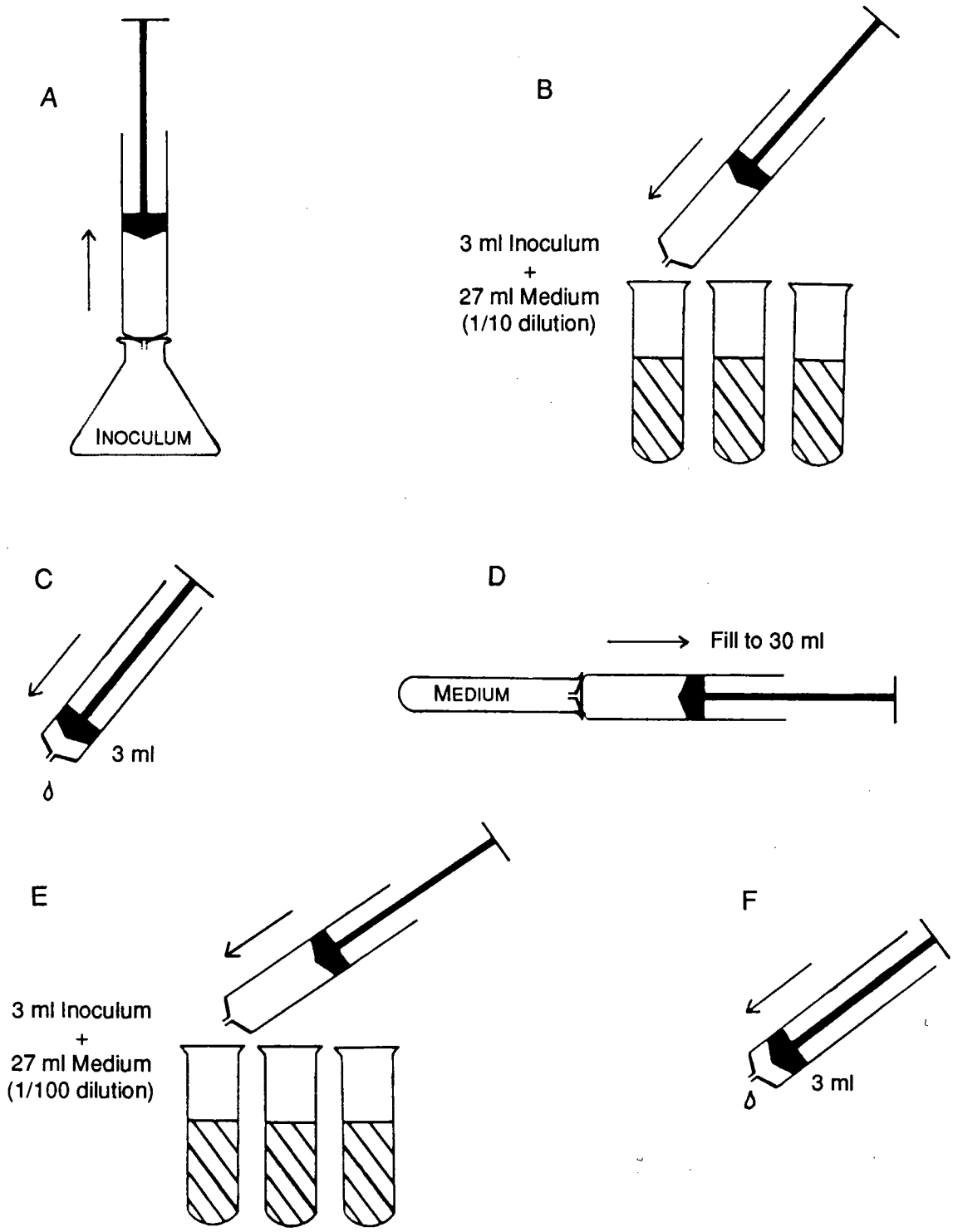

Figure 3.2: The steps involved in the Serial Dilution-Culture Technique (Throndsen, 1978).

was repeated to produce a dilution inoculum of 100:1. The result is a serial dilution of 10^{-1}, 10^{-2}, and 10^{-3} inocula with three replicates for each dilution step. This entire procedure is repeated for each region.

The test tubes containing the sediment dilutions were stored in an incubation chamber at 16°C under a 14:10 light:dark cycle at an irradiance of about 35 $\mu E \cdot m^{-2} \cdot s^{-1}$ measured with a (LiCor Model LI-185 ^{TM} light meter). Culture tubes were randomized daily to reduce the effects of possible light intensity variations emitted along the length of the fluorescent lights.

Direct counts were performed every three days, beginning on day 1. An aliquot was taken from each suspended test tube, fixed with Lugol's solution, allowed to settle in a two ml settling chamber and viewed under an inverted microscope (Utermohl method; Hasle, 1978). The counts performed on day 1 provided the initial phytoplankton concentrations data for the three regions listed in Table 3.0. The aliquot quantity varied depending on the phytoplankton abundance in each dilution. Counts were made on low, medium and high power and converted accordingly to cells$\cdot L^{-1}$. The experiment was terminated when the counting procedure was rendered inaccurate due to the clumping of phytoplankton and increase in bacteria during the senescent phase on day thirteen.

Results were plotted using the Sigmaplot 4 program. One-Factor and Two-Factor Analysis of Variance (Systat 5.0 program), along with post-hoc Tukey and Student Newman-Keuls tests, were used to determine the effect of region and dilution on the starting concentration and lag phase of the phytoplankton groups generated from water-sediment interface samples. The concentrations of phytoplankton groups/species were transformed where necessary.

3.3: RESULTS

The relative sediment grain size classes varied across the core samples collected from regions I, II, and III (Fig. 3.3). Seventy-nine percent of the total sediment collected from region I fell into the very coarse sand to gravel classification greater than 1000 μm (Wentworth, 1922). This category consisted of angular-shaped rocks and shell fragments one to two cm in diameter. In region II, the size classifications of sediment grain size ranged from coarse sand to silt. The two largest categories fell into the size classifications of coarse sand (37.9%) and medium sand (29.3%). The shape of the sediment from region II consisted of both angular and rounded-spherical grains. In region III, the two largest sediment grain size categories fell into the fine sand classification (31.7%, 150 - 250 μm) and the very fine sand classification (30.5%, 63 - 150 μm). The highest percentage of silt (< 63 μm) was found in region III and the sediment grain shape in every size classification consisted of well-rounded, spherical grains.

Considering a single phytoplankton group/species the statistical comparison (ANOVA) shows no significant difference, with the exception of *Skeletonema costatum,* between of the mean phytoplankton concentrations among the water-sediment interface samples of regions I, II, and III (Table 3.1). However, the high variability found within the mean number of each phytoplankton group/species may have influenced the absence of a difference found in the statistical test. The concentrations of phytoplankton groups/species were usually higher than those in regions I and II, with the exceptions of *Chaetoceros laciniosum*, Cyst 2, and *Thalassiosira nordenskioeldii.* A higher number of phytoplankton species were found in region III. For example, resting spores of *Chaetoceros* spp. such as *Chaetoceros debile, Ch. didymus, Ch. laciniosum,* and *Ch. radicans* were found in region III only.

Considering a single region the variations among groups/species are significant. An ANOVA comparison reveals that a statistical difference lies between the mean concentration of each phytoplankton group/species within region I ($P = 0.005$), within

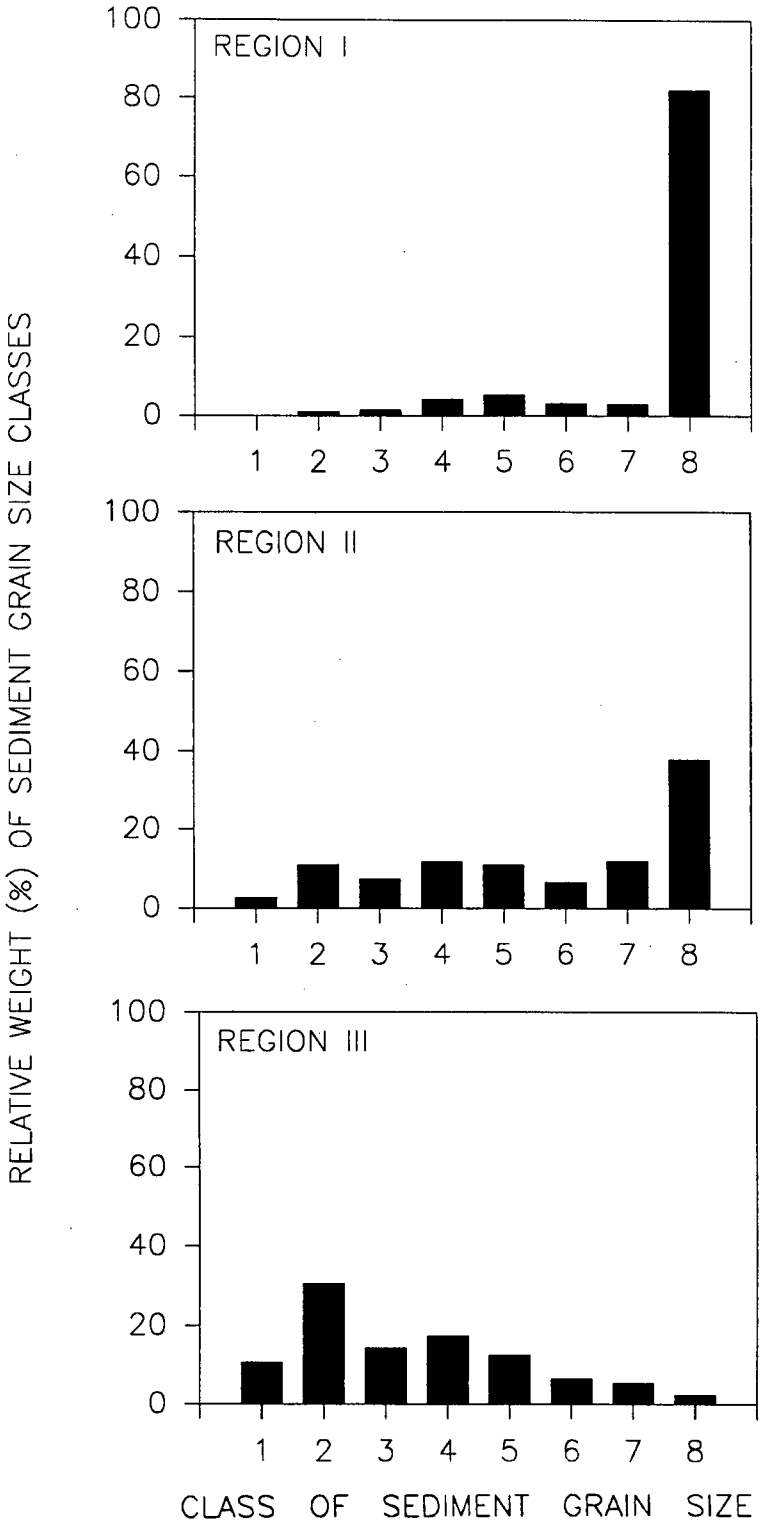

Figure 3.3: Relative weight (%) of sediment grain size classes of core samples collected from regions I, II, and III. Class sizes: 1 = < 63 µm, 2 = 63 - 150 µm, 3 = 150 - 180 µm, 4 = 180 - 250 µm, 5 = 250 - 300 µm, 6 = 300 - 355 µm, 7 = 355 - 425 µm, 8 = > 425 µm.

TABLE 3.0: Statistical comparisons of mean concentrations of phytoplankton species present in the water-sediment interface samples of regions I, II, and III. (M = mean ln cells•ml sediment^{-1}, S.D. = standard deviation, n = 3, level of significance = 0.05).

Phytoplankton species/group	Region I M (S.D.)	Region II M (S.D.)	Region III M (S.D.)	ANOVA P
Chaetoceros convolutum	0.00 (0.00)	0.00 (0.00)	0.768 (1.32)	0.42
Chaetoceros debile	0.00 (0.00)	0.00 (0.00)	2.36 (4.08)	0.42
Chaetoceros debile spores	0.00 (0.00)	0.00 (0.00)	4.94 (4.29)	0.08
Chaetoceros didymus spores	0.00 (0.00)	0.00 (0.00)	5.25 (4.62)	0.08
Chaetoceros gracile	0.00 (0.00)	0.00 (0.00)	2.89 (5.01)	0.42
Chaetoceros laciniosum	2.59 (4.48)	0.00 (0.00)	1.58 (2.75)	0.60
Chaetoceros laciniosum spores	0.00 (0.00)	0.00 (0.00)	5.25 (4.62)	0.08
Chaetoceros radicans	0.00 (0.00)	0.00 (0.00)	2.13 (3.68)	0.42
Chaetoceros radicans spores	0.00 (0.00)	0.00 (0.00)	4.25 (3.68)	0.08
Chaetoceros septentrionale	0.00 (0.00)	0.00 (0.00)	4.62 (4.04)	0.08
Chaetoceros sociale	3.36 (5.81)	0.00 (0.00)	3.54 (3.12)	0.31

TABLE 3.0 cont'd: Statistical comparisons of mean concentration of phytoplankton species present in the water-sediment interface samples of regions I, II, and III. (M = mean ln cells•ml sediment^{-1}, S.D. = standard deviation, n = 3, level of significance = 0.05).

Phytoplankton species/group	Region I M (S.D.)	Region II M (S.D.)	Region III M (S.D.)	ANOVA P
Cyst 1	4.99 (0.403)	5.48 (4.75)	6.97 (0.55)	0.68
Cyst 2	2.09 (3.63)	0.00 (0.00)	0.00 (0.00)	0.42
Skeletonema costatum	4.31 (3.74)	3.18 (2.75)	11.39 (0.02)	0.02
Thalassiosira nordenskioeldii	0.00 (0.00)	3.17 (2.75)	0.00 (0.00)	0.08

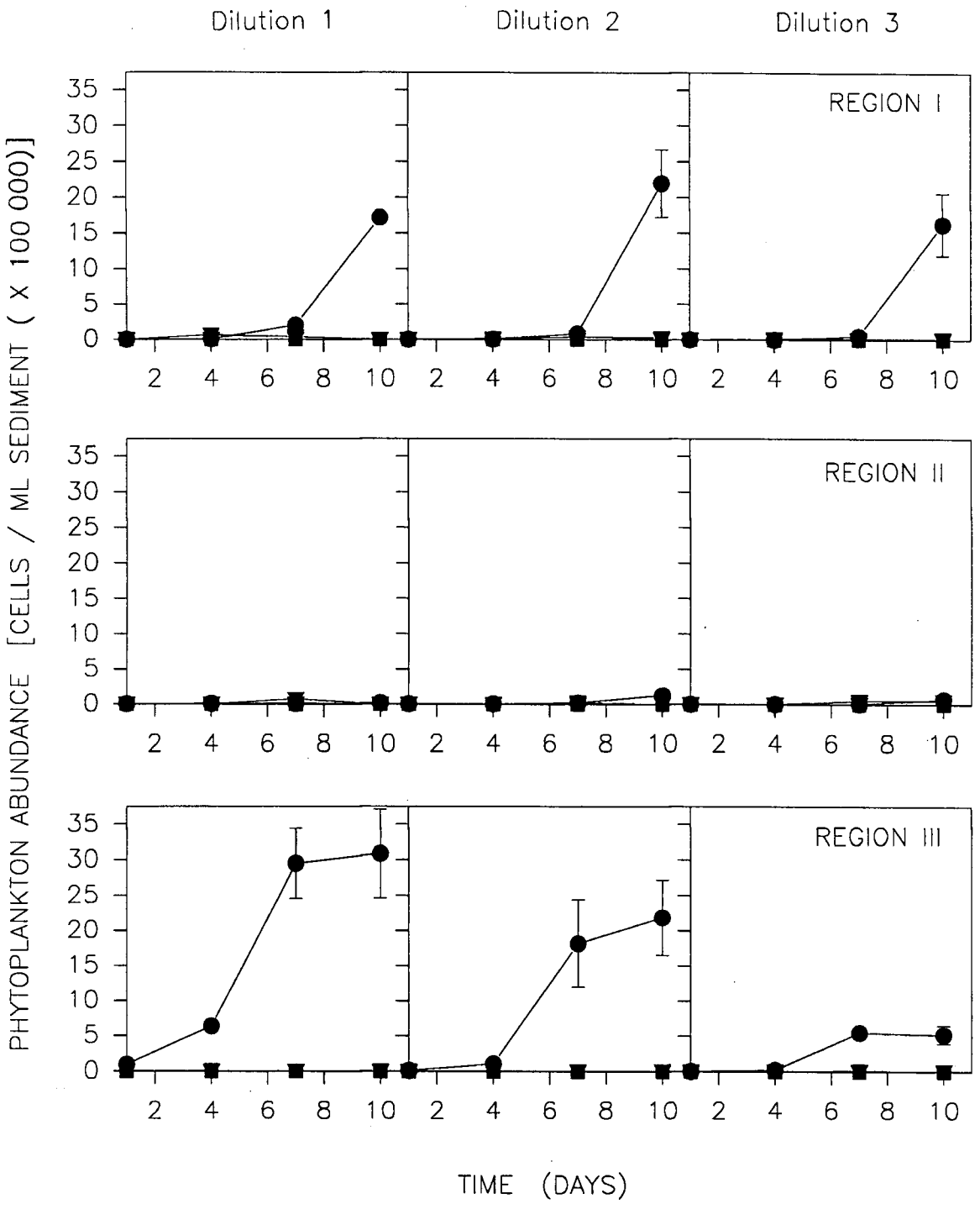

Figure 3.4: Growth curves of phytoplankton groups generated from the incubation of water-sediment interface samples collected from regions I, II, and III. ● = diatoms, ▽ = flagellates, ▼ = nanoflagellates, □ = heterotrophs. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, and Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

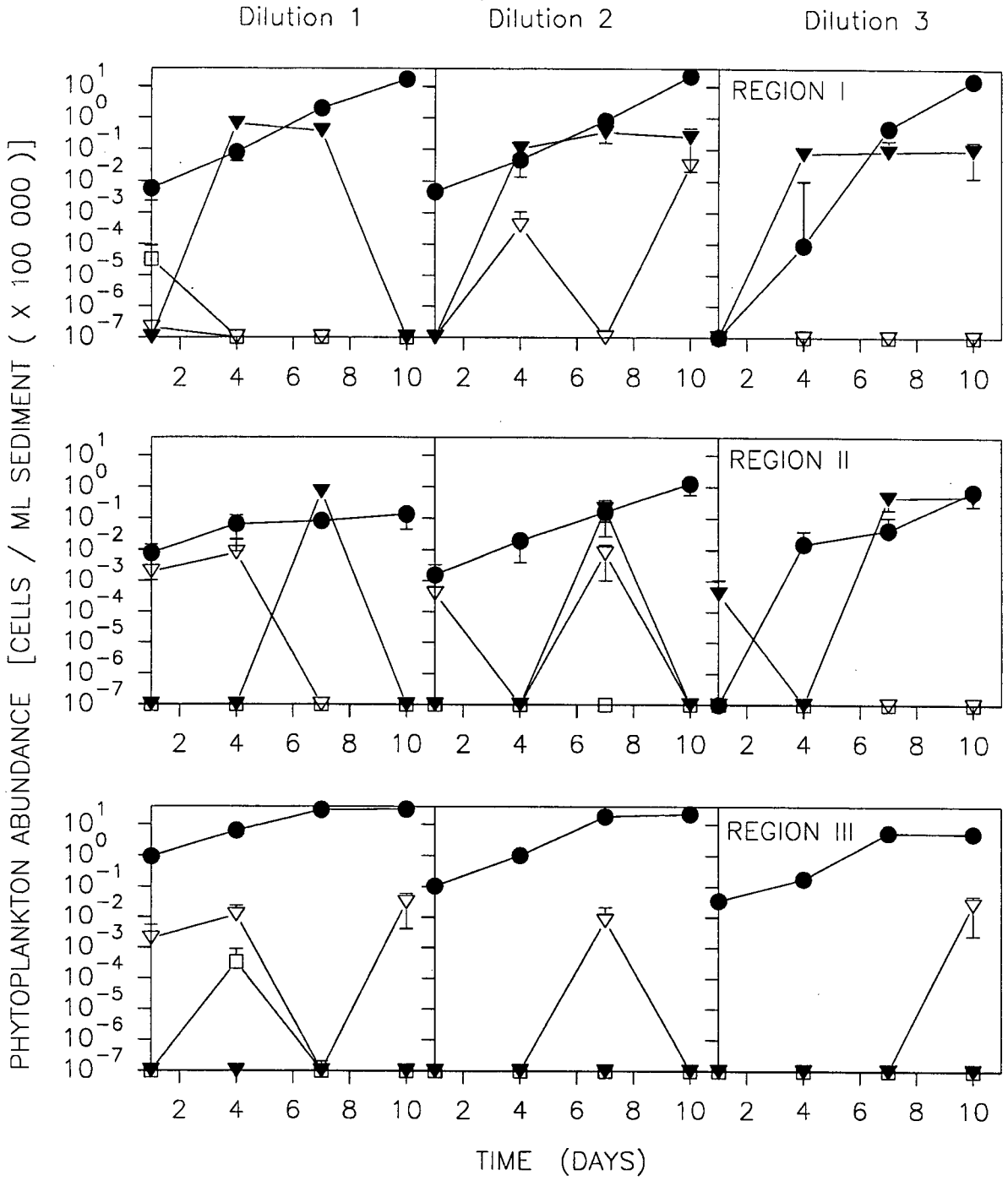

Figure 3.5: Growth curves of phytoplankton groups generated from the incubation of water-sediment interface samples collected from regions I, II, and III. ● = diatoms, ▽ = flagellates, ▼ = nanoflagellates, □ = heterotrophs. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

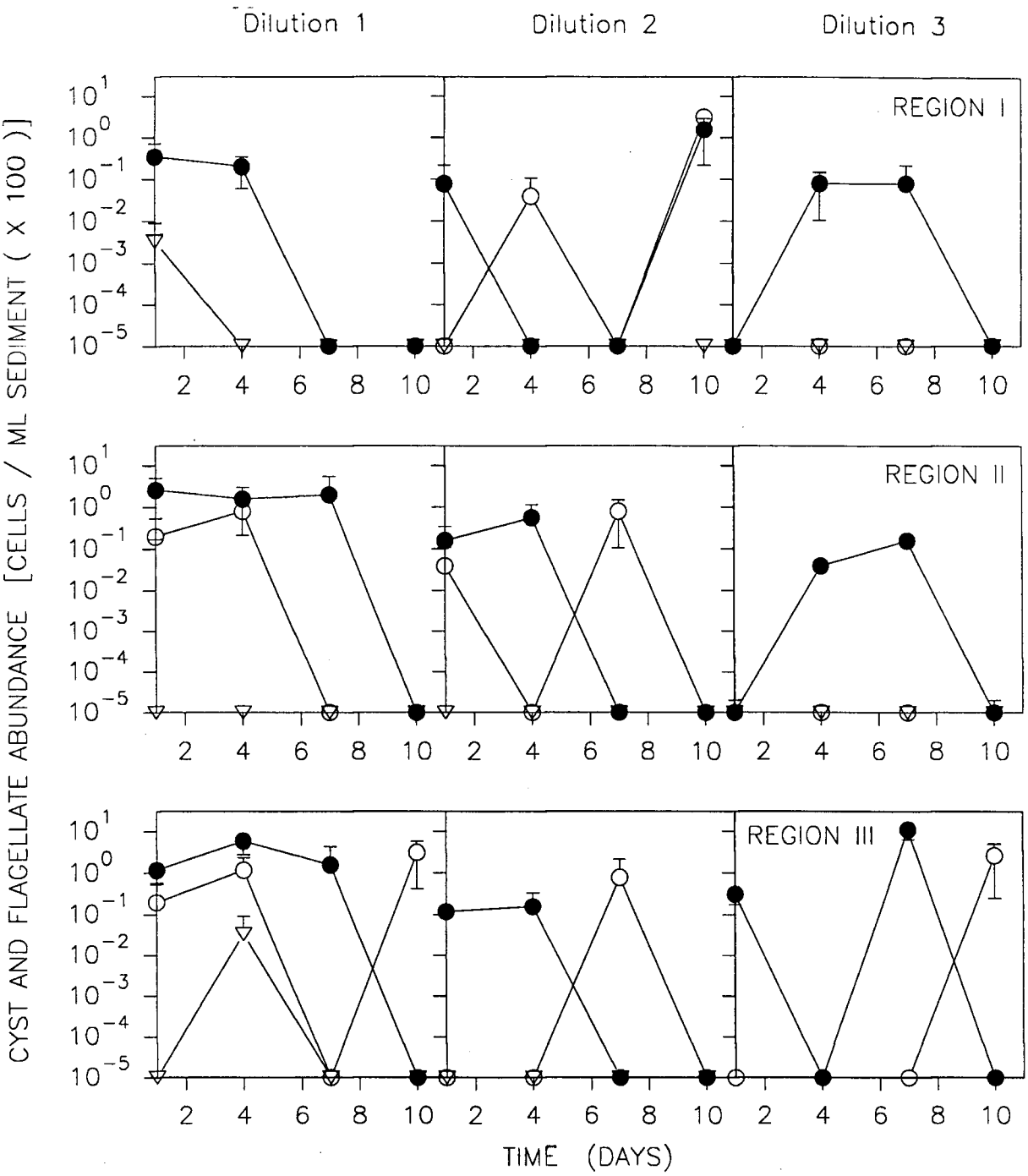

Figure 3.6: The abundance of cysts and flagellates observed in the incubated water-sediment interface samples from regions I, II, and III. ● = cysts, ○ = flagellates, ▽ = heterotrophs. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

region II (P = 0.006), and within region III (P = 0.033). Post hoc Tukey test results did not distinguish between the mean concentrations of phytoplankton group/species within each region. However, *Skeletonema costatum* and Cyst 1 were observed to have higher mean concentrations than other groups or species within each region.

The low abundance of several phytoplankton groups/species present in a certain region or dilution created noise in the estimates of phytoplankton numbers over the time period of the experiment. The phytoplankton numbers present initially in region III fall above the 200 number counting limit required to achieve an accepted degree of accuracy of 15 % (Lund *et al.*, 1958). However, some of the initial concentrations of "rare" phytoplankton groups/species or the groups/species of the lower dilutions fell below the counting limit of accuracy and therefore should be analyzed with skeptism. In general, the mean numbers fluctuating below the 10^{-2} and 10^{-1} values on the x-axis of the log scale plots of Figures 3.5, 3.6, 3.7, 3.8, and 3.9 can be considered to be inaccurate.

The diatom group appeared to suppress the growth of the other phytoplankton groups, such as flagellates and nanoflagellates, present in the incubation of the water-sediment interface samples collected from regions I, II, and III (Fig. 3.4). Very little growth was observed in samples from region II relative to samples from region I and III. The initial concentrations or "inocula" of the diatom groups on day one of the experiment were very similar in region I and II and much higher in region III as seen on the log scales of Fig. 3.5. In region III, stationary phase of the diatom group was initiated on day seven regardless of the different growth rates observed in each dilution (Fig. 3.4). The onset of stationary phase in region III may be due to an inhibitory effect produced by the increased amounts of bacteria or pennate diatom observed on day seven and ten. By day thirteen, the formation of phytoplankton aggregates was so extensive in all three regions that counting procedures were rendered inaccurate. An increase in a red-pigmented flagellate germling on day thirteen was observed in regions I and III. Nanoflagellates reached their highest concentrations in regions I and II (Fig. 3.5).

Fig. 3.6 reveals a decrease in the abundance of "unhatched" cysts by day seven or ten in dilutions one and two in all three regions. The sporatic increases and decreases of cyst abundance in dilution three may be attributed to the low probabilities of sampling cells in small volumes. The flagellate abundance did not show any obvious trend but seemed to appear sporatically. Increases were observed on day seven or ten in region I (dilution two), in region II (dilution two), and in region III (dilution one, two, and three).

No statistical difference was found between the mean concentrations of *Skeletonema costatum*, *Chaetoceros* spp., and *Thalassiosira nordenskoieldii* present (day 1) in the water-sediment interface samples collected from regions I and II (Table 3.1). In region III the mean concentrations of *S. costatum*, *Chaetoceros* spp. and *T. nordenskioeldii* present (day 1) in the water-sediment interface samples differed significantly ($P < 0.001$).

Fig. 3.7, 3.8, and 3.9 reveal the succession of *Skeletonema costatum*, and *Chaetoceros* spp., *Thalassiosira nordenskioeldii* generated from core samples from each region. A lag phase (growth phase slower than the exponential growth phase) is exhibited by *Thalassiosira nordenskioeldii* in region I (Fig. 3.7) and III (Fig. 3.9). In region II a lag phase was exhibited by *Chaetoceros* spp.and *Thalassiosira nordenskioeldii* in dilutions one and two and by all three species in dilution three. The lower initial phytoplankton concentrations found in dilution three and in regions I and II may contribute to the lag phase exhibited by *Chaetoceros* spp. and *Thalassiosira nordenskioeldii*.

Auxospores of *Skeletonema costatum* were formed in region I and III and not in region II (Fig. 3.10). A two-way ANOVA comparison and post hoc Student-Newaman Keuls test of the ratio of auxospore to vegetative cells of *Skeletonema costatum* revealed a similarity between region I and III and significant difference between region II ($P = 0.005$; Table 3.2). The highest ratio of auxospores to vegetative cells was observed on day four in regions I and III. Dilutions one and two had the highest auxospore ratio in region I, while dilutions two and three had the highest ratio in region III. The auxospore

TABLE 3.1: Statistical comparison of the mean concentrations (ln cells• ml sediment^{-1}) of *Skeletonema costatum*, *Chaetoceros* spp., and *Thalassiosira nordenskioeldii* present (day 1) in the water-sediment interface samples collected from regions I, II, and III. M = mean, S.D. standard deviation, n = 3, level of significance = 0.05).

	Skeletonema costatum M (S.D.)	*Chaetoceros* spp. M (S.D.)	*Thalassiosira nordenskioeldii* M (S.D.)	P
REGION I				
initial concentration	4.31 (3.74)	3.64 (3.15)	0.00 (0.00)	0.21
REGION II				
initial concentration	3.18 (2.75)	0.00 (0.00)	3.17 (2.75)	0.19
REGION III				
initial concentration	11.39 (0.02)	7.30 (0.80)	0.00 (0.00)	<0.001

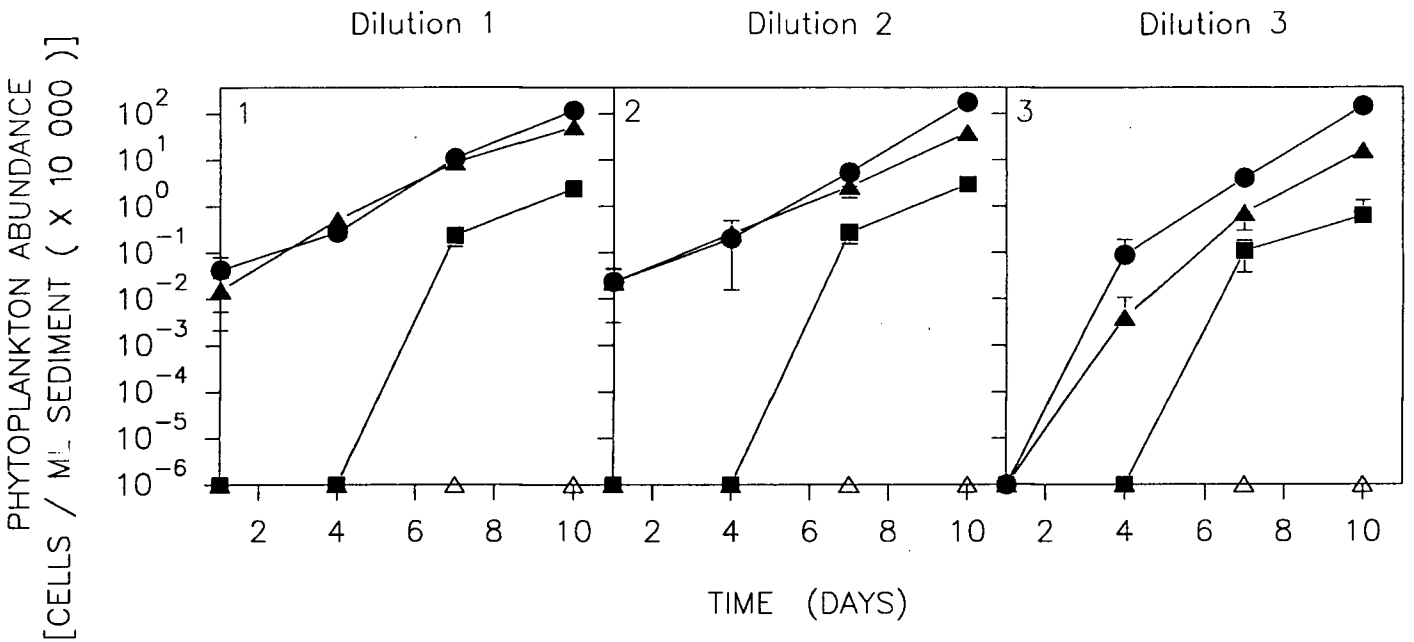

Figure 3.7: Growth curves of *Skeletonema costatum*, *Chaetoceros* spp., *Thalassiosira nordenskioeldii* generated from the incubation of water-sediment interface samples from region I. ● = *Skeletonema costatum*, ▲ = *Chaetoceros* spp., △ = *Chaetoceros* spp. resting spores, ■ = *Thalassiosira nordenskioeldii*. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

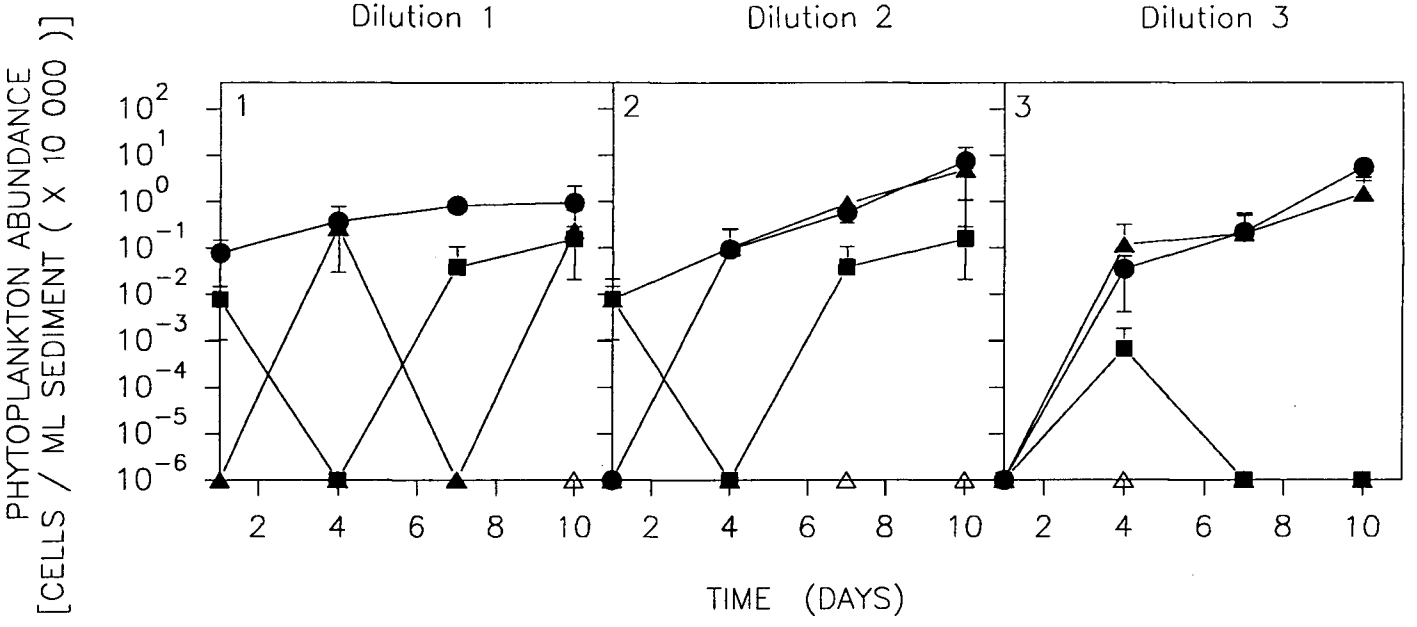

Figure 3.8: Growth curves of *Skeletonema costatum*, *Chaetoceros* spp., *Thalassiosira nordenskioeldii* generated from the incubation of water-sediment interface samples from region II. ● = *Skeletonema costatum*, ▲ = *Chaetoceros* spp., △ = *Chaetoceros* spp. resting spores, ■ = *Thalassiosira nordenskioeldii*. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

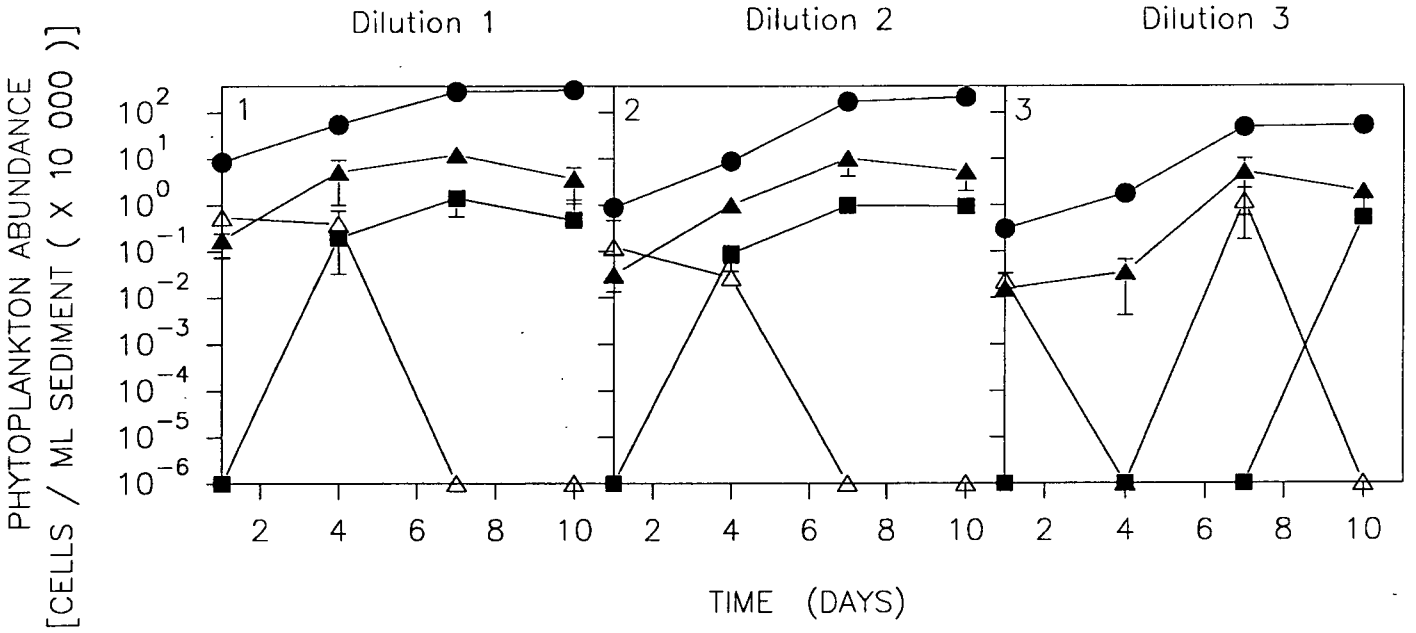

Figure 3.9: Growth curves of *Skeletonema costatum*, *Chaetoceros* spp., *Thalassiosira nordenskioeldii* generated from the incubation of water-sediment interface samples from region III. ● = *Skeletonema costatum*, ▲ = *Chaetoceros* spp., △ = *Chaetoceros* spp. resting spores, ■ = *Thalassiosira nordenskioeldii*. Dilution 1 = 10^{-1}, Dilution 2 = 10^{-2}, Dilution 3 = 10^{-3} of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

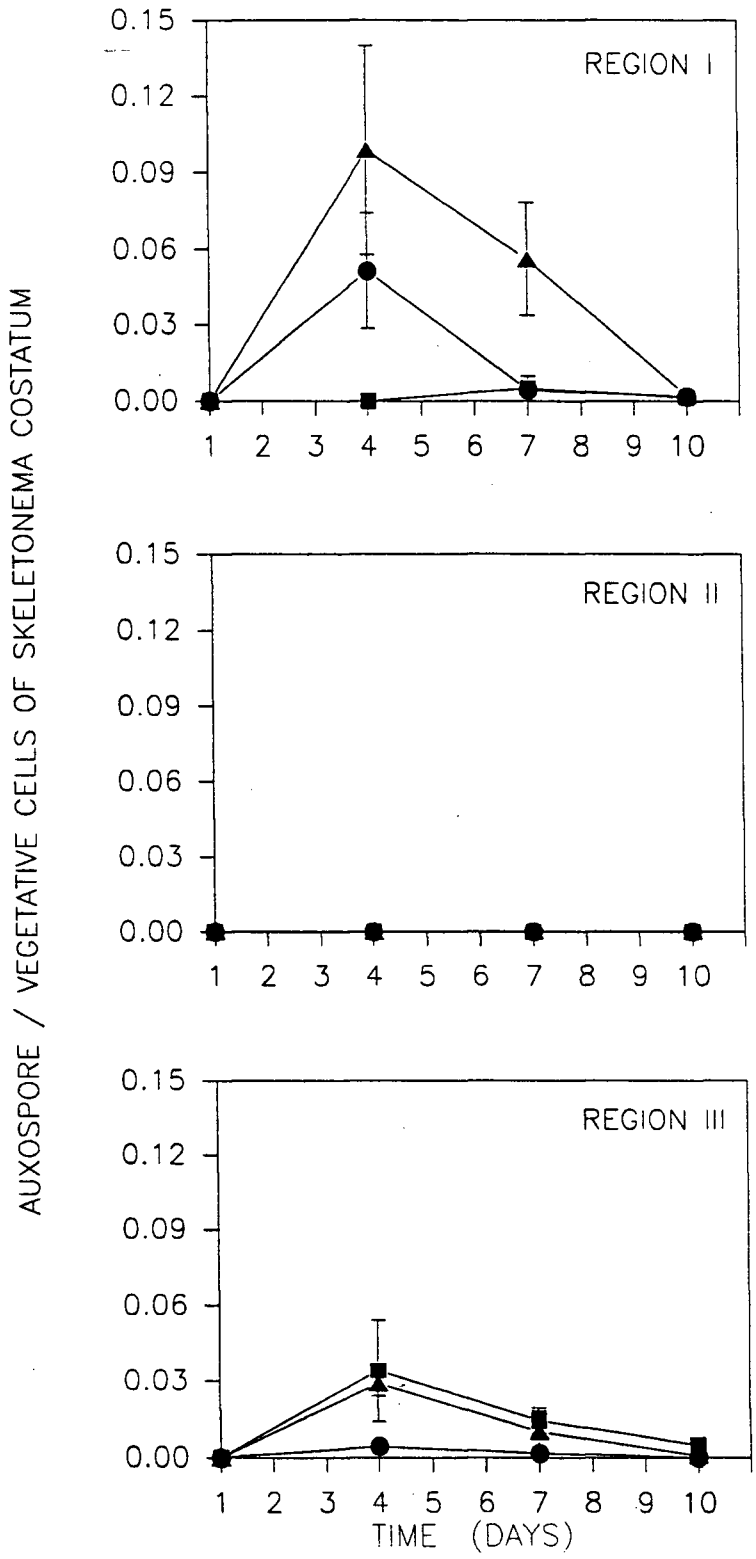

Figure 3.10: The ratio of auxospore / vegetative cells of *Skeletonema costatum* generated from water-sediment interface samples collected from regions I, II, and III. ● = dilution one (10^{-1}), ▲ = dilution two (10^{-2}), ■ = dilution three (10^{-3}) of sediment inoculum (1 ml). Error bars = ± 1 standard deviation.

TABLE 3.2: Comparison of the ratio of auxospore/vegetative cells of *Skeletonema costatum* generated from water-sediment interface samples between Regions I, II, and III. (n = 9, level of significance for Student-Newman-Keuls test = 0.05).

	REGION II		REGION III		REGION I	P
Ranked means	0.000	≠	0.452	=	0.483	0.005
Standard Deviations	0.000		0.247		0.482	

TABLE 3.3: Statistical comparison of the mean cell diameter of pre-auxospore cells and post-auxospore cells of *Skeletonema costatum* generated from the incubation of water-sediment interface samples. S.D. = Standard Deviation, level of significance = 0.05.

	Mean (μm) (S.D.)	t-test P
Pre-auxopsore	7.86 (3.32)	< 0.001
Post-auxospore	19.89 1.17	

ratio from day four to day ten appeared to decline at a similar rate within each region. The mean diameter of pre-auxospore cells was significantly different from the mean diameter of post-auxopsore cells ($P = < 0.001$; Table 3.3).

3.4: DISCUSSION

Sediment analysis

The different hydrographic conditions found in regions I, II, and III result in the different settlement rates of sediment of varying grain size and shape in each region. The two-layer estuarine flow in region III acts as a sediment trap and as a result this region contains the largest amount of fine silt (Fig. 3.3). In contrast, Skookumchuck Narrows (region I), a tidally scoured basin, consists mainly of sediment (78.8%) greater than the 1000 μm size and is categorized as very coarse sand and gravel. Sediment smaller than this category requires tidal current speeds less than ten to twenty cm•second^{-1} in order to be deposited (Heezen and Hollister, 1964). In region I the water currents will remain above the speed of ten cm•second^{-1} much of the time. Hence a low percentage (21.2%) of sediment smaller than the 1000 μm size was found in the core sample. Region II appears to be an intermediate region as it contained both coarse sand (37.9%) and silt (2.6%). The source of surface lateral transport in this region comes from the flood tidal jet generated from the sill at Skookumchuck Narrows (Sill 1) and a tidal ebb current forced over the sill at Tzoonie Narrows (Sill 2) (Fig. 1.4). This lateral transport may keep sediment particles in suspension longer and eventually transport the particles to a region outside the influence of the tidal jet.

Comparison of phytoplankton groups/species present at the water-sediment interface

Phytoplankton act as silt particles in terms of their transportation and settlement and tend to accumulate in low turbulent energy fjords (Dale, 1976). Since region III contains the largest amount of silt and phytoplankton relative to regions I and II, region III acts as both a sediment and phytoplankton trap.

A statistical comparison (ANOVA) revealed no difference between the mean log concentration of each phytoplankton group/species across the three regions (Table 3.0). However, in general the mean log concentrations of each phytoplankton species was

observed to be relatively higher in region III than in region I and II. The greater accumulation of phytoplankton at the water-sediment interface in region III depends on the extent to which rapid downward transport mechanisms operate. Possible mechanisms operating in region III may include the two-layer estuarine flow of the shallow-silled fjord, retention of grazers and subsequent increase in fecal pelletization, greater fresh water run-off and flocculation/aggregation production, decreased dissolution of diatom frustules due to increased silica concentration in sediments (Roelofs, 1983). The greater accumulation of phytoplankton in a localized area such as region III may serve as a "seed bed".

The anoxic state of the water-sediment interface of region III may filter out certain phytoplankton species and associated resting stages, such as *Leptocylindrus danicus*, that lose their viability in the presence of low oxygen, high ammonium, H_2S, and decomposing organics (Davis *et al.*, 1980). The phytoplankton cells that exist in the region III core sample collected in February (before the spring bloom fall out) represents phytoplankton that have sedimented out since the last resuspension event due to a deep water replacement event. The warm bottom temperature in region III prior to deep water replacement in April of 1991 indicates that the previous deep water renewal probably took place in the summer in 1990 (Pond, unpublished data, 1991). Table 3.0 lists the phytoplankton that survived the over-wintering period of hypoxic water-sediment interface conditions of region III. The diatoms present included *Chaetoceros* spp., *Skeletonema costatum*, and *Thalassiosira nordenskioeldii*, along with two cyst types. Nannoflagellates were not observed at any time during the incubation experiment in region III (Fig. 3.5).

Resting spores were found only in the water-sediment interface samples of region III and belonged to the genus *Chaetoceros*. The formation of resting spores in this region may have been promoted by the prolonged nutrient-depleted condition of the surface waters between June and September (Fig. 2.4 and 2.5, Table 2.1) (Von Stosch, 1979;

Davis *et al.*, 1980; French and Hargraves, 1985). Hargraves and French (1983) have suggested that resting spore formation may be a mechanism performed to avoid damage caused by photo-oxidative effects and metabolic imbalance in the presence of highly irradiated, nutrient-depleted surface waters. The increased density of the heavily armoured, double theca frustule will increase sinking rates of resting spores and provide rapid tranport to the benthos compared to that of vegetative cells (Davis *et al.*, 1980; Hargraves and French, 1983).

Resting spores of *Chaetoceros laciniosum* (3.33% of total phytoplankton biomass) and *Chaetoceros radicans* (< 1% total phytoplankton biomass) appeared on September 25 in the plankton samples in region I. They appeared in September, when decreasing temperatures, photoperiod, and light levels may have promoted their formation (Von Stosch, 1979; French and Hargraves, 1985). The strong lateral transport and minimal slack tide period that exists in region I will lengthen the suspension time of fast-sinking resting spores. The documentation of the formation and sedimentation of diatom resting spores in the field is rare since the formation and sedimentation of resting spores occurs faster than the frequency of sampling (Davis *et al.*, 1980). The weaker lateral transport present in regions II and III will allow a faster vertical separation of resting spores from planktonic vegetative cells since sinking rates of the former exceed those of the latter by five to six times (Bienfang pers. comm. in Davis *et al.*, 1980).

If vertical migration patterns of herbivores exhibit an avoidance of the outgoing surface layer of the two-layer estuarine system they will be retained in region III. The incorporation of resting spores into fecal pellets of herbivores, retained in region III, may provide a rapid transport to the sediments (Hargraves and French, 1983) and also an alternative explanation for the absence of resting spores in the planktonic samples. Davis *et al.* (1980) also found that *Leptocylindrus danicus* appeared to sink unmolested via transportation through grazers in the CEPEX controlled experiment in Saanich Inlet, B.C.

Chaetoceros convolutum, *Skeletonema costatum*, and *Thalassiosira nordenskioeldii* are the only diatom species present not known to form true resting spores. Resting spores generally have double theca and restricted contact between the spore interior and external environment, and therefore differ morphologicaly from their corresponding vegetative cells (Hargraves, 1984), as opposed to resting cells which are structurally similar to vegetative cells (Hargraves, 1979). *S. costatum* present in the sediments of Narragansett Bay were found to be physiologically similar to most diatom resting spores (Hargraves and French, 1975). The most salient morphological characteristics of the Narragansett Bay benthic cells of *S. costatum* were the heavily silicified frustule and the compaction of cellular contents. The cellular contents of *S. costatum* in the core samples of all three regions were observed to be compact and drawn away from the frustule. Hargraves and French (1975) suggested that *S. costatum* formed a "physiological" resting spore. *T. nordenskioeldii* is also thought to form resting spores morphologically similar to their vegetative cells (Hargraves, 1976; Syvertsen, 1979). Normally "physiological" resting spores may have problems sinking away from adverse surface conditions compared to the true resting spores, however, the high sinking rates of *S. costatum* may increase the survival of planktonic-benthic transport and explain the high numbers of *S. costatum* in the core samples, compared to other species.

Approximately seventy-three species of the *Chaetoceros* genus form resting spores and belong to the subgenus Hyalochaete (solid setae) (Hargraves, 1984). Although, *Chaetoceros concavicorne* belongs to the subgenus Phaeoceros (hollow setae) it may also form a "physiological" resting spore, as it did not lose its viability during the time spent in the harsh benthic conditions of region III. *Ch. concavicorne* present in the core samples of region III grew once it was exposed to culture medium.

For most diatoms the formation of resting spores is an asexual process (Davis, 1980; French and Hargraves, 1985), therefore, the formation of resting spores does not cause a marked decrease in cell numbers. However, Davis *et al.* (1980) found that *Leptocylindrus*

danicus formed resting spores at low nitrate levels (< 0.5 μM) following sexual reproduction and the associated formation of auxospores. Subsequent lab experiments revealed that the vegetative cells plus resting spore cells exhibited a marked decrease in numbers after the formation of resting spores. This obligate route through sexual reproduction and the marked decrease in number of cells forming resting spores limits the success of *L. danicus* accumulating in the sediments. Although the resting spores were not observed initially, *L. danicus* was present during the incubation experiment in regions I and III.

Comparison of phytoplankton groups/species cultured from water-sediment interface samples of regions I, II, and III

Diatoms appeared to suppress the growth of flagellates in all dilutions during the incubation experiment (Fig. 3.4). If the flagellates were not suppressed an increase in the number of empty cysts should have been associated with an increase in the number of flagellates present. If vegetative growth took place an expential growth curve would have been exhibited by the flagellates. The number of empty cysts increased over the ten day experiment, however, no obvious trends in the increase of flagellate abundance was observed over the ten day experiment (Fig. 3.6). Cell division in a red-pigmented flagellate germling was observed in the cultures of regions I and III after the termination of the experiment when growth conditions were not suitable for other phytoplankton groups/species.

The initial concentration, lag time, and successive growth of the phytoplankton species from the water-sediment interface samples may dictate the timing and initation of the spring bloom in overlying waters. A spring bloom in the Strait of Georgia begins in March and April and is dominated by *Skeletonema costatum* and *Thalassiosira* spp. and eventually by *Chaetoceros* spp. (Harrison *et al.*, 1983). A similar but smaller bloom sometimes occurs in the fall.

The greater accumulation of one species over the others in the different regions may affect the order of appearance of species involved in the spring planktonic succession proceeding resuspension. In region III *Skeletonema costatum* had a higher mean concentration in the water-sediment interface samples (day 1) and reached the highest final concentrations (day 10) relative to *Chaetoceros* spp. and *Thalassiosira nordenskioeldii* (Table 3.1). In region I *T. nordenskioeldii* exhibited a lower mean concentration and longer length in lag phase relative to *S. costatum* and *Chaetoceros* spp. in the incubation experiment (Fig. 3.7). As a result the final concentrations (day 10) of *T. nordenskioeldii* were lower than those of *S. costatum* and *Chaetoceros* spp.

Auxospore formation in Skeletonema costatum

Auxospores of *Skeletonema costatum* formed in regions I and III and not in region II (Fig. 3.10). The maximum mean ratio of auxospore to vegetative cells (day four) did not differ significantly between regions I and III (Table 3.2). An optimal concentration may be necessary to meet the requirements of successful auxospore formation, since the more concentrated dilution of region III did not give rise to the largest ratio of auxospore to vegetative cells. In region I, the largest number of auxospores was produced in dilution two, whereas in region III, the largest number was produced in dilution three. The initial concentration of vegetative *S. costatum* cells may have been too low in region II to induce auxosporylation.

The auxospores of *Skeletonema costatum* had formed between day one and day three of the experiment. Several large vegetative cells were attached to the hemispherical auxospore cells on day three, signifying that asexual cell division had taken place since the time of auxospore formation. Therefore, the auxospores probably formed around day two of the experiment. Smith (1966) observed that auxospores of *Coscinodiscus concinnus* could form within 36 to 76 hours. Smith aslo observed that concentrations of male gametes peaked a day or two before auxospores were formed.

The exposure of *Skeletonema costatum* to the experimental conditions such as an increase in light intensity and temperature and a change in photoperiod (Holmes, 1966) and ambient nutrient concentration (Harrison, 1973) may have induced the formation of auxospores. Auxospore formation in *Coscinodiscus concinnus* was found to be induced over limited ranges of temperature (15-25°C) and light intensity (> 0.01 ly/min) and was accelerated by shorter photoperiods (Holmes, 1966). Auxospores formed within in 36 hours on a shorter photoperiod (8 hrs light) as opposed to 76 hours on a longer photoperiod (12 - 16 hrs light). The optimal temperature and light intensity ranges for auxosporylation widened under a shorter photoperiod. Harrison (1973) found that the sexual reproduction cycle in *S. costatum* took twice as long at 12°C than those at 18°C. In this investigation, the auxospores of *S. costatum* were formed after a senescent batch inoculum was exposed to limiting levels (< 2 μM) and subsequent increases of silicate concentrations. The synchronization of the sexual reproductive cycle was influenced by how long the batch inoculum had been senescent. The synchronization of *S. costatum* auxospore formation in this study may have been influenced by the recovery from a senescent phase, experienced during the over-wintering period at the water-sediment interface. Therefore, auxospores may form during periods of shorter daylight hours, broader temperature and light ranges, and a change in nutrient conditions, such as those that occur in the spring or autumn.

The mean cell diameter (7.86 μm) of the *Skeletonema costatum* cells on day one in region III was significantly different than the mean cell diameter (19.89 μm) of the post-auxospore (large) population observed on day three (Table 3.3). The increase in cell size during auxospore formation, triggered by experimental conditions, may have ecological significance with respect to the seasonal size changes of diatoms. The resuspension of small-sized benthic cells into overlying waters of optimal growth conditions during the spring may trigger auxospore formation. A population undergoing rapid increases in cell numbers during a spring bloom would benefit from the formation of auxospores and

consequent restitution of a large-sized population. Harrison (1973) found that the wide-diameter post-auxospore cells had higher growth rates than the thin-diameter pre-auxospore cells. Billinger (1977) found that size restitution of the planktonic population of *Stephanodiscus astraea* in a reservoir in England took place in autumn. The winter population maintained its large size until the spring when rapid growth took place. As a result of the rapid growth, the cell diameter of *S. astraea* decreased quickly. In the late summer, cell growth was slower relative to that in spring and as a consequence the reduction of size proceeded much slower. Therefore, the spring bloom, which undergoes rapid cell growth and decreases in cell diameter, may be seeded by a large cell-sized population that persisted throughout the winter, or by a small cell-sized sedimented population that underwent resuspension and auxosporylation in the spring.

The small-diameter cells of *Skeletonema costatum* found in the February water-sediment interface samples indicate that sedimentation of smaller cells is favoured over large cells. The large cells may be selectively grazed (Frost, 1972) before they have a chance to settle, or they may require winter mixing in order to remain suspended in the overlying waters during the winter period (Round, 1982).

Establishment of a new large-sized population of *Stephanodiscus* through the formation of auxospores, followed by a decay of the old small-sized (pre-auxospore) population was recorded in an English reservoir (Round, 1982). A similar trend of old (small pre-auxospore) and new (large post-auxospore) populations of *Skeletonema costatum* was observed in the incubation of water-sediment interface samples. For example, by day ten of the experiment small cells of *S. costatum* were not observed. The rate of decline or dilution of the auxospores with vegetative cells between day 4 and day 10 was similar between dilution one and two in region I and dilution two and three in region III. However, these declines or dilution rates of the small-sized population differed between regions.

Large-diameter cells (or possibly auxospores) of *Thalassiosira nordenskioeldii* were observed on day ten of the experiment. Prior to this time, cells with very small diameters were observed. The delayed formation of auxospores in *T. nordenskioeldii* compared to that of *S. costatum* may influence the time of appearance of these species in the local spring succession.

CONCLUSIONS

1. Physical profiles of temperature and salinity between June and September reveal region I as well-mixed, region II as weakly stratified, and region III as well-stratified. Stratified conditions set in earlier (June) and remain longer in region III than in any other regions sampled in Sechelt Inlet (Taylor *et al.*, 1991).

2. The depths of the one percent light levels were generally deeper in region I and more shallow in region III. The changes in depths of the one percent light level over the sampling period in regions II and III exhibit a similar pattern.

3. The ambient nitrate and ammonium concentrations in region I remain above the limiting levels for phytoplankton. Ambient nitrate and ammonium concentrations remained low or undetectable on July 8 and July 22 in the surface waters of region II and between June 9 to August 26 in region III. Phosphate was always present in the surface waters of each region.

4. The surface waters of region III appear to be nitrogen-deficient. Phytoplankton in this region must be able to control their position in the water column in order to optimize light levels above the nitricline/pycnocline and not become nitrogen-limited.

5. The nitrogen to phosphate ratios in the sampled regions of Sechelt Inlet are lower than the average plankton ratio (16:1; Redfield *et al.*, 1963).

6. Diatoms exhibited the highest relative biomass in regions I and II over the sampling period. In region I the sharp fluctuations of the diatom biomass observed between sampling trips reflect the extreme changes in physical conditions. In region III the ratio of diatom to dinoflagellate biomass is closer to a one to one ratio than those in regions I and II. Nanoflagellates reached their highest relative biomass in regions I and III, while ciliates reached their highest relative biomass in region III. A reciprocal codominance of diatom to dinoflagellate biomass between sampling trips is seen in each region.

7. The formation of thin horizontal layers by the three groups: dinoflagellates, other photosynthetic flagellates, and diatoms was observed in regions II and III. The pronounced horizontal layers produced by these groups in region III show an avoidance of the nutrient-depleted surface waters before the September sampling trips. Although small, the biomass present in the top few metres of region III may serve as an "inoculum" for region II during ebb tide events. These three groups did not avoid the surface waters in region I and II.

8. Phytoplankton species comprising the top ninety percent of the total phytoplankton biomass were assigned a successional stage type characterized by Margalef (1967). A temporal succession was observed in the source waters of region I since a gradual increase in stage three and a decrease in stage one phytoplankton is observed. In general the changes in stages of phytoplankton in region II (resident community) were minimal and did not reflect those in region I (source community) and region III (resident community). This observation is in agreement with the characterization of phytoplankton compositon in shallow-silled fjords of low flushing rates and freshwater inflow in that these communities generally have an autochthonous origin (Gowen, 1984). Autochthonous input may arise from the transportation of surface phytoplankton from region III on ebb tide or the resuspension of sedimented phytoplankton during seasonal

flushing events. However, the potential for allochthonous origin of a phytoplankton bloom exists if a sequence of events, such as reduced competition and grazing for allochthonous species and appropriate nutrient and stability conditions prevail. Region II contained the highest amount of stage one species probably due to the diatom population present inside the sill entrance (Taylor *et al.*, 1991). The phytoplankton community of region III maintained a forty percent biomass of stage three species and appeared resistant to any temporal changes in phytoplankton community strucure.

9. A qualitative comparison of the phytoplankton community in Sechelt Inlet to those in the Northern Strait of Georgia (Haigh, 1991) and those in Norwegian fjords of the same lattitude (Smayda, 1980) reveals similarities. However, direction and rates of succession vary between fjord and source water and therefore the species succession varies with any one point in time.

9. *Heterosigma akashiwo* and *Dictyocha fibula* make up the top 47% of the total phytoplankton biomass in region I on July 22 and appeared to inhibit the presence of other phytoplankton species.

10. The June and September diatom blooms in region III consisted of large benthic and post-bloom oceanic diatoms such as *Pleurosigma* sp., and *Rhizosolenia setigera*, *Chaetoceros decipiens*, and *Naviculae wawrickae* respectively.

11. Region II is considered a "transition" zone because it is located at the mixing boundary of bodies of water (regions I and III). Region III is also considered a "transition" zone because of the large amount of freshwater and saltwater mixing. As a result these regions contained the highest number of phytoplankton species in the top ninety percent of the biomass.

12. Region II contained the highest number of heterotrophs in the top ninety percent of the biomass. Region III contained the lowest number of heterotrophs.

13. The highest concentrations of *H. akashiwo* were generally found in region II. In 1989 *H. akashiwo* reached its highest concentrations outside the entrance to Sechelt Inlet in early September. An "inoculum" was transported through region I, however, fish-killing concentrations were not obtained.

14. *Prorocentrum minimum* appeared to form an autochthonous population in region III reaching its highest concentrations in late August. *Protogonyaulax tamarensis* reached its highest concentration in region II and was present in the flood waters at the entrance to Sechelt Inlet on August 10 and September 25. *Dinophysis fortii* and *D. acuminata* generally appeared in region III, forming a subsurface layer.

15. *Chaetoceros convolutum* and *Ch. concavicorne* maintained fish-killing concentrations in region II until July 22 when the population sank below nine metres. A subsurface population remained at the 6 to 9 metre depth interval until September 25 when the resuspended population reached its highest concentrations in surface waters of region II. The distribution of *Nitzschia pungens* was similar to that of *Ch. convolutum* and *Ch. concavicorne.*

16. Region I had the highest amount of coarse grain sediment while region III had the highest amount of silt particles. In general, region III was observed to contain a greater amount of phytolankton present at the water-sediment interface, relative to that of the other regions. Resting spores were present only in region III.

17. Diatoms, such as *Skeletonema costatum*, *Chaetoceros* spp., and *Thalassiosira nordenskioeldii* were the dominant phytoplankton species generated from the water-sediment interface samples. Flagellates seemed to be suppressed by the diatoms.

18. Auxospores of *Skeletonema costatum* were formed in the incubation experiments on the core samples collected from region I and III. The mean diameter of pre-auxospore cells was significantly different (lower) from the mean diameter of the post-auxospore cells.

REFERENCES

Anonymous. 1989. Canadian Tide and Current Tables. Volume 5. Juan de Fuca Strait and Strait of Georgia., Canada Dept. Fisheries and Oceans.

Anderson, D.M. and F.M.M. Morel. 1979. The seeding of two red tide blooms by the germination of benthic *Gonyaulax tamarensis* hypnocysts. Estuarine Coastal Mar. Sci. 8: 279-293.

Anderson, D.M., S.W. Chisholm, and C.J. Watras. 1983. Importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. Mar. Biol. 76: 179-189.

Anderson, D.M. and B.A. Keafer. 1985. Dinoflagellate cyst dynamics in coastal and estuarine waters. Anderson, White, and Baden (Eds.) In: Toxic Dinoflagellates. Elsevier Science Publishing Co.

Anderson, D.M., S.W. Chisholm, and C.J. Watras. 1983. Importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. Mar. Biol. 76: 179-189.

Antia, N.J., P.J. Harrison, and L. Oliveira. 1991. The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. Phycologia 30 (1): 1-89.

Bates, S.S., C.J. Bird, A.S.W. DeFreitas, R. Foxall, M.W. Gilgan, L.A. Hanic, G.E. Johnson, A.W. McCulloch, P. Odense, R. Pocklington, M.A. Quilliam, P.G. Sim, J.C. Smith, D.V. Subba Rao, E.C.D. Todd, J.A. Walter, and J.L.C. Wright. 1989. Pennate diatom *Nitzschia pungens* as the primary source of domoic acid, a toxin in shell fish from eastern Prince Edward Island, Canada. Can. J. Fish. Aquat. Sci. 46:1203-1215.

Bell, G.R., 1961. Penetration of spines from a marine diatom into the gill tissue of Lingcod (*Ophiodon elongatus*). Nature 192: 279-280.

Bell, G.R., W. Griffioen, O. Kennedy. 1974. Mortalities of pen-reared salmon associated with blooms of marine algae. In: Gaines, G. and F.J.R. Taylor. 1986. A mariculturist's guide to potentially harmful marine phytoplankton of the pacific coast of North America. Information Report No. 10. Prepared for the Marine Resources Section Fisheries Branch B.C. Ministry of Environement.

Billinger, E. G. 1977. Seasonal size changes in certain diatoms and their possible significance. Br. Phycol. J. 12: 233-239.

Binder, B.J. and D.M. Anderson. 1987. Physiological and environmental control of germination in *Scrippsiella trochoidea* (Dinophyceae) resting cysts. J. Phycol. 23: 99-107.

Black, E. 1989. The Sechelt Inlet water quality program. Aquaculture Information Bulletin No. 14. Ministry of Agriculture and Fisheries.

Brett, J.R., W. Griffioen, and A. Solmie. 1978. The 1977 crop of salmon reared on the Pacific Biological Station experimental fish farm. Fish. Mar. Ser. Res. Tech. Rep. 845 p.17.

Brooks, V., 1989. B.C. Salmon Farmers Association. The Fish Farm News. 2 (10) p. 14.

Caine, G. 1988. Guidelines for selecting a fish farming site. Aquaculture Information Bulletin No. 10.

Carlsson, P., E. Graneli, and P.J. Hansen. 1989. Grazer elimination through poisoning: one of the mechanisms behind *Chrysochromulina polylepis* blooms? Abstracts from the Fourth International conference on Toxic Marine Phytoplankton. Sweden. p. 38.

Carreto, J.I., M.O. Carignan, G. Daleo, and S.G. De Marco. 1990. Occurrence of mycosporine-like amino acids in the red-tide dinoflagellate *Alexandrium excavatum*: UV-photoprotective compounds? J. Plankt. Research. 12: 909-921.

Cembella, A.D. 1989. Occurrence of okadaic acid, a major diarrheic shellfish toxin, in natural populations of *Dinophysis* spp. from the eastern coast of North America. J. Appl. Phycology 1: 307-310.

Chang, F.H., C. Anderson, and N.C. Boustead. 1990. First record of a *Heterosigma* (Raphidophyceae) bloom with associated mortality of cage-reared salmon in Big Glory Bay, New Zealand. New Zeal. J. Mar. Fresh. Res. 24: 461-469.

Cochlan, W.P. 1986. Seasonal study of uptake and regeneration of nitrogen on the Scotian Shelf. Cont. Shelf. Res. 5: 555-577.

Cochlan, W.P. 1989. Nitrogen uptake by marine phytoplankton: the effects of irradiance, nitrogen supply and diel periodicity. Ph.D. Thesis. Department of Oceanography. University of British Columbia.

Conway, H.L. and P.J. Harrison. 1977. Marine diatoms grown in chemistats under silicate or ammonium limitation. IV. Transient response of *Chaetoceros debile*, *Skeletonema costatum*, and *Thalassiosira gravida* to a single addition of the limiting nutrient. Mar. Biol. 43: 33-43.

Costas, E., M. Navarro, V. Lopez-Rodas. 1990. An environment-synchronized internal clock controlling the annual cycle of dinoflagellates. Graneli, E., B. Sundstrom, L. Edler, and D.M. Anderson. (Eds.) In: Toxic Marine Phytoplankton. Elsevier Science Publishing Co., Inc. New York.

Cullen, J.J., M. Zhu, R.F. Davis and D.C. Pierson. 1985. Vertical migration, carbohydrate synthesis, and nocturnal nitrate uptake during growth of *Heterocapsa niei* in a laboratory water column. Anderson, White, and Baden (Eds) In: Toxic Dinoflagellates. Elsevier Science Publishing. Oxford.

Cupp, E.E. 1943. Marine Plankton Diatoms of the West Coast of North America. University of California Press, Berkeley, pp. 237.

Dale, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. Rev. Palaeobot. Palynology 22: 39-60.

Davis, C.O., J.T.Hollibaugh, D.L.R. Seibert, W.H. Thomas, and P.J. Harrison. 1980. Formation of resting spores by *Leptocylindrus danicus* (Bacillariophyceae) in a controlled experimental ecosystem. J. Phycol. 16: 296-302.

D'Elia, C.F., J.G. Sanders, and W.R. Boynton. 1986. Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. Can. J. Fish. Aquat. Sci. 43: 397-406.

Dortch, Q. and J.R. Postel. 1989. Phytoplankton - nitrogen interactions. (Eds.) M.R. Landry and B.M. Hickey In: Coastal Oceanography of Washington and Oregon. Elsevier Science Publishers. Amsterdam. pp. 139-173.

Dugdale, R.C. and J.J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity . Limnol. Oceanogr., 12: 196-206.

Endo, T. and H. Nagata. 1984. Resting and germination of cysts of *Peridinium* sp. (Dinophyceae). Bull. Plankt. Soc. Japan. 31: 23-33.

Erard-Le Denn, E. and M. Ryckaert. 1990. Trout mortality associated to *Distephanus speculum*. Graneli, E., B. Sundstrom, L. Edler, and D.M. Anderson (Eds). In: Toxic Marine Phytoplankton. Elsevier. New York.

Eppley, R.W., E.H. Renger, E.L. Venrick, and M.M. Mullin. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the N. Pacific Ocean. Limnol. Oceanogr., 18: 534-551.

French, F.W. and P.E. Hargraves. 1980. Physiological characteristics of plankton diatom resting spores. Mar. Biol. Letters (1): 185-195.

French, F.W. III and P.E. Hargraves. 1985. Spore formation in the life cycles of the diatoms *Chaetoceros diadema* and *Leptocylindrus danicus*. J. Phycol. 21: 477-483.

Frost, B.W. 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17: 805-815.

Gaines, G. and F.J.R. Taylor. 1986. Information Report No. 10. Province of B.C., Ministry of Environment Marine Resources Section, Fisheries Branch.

Gatzke, R. 1988. Effects of irradiance and temperature on *Chaetoceros convolutus*. BSc Honors Thesis, University of British Columbia, pp. 21.

Gormican, S.J. 1989. Water circulation, dissolved oxygen, and ammonia concentrations in fish net-cages. MSc. thesis, University of British Columbia. pp. 61.

Gowen, R.J., P. Tett, K.J. Jones. 1983. The hydrography and phytoplankton ecology of Loch Ardbhair: a small sea-loch on the westcoast of Scotland. J. Exp. Mar. Biol. Ecol. 71: 1-16.

Gowen, R. 1984. The ecology of phytoplankton in Scottish coastal waters with particular reference to toxic species and their importance to mariculture. A final report for the Highlands and Island Development Board. Scottish Marine Biological Association. Oban, Scotland. pp. 1-92.

Guillard, R.R.L. and P. Kilham. 1977. The ecology of marine planktonic diatoms. D. Werner (Ed). In: The Biology of Diatoms. University of California Press, Berkely, pp. 372-469.

Haigh, R. 1988. The effect of stratification on microplankton. MSc. University of British Columbia.

Hallegraeff, G.M. 1991. Aquaculturists' guide to harmful australian microalgae. CSIRO Division of Fisheries, Fishing Industry Training Board of Tasmania inc. Australia.

Hargraves, P.E. 1976. Studies on marine plankton diatoms. II. Resting spore morphology. J. Phycol. 12 (1): 118-128.

Hargraves, P.E. and F.W. French. 1983. Diatom resting spores: significance and strategies. G.A. Fryxell (Ed) In: Survival and Strategies of the Algae. Cambridge University Press, New York.

Harrison, P.J. 1973. Continuous culture of the marine diatom *Skeletonema costatum* (Grev.) Cleve under silicate limitation. Ph.D. Thesis. University of Washington.

Harrison, P.J., R.E. Waters, and F.J.R. Taylor. 1980. A broad spectrum artificial medium for coastal and open ocean phytoplankton. J. Phycol. 16: 28-35.

Harrison, P.J., J.D. Fulton, F.J.R. Taylor and T.R. Parsons. 1983. Review of the biological oceanography of the Strait of Georgia: Pelagic environment. Can. J. Fish. Aquat. Sci. 40: 1064-1094.

Harrison, W.G., T. Platt, and M.R. Lewis. 1987. f-ratio and its relationship to ambient nitrate concentration in coastal waters. J. Plankton Res. 9: 235-248.

Hasle, G.R. 1978. Using the inverted microscope. In: Phytoplankton Manual. Monographs on oceanographic methodology 6, (A. Sournia, ed.), UNESCO pp. 191-196.

Hatano, S., Y. Hara, and M. Takahashi. 1983. Preliminary study on the effects of photoperiod and nutrients on the vertical migratory behaviour of a red tide flagellate, *Heterosigma akashiwo*. Jap. J. Phycol. 31: 263-269.

Heezen, B.C. and C. Hollister. 1964. Deep-sea current evidence from abyssal sediments. Mar. Geol. 1: 141-174.

Hicks, B. 1988. What is a diagnosis? Canadian Aquaculture. July/August, p.A19

Holmes, R.W. 1967. Auxospore formation in two marine clones of the diatom genus *Coscinodiscus*. Amer. J. Bot. 54: 163- 168.

Ignatiades, L. 1969. Annual cycle, species diversity and succession of phytoplankton in lower Saronicos Bay, Aegean Sea. Mar. Biol. 3: 196-200.

Imai, I. and K. Itoh. 1986. A preliminary note on the cysts of *Chattonella* (Raphidophyceae), red tide flagellates, found in bottom sediment in Suo-nada, Western Seto Inland Sea, Japan. Bull. Plankt. Soc. Japan. 33: 61-63.

Jones, K.J. and Gowen, R.J. 1985. The influence of advective exchange on phytoplankton in Scottish fjordic sea-lochs. (Eds) Anderson, D.M., A.W.White, D.G. Baden. In: Toxic Dinoflagellates, Elsevier, New York, pp. 207-212.

Jones, K.J., L. Cabecadas, R.J. Gowen, N. Robertson and P. Tett. 1981. Phytoplankton, nutrients and hydrography in Loch Fyne and approaches. In: Gowen, R. 1984. A final report for the Highlands and Islands Development Board. Scottish Marine Biological Association. Oban, Scotland.

Kennedy, W.A., C.T. Shoop, W. Griffioen, and A. Solmie. 1976. The 1974 crop of salmon reared on the Pacific Biological Station experimental fishfarm. Fish Mar. Ser. Res. Tech. Rep. 612: p. 19.

Larson, J. and O. Moestrup. 1989. Guide to toxic and potentially toxic marine algae. The Fish Inspection Service, Ministry of Fisheries, Denmark. pp. 1-61.

Lassus, P., M. Bardouil, I. Truquet, C. Le Baut, M. J. Pierre. 1985. *Dinophysis acuminata* distribution and toxicity along the southern Brittany coast (France): correlation with hydrological parameters. (Eds) Anderson, D. M., A.W. White, D.G. Baden. In: Toxic Dinoflagellates Elsevier, New York, pp. 159-164.

Lazier, J.R.N. 1963. Some aspects of the oceanographic structure in the Jervis Inlet system. MSc. thesis, University of British Columbia 54 pp.

Lewis, J., P. Tett, and J.D. Dodge. 1985. The cyst-theca cycle of *Gonyaulax polyedra* (*Lingulodinium machaerophorum*)in Creran, a Scottish west coast Sea-Loch. Anderson, White and Baden. (Eds.) In: Toxic Dinoflagellates. Elsevier Science Publishing Co.

Lund, J.W.G., C. Kipling, and E.D. Le Cren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143- 170.

Malone, T.C. 1980. Algal Size. I. Morris. (Ed) In: The Physiological Ecology of Phytoplankton. Blackwell Scientific Publications. London.

Marasovic I. 1989. Encystment and excystment of *Gonyaulax polyedra* during a red tide. Estuarine, Coastal Shelf Sci 28: 35-41.

Margalef, R. 1958 Temporal succession and spatial heterogeneity in phytoplankton. (Ed) A.A. Buzzati-Travoso In: Perspectives in Marine Biology. Univ. Calif. Press, Berkeley, pp. 323-349.

Margalef, R. 1963. Succession in marine populations. Adv. Frontiers Pl. Sci. 2: 137-188.

Margalef, R. 1967. The food web in the pelagic environment. Helgolander Wiss. Meeresunters. 15: 548-559.

Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, 1 (4): 493-509.

Matsuoka,K., Y.Fukuyo, and D.M. Anderson. 1989. Methods for modern dinoflagellate cyst studies. Okaichi, Anderson, and Nemoto (Eds.) Red Tides: Biology, Environmental Science, and Toxicology. Elsevier Science Publishing Co.

Matsuoka, K., Y. Fukuyo, M.H. Jaafar, and M.W.R.N. De Silva. 1989. Occurrence of the cyst of *Pyrodinium bahamense* var. *compressum* in surface sediments of Brunei Bay. G.M. Hallegraeff and J.L. Maclean (Eds.) In: Biology, epidemiology and management of *Pyrodinium* red tides. ICLARM Conference Proceddings 21 p 286 Fisheries Departmen, Ministry of Development, Brunei Darussalam, and International Center for Living Aquatic Resources Management, Manila, Philippines.

McCarthy, J.J., W.R. Taylor and J.L. Taft. 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay. 1. Nutrient availability and phytoplankton preferences. Limnol. Oceanogr. 22: 996-1011.

Metaxas, A. and A.G. Lewis. 1991. Interactions between two species of marine diatoms: effects on their individual copper tolerance. Marine Biology. 109: 407-413.

Nakamura, Y, T. Umemori, M. Watanabe, D.M. Kulis and D.M. Anderson. 1990. Encystment of *Chattonella antiqua* in Laboratory cultures. J. Oceanographical Society of Japan. 46 (2): 35-43.

Nichols, P.D., J.K. Volkman, G.M. Hallegraeff, and S.I. Blackburn. 1987. Sterols and fatty acids of the red tide flagellates *Heterosigma akashiwo* and *Chattonella antiqua* (Raphidophyceae). Phytochemistry 26: 2537-2541.

Okaichi, T. 1985. Fish kills due to the red tides of *Chattonella*. Bull. Ar. Sci. 37 p.772.

Owen, K.C. and D.R. Norris. 1982. Benthic resting cysts of *Gonyaulax monilata* Howell and their relationship to red tides in the Indian River, Florida. Florida Sciences, 45: 227-233.

Paasche, E. and S. Kristiansen. 1982. Nitrogen nutrition of the phytoplankton in the Oslofjord. Estuarine, Coastal Shelf Sci. 14: 237-249.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press. Oxford.

Parsons, T.R., M. Takahashi, and B. Hargrave. 1977. Biological oceanographic processes, 2nd ed. Pergamon Press, Oxford, New York.

Perry, M.J. and R.W. Eppley. 1981. Phosphate uptake by phytoplankton in the central North Pacific Ocean. Deep-Sea Res. 28: 39-49.

Pianka, E.R. 1970. On r- and k-selection. Am. Nat. 104: 592-597.

Pickard, G.L. 1961. Oceanographic features of inlets in the British Columbia Coast. J. Fish. Res. Bd. Can. 18: 907-999.

Pratt, D.M. 1966. Competition between *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay and in culture. Limnol. Oceanogr. 11: 447-455.

Putt, M. and D.K. Stoecker. 1989. An experimentally determined carbon:volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34: 1097-1103.

Raven, J.A. and K. Richardson. 1984. Dinophyta: a cost-benefit analysis. New Phytol. 98: 259-276.

Rensel, J.E., W.A. Clark, and R.A. Pastorok. 1990. Nutrients and phytoplankton in Puget Sound. Report prepared for U.S. Environmental Protection Agency Seattle, Washington.

Rijstenbil, J.W. 1989. Competitive interaction between *Ditylum brightwelli* and *Skeletonema costatum* by toxic metabolites. Neth. J. Sea Res. 23: 23-27.

Roelofs, A.K., 1983. The distribution of diatoms in the surface sediments of British Columbia, Canada. Ph.D. Thesis. University of British Columbia.

Round, F.E. 1982 Auxospore structure, initial valves and the development of populations of *Stephanodiscus* in Farmoor Reservoir. Ann. Bot. 49: 447-459.

Ryther, J. H. and W.M. Dunstan. 1971. Nitrogen, phosphorus and eutrophication in the coastal marine environment. Science 1717: 1008-1013.

Sakshaug, E. and Y. Olsen. 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. Can. J. Fish. Aquat. Sci. 43: 389-396.

Sancetta, C. 1989. Processes controlling the accumulation of diatoms in sediments: a model derived from British Columbian fjords. Paleoceanography, 4: 235-251.

Skjoldal, H.R. and P. Wassmann. 1986. Sedimentation of particulate organic matter and silicum during spring and summer in Lindaspollene, Western Norway. Mar. Ecol. Prog. Ser. 30: 49-63.

Smayda, T.J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Ann. Rev. 8: 353-414.

Smayda, T.J. 1978. Phytoplankton conversions. Sournia, A. (Ed) In: Phytoplankton Manual, Unesco, United Kingdom.

Smayda, T.J. 1980. Phytoplankton species succession. D.J. Anderson, P. Greig-Smith, F.A. Pitelka (Eds) In: The Physiological Ecology of Phytoplankton. Blackwell Sientific Publications, Oxford.

Smethie, W.M.Jr. 1987. Nutrient regeneration and denitrification in low oxygen fjords. Deep-Sea Research. 34 (5/6): 983-1006.

Smith, W. 1966. Short-term temperature and light conditions associated with auxospore formation in the marine centric diatom *Coscinodiscus concinnus*. Nature, 209 (5019): 217-218.

Steidinger, K.A. 1975. Implications of dinoflagellae life cycles on initiation of *Gymnodinium breve* red tides. Environ. Letters, 9: 129-139.

Steidinger, K.A. 1983. A re-evaluation of toxic dinoflagellate biology and ecology. Round and Chapman (Eds.) In: Progress in Phycological Research. Elsevier.

Sutherland, T.F. and F.J.R. Taylor. 1990. Are harmful flagellate blooms in Sechelt Inlet, B.C., autochthonous? Bull. Aquacul. Assoc. Cananda 90-4: 22-26.

Syrett, P.J. 1981. Nitrogen metabolism of microalgae. In: Platt, T. (Ed) Physiological Bases of Phytoplankton Ecology. Can. Bull. Fish. Aquat. Sci. 210: 182-210.

Taylor, F.J.R., R. Haigh, T.F. Sutherland, and J. Ramirez. 1991. Draft report of the harmful algal research project in Sechelt Inlet, B.C., 1988-1990. Report prepared for the British Columbia Ministry of Environment.

Tett, P., R. Gowen, B. Granthan, and K. Jones. 1981. A summary of the final report on the investigation of phytoplankton in Loch Striven 1980, including a report on histopathological features of the experimental salmon by R.J. and A.M. Bullock. In: Gowen, R. 1981. A final report for the Highlands and Islands Development Board. Scottish Marine Biological Association. pp. 1-92.

Thomson, R.E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 pp.

Throndsen, J. 1978. The dilution-culture method. Sournia, A. (Ed) In: Phytoplankton Manual. Unesco, United Kingdom.

Tomas, C.R. 1978. *Olisthodiscus luteus* (Chrysophyceae) I. Effects of salinity and temperature on growth, motility and survival. J. Phycol. 14: 309-313.

Toyoshima, T., M. Shimada, H.S. Ozki, T. Okaichi, and T.H. Murakami. 1987. Histological alterations to gills of yellowtail, *Seriola quinqueradiata*, following exposure to the red tide species *Chatonella antiqua*. T. Okaichi, D.M. Anderson, T. Nemoto. Elsevier, New York.

Tyler, M.A., DW. Coats, and D.M. Anderson. 1982. Encystment in a dynamic environment: deposition of dinoflagellate cysts by a frontal convergence. Mar. Ecol. Prog. Ser. 7: 163-178.

Von Stosch, H.A., 1982. On auxospore envelopes in diatoms. Bacillaria. 5: 127-156.

Von Stosch, H.A. and K. Fecher. 1979. "Internal thecae" of *Eunotia soleirolii* (Bacillariophyceae): development, structure and function as resting spores. J. Phycol. 15: 233- 243.

Wada, M, A. Miyazaki and T. Fujii. 1985. On the mechanisms of diurnal vertical migration behaviour of *Heterosigma akashiwo* (Raphidophyceae). Plant Cell Physiol. 26 (3): 431-436.

Walker, L.M. and K.A. Steidinger. 1979. Sexual reproduction in the toxic dinoflagellate *Gonyaulax monilata*. J. Phycol. 15: 312-315.

Wall, D. and B. Dale. 1969. The "hystrichosphaerid" resting spore of the dinoflagellate *Pyrodinium bahamense*, Plate, 1906. J. Phycol. 5 (2): 140-149.

Walsby, A.F. and C.S. Reynolds. 1980. Sinking and floating. I. Morris (Ed) In: The physiological ecology of phytoplankton. Blackwell Scientific Publications Oxford.

Wassmann, P. 1991. Dynamics of primary production and sedimentation in shallow fjords and polls of Western Norway. (Ed) M. Barnes, Oceanogr. Mar. Biol. Annu. Rev., 29: 87-154. Aberdeen University Press.

Watanabe, M.M., M. Watanabe, and Y. Fukuyo. 1982. Encystment and excystment of red tide flagellates I. Induction of encystment of *Scrippsiella trochoidea*. Res. Rep. Natl. Inst. Environ. Stud. 30: 27-42.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments: Jour. Geology. 30:377-392. In: Krumbein, W. C. and F. J. Pettijohn. Manual of sedimentary petrography. (Ed) K. F. Mather. The Century Earth Science Series, New York. 1938.

Weston, D. 1988. The impact of mariculture on the environment. Technical Report. Washington.

Yamochi, S. and T. Abe. 1984. Mechanisms to initiate a *Heterosigma akashiwo* red tide in Osaka Bay. II. Diel vertical migration. Marine Biology, 83: 255-261.

Yamochi, S. 1989. Mechanisms for outbreak of *Heterosigma akashiwo* red tide in Osaka Bay. T. Okaichi, D.M. Anderson, T. Nemato (Eds) In: Red Tide: Biology, Environmental Science, and Toxicology. Elsevier Science Publishing Co. New York.

APPENDIX 1.1: Diatom biomass ($\mu gC \cdot L^{-1}$) at each depth inteval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
June 9			
0-3	561.98	66.55	0.14
3-6	132.45	87.64	4.61
6-9	191.43	103.13	9.81
9-12	141.39	74.15	275.26
12-15	94.62	42.99	3.88
15-18	211.13	43.17	0.68
TOTAL	1333.01	417.63	294.39
June 25			
0-3	84.56	508.63	0.45
3-6	46.30	293.89	24.55
6-9	60.32	727.22	196.20
9-12	78.54	462.96	72.12
12-15	93.82	173.47	37.73
15-18	77.25	185.79	9.09
TOTAL	440.79	2351.95	340.13
July 8			
0-3	134.43	1602.40	215.90
3-6	85.19	601.48	173.87
6-9	75.65	315.64	139.83
9-12	53.72	180.04	68.31
12-15	36.52	139.43	32.02
15-18	99.40	82.45	17.17
TOTAL	484.91	2921.44	647.11
July 22			
0-3	6.40	122.55	1.70
3-6	4.26	72.08	10.33
6-9	4.02	56.01	25.63
9-12	7.21	51.18	32.71
12-15	3.25	109.84	32.39
15-18	0.68	37.57	5.73
TOTAL	25.82	449.24	108.49

APPENDIX 1.1 cont'd: Diatom biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
August 10			
0-3	12.61	317.41	13.62
3-6	22.34	110.63	25.51
6-9	15.85	152.90	24.19
9-12	9.44	72.84	44.72
12-15	9.18	120.02	5.73
15-18	9.14	6.30	4.64
TOTAL	78.57	780.10	118.41
August 26			
0-3	107.12	1704.76	53.67
3-6	82.20	423.37	106.90
6-9	86.73	233.27	17.32
9-12	147.88	108.86	3.30
12-15	120.67	38.48	2.43
15-18	113.22	14.78	3.17
TOTAL	657.81	2523.52	186.79
September 8			
0-3	23.53	147.04	1.24
3-6	13.29	101.44	43.19
6-9	6.76	48.07	3.97
9-12	18.00	5.99	1.86
12-15	9.91	0.78	1.84
15-18	7.83	1.10	3.51
TOTAL	79.32	304.41	55.61
September 25			
0-3	168.90	352.03	95.49
3-6	98.55	111.29	41.86
6-9	55.99	106.76	2.47
9-12	51.97	73.80	2.96
12-15	50.74	22.93	4.47
15-18	42.82	5.13	8.79
TOTAL	468.97	671.94	156.04

APPENDIX 1.2: Dinoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
June 9			
0-3	4.34	49.73	203.67
3-6	6.69	31.28	33.72
6-9	3.02	12.78	16.67
9-12	2.18	7.85	12.55
12-15	3.09	4.19	6.60
15-18	1.14	5.62	2.67
TOTAL	9.39	104.42	244.08
June 25			
0-3	7.25	108.96	48.47
3-6	0.30	14.82	126.77
6-9	1.36	41.73	52.46
9-12	2.11	10.97	35.04
12-15	1.63	4.61	4.86
15-18	3.40	10.36	1.12
TOTAL	16.06	191.45	268.72
July 8			
0-3	0.24	45.48	66.58
3-6	4.35	7.02	69.28
6-9	0.27	11.21	28.86
9-12	0.61	5.55	21.18
12-15	0.19	6.67	3.51
15-18	4.11	2.27	3.87
TOTAL	9.77	78.20	193.28
July 22			
0-3	10.81	93.11	26.00
3-6	10.80	37.05	59.58
6-9	15.94	30.70	40.60
9-12	6.65	7.43	24.36
12-15	8.56	10.43	5.34
15-18	5.54	9.71	1.24
TOTAL	58.30	188.44	157.12

APPENDIX 1.2 cont'd: Dinoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
August 10			
0-3	26.86	287.99	115.19
3-6	59.62	152.89	50.37
6-9	43.04	26.44	86.20
9-12	43.65	8.17	66.50
12-15	40.09	19.92	13.59
15-18	19.27	6.20	2.12
TOTAL	232.54	501.60	333.98
August 26			
0-3	7.28	46.04	36.78
3-6	8.94	15.18	79.93
6-9	5.41	9.32	32.67
9-12	6.79	4.80	2.54
12-15	6.63	2.88	1.62
15-18	5.20	3.29	0.15
TOTAL	40.25	81.51	153.69
September 8			
0-3	4.87	68.78	44.69
3-6	1.98	32.84	62.17
6-9	9.41	8.09	8.58
9-12	13.76	2.77	0.37
12-15	18.88	1.15	8.58
15-18	26.20	1.59	0.33
TOTAL	75.10	115.21	124.73
September 25			
0-3	9.32	87.94	51.99
3-6	7.53	38.85	21.44
6-9	6.70	10.11	2.54
9-12	9.01	4.07	1.44
12-15	25.57	3.92	1.64
15-18	12.78	0.00	2.01
TOTAL	70.90	144.90	81.06

APPENDIX 1.3: Heterotrophic dinoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
June 9			
0-3	2.91	0.22	0.22
3-6	2.43	3.02	11.17
6-9	2.70	1.16	4.19
9-12	1.46	1.35	7.53
12-15	1.46	0.00	6.32
15-18	0.12	1.28	2.37
TOTAL	11.07	7.03	31.80
June 25			
0-3	4.41	8.90	7.85
3-6	23.22	10.16	58.15
6-9	4.36	11.97	13.61
9-12	3.28	14.44	6.68
12-15	4.21	1.36	2.80
15-18	5.60	6.90	0.00
TOTAL	45.08	53.73	89.08
July 8			
0-3	0.00	29.86	22.82
3-6	0.22	43.92	10.62
6-9	3.28	44.30	2.60
9-12	0.00	0.00	2.26
12-15	0.00	0.00	0.00
15-18	0.00	0.93	1.08
TOTAL	3.50	119.01	39.38
July 22			
0-3	0.22	14.51	18.34
3-6	3.23	11.52	13.10
6-9	1.08	6.93	5.36
9-12	2.15	16.85	0.81
12-15	1.35	12.82	3.36
15-18	0.00	0.48	0.00
TOTAL	8.03	63.10	40.97

APPENDIX 1.3 cont.d: Heterotrophic dinoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989

Depth (m)	Region I	Region II	
August 10			
0-3	4.59	26.11	15.66
3-6	10.79	17.40	8.52
6-9	4.86	0.22	2.76
9-12	7.72	1.76	25.81
12-15	0.22	7.18	12.61
15-18	0.97	0.00	15.80
TOTAL	29.14	52.67	81.15
August 26			
0-3	0.00	9.23	0.22
3-6	0.12	24.79	1.56
6-9	0.37	17.93	0.88
9-12	0.25	1.81	0.11
12-15	0.36	0.47	0.11
15-18	0.12	2.46	0.11
TOTAL	1.23	56.69	3.00
September 8			
0-3	0.00	5.54	0.03
3-6	0.00	0.30	0.08
6-9	0.49	3.99	0.00
9-12	0.00	1.35	0.00
12-15	0.00	0.00	0.00
15-18	0.00	0.00	0.12
TOTAL	0.49	11.18	0.24
September 25			
0-3	0.00	3.08	3.01
3-6	0.00	0.57	1.10
6-9	0.00	6.97	0.11
9-12	0.00	0.46	0.00
12-15	0.00	0.11	0.00
15-18	0.10	0.00	0.11
TOTAL	15.63	15.53	4.33

APPENDIX 1.4: Nanoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September 1989.

Depth (m)	Region I	Region II	Region III
June 9			
0-3	4.83	37.36	7.70
3-6	4.64	15.29	9.01
6-9	2.83	17.78	6.13
9-12	3.81	10.94	6.98
12-15	1.50	5.18	3.58
15-18	3.17	3.04	1.56
TOTAL	20.78	89.60	34.96
June 25			
0-3	287.86	1432.46	262.91
3-6	276.00	359.04	825.86
6-9	494.34	281.86	270.75
9-12	436.02	257.42	370.08
12-15	285.31	140.76	264.32
15-18	776.04	137.28	211.45
TOTAL	255.56	260.88	220.54
July 8			
0-3	13.78	43.02	18.51
3-6	12.61	14.86	11.20
6-9	14.19	10.47	9.15
9-12	13.18	13.43	2.73
12-15	8.13	3.80	3.02
15-18	6.86	6.33	2.52
TOTAL	68.76	91.91	47.13
July 22			
0-3	17.21	44.74	57.63
3-6	26.42	14.86	23.10
6-9	13.12	10.36	29.84
9-12	29.81	13.88	10.72
12-15	15.99	4.48	4.24
15-18	8.07	6.79	1.24
TOTAL	110.63	95.11	126.77

APPENDIX 1.4 cont'd: Nanoflagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
August 10			
0-3	12.42	228.53	84.97
3-6	18.17	73.08	29.42
6-9	66.22	73.13	17.46
9-12	26.98	35.14	5.11
12-15	12.87	39.19	5.41
15-18	17.60	55.99	10.86
TOTAL	154.25	505.05	153.23
August 26			
0-3	12.30	60.34	119.44
3-6	20.18	27.50	69.89
6-9	6.47	28.85	24.53
9-12	16.77	19.31	2.53
12-15	21.60	11.62	1.75
15-18	12.02	1.91	2.64
TOTAL	89.35	149.53	220.78
September 8			
0-3	5.63	15.67	155.15
3-6	3.65	16.14	7.95
6-9	2.65	8.63	1.88
9-12	1.86	8.85	1.28
12-15	2.16	5.19	1.26
15-18	1.05	1.97	1.38
TOTAL	16.99	56.45	168.90
September 25			
0-3	0.00	6.40	18.60
3-6	8.13	8.78	10.24
6-9	3.83	6.64	1.89
9-12	6.32	12.48	1.19
12-15	3.48	8.84	0.20
15-18	0.39	1.66	0.14
TOTAL	29.12	44.80	32.26

APPENDIX 1.5: Photosynthetic flagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989 (Photosynthetic flagellates = *Dictyocha speculum*, *Eutreptiella* spp., *Heterosigma akashiwo*, and Prasinophyte sp.)

Depth (m)	Region I	Region II	Region III
June 9			
0-3	3.60	4.09	0.00
3-6	0.00	25.48	77.98
6-9	1.70	3.03	13.35
9-12	3.81	7.78	4.45
12-15	0.64	2.92	8.26
15-18	1.33	1.32	4.87
TOTAL	11.07	44.63	108.91
June 25			
0-3	0.42	0.83	0.00
3-6	0.00	0.11	3.57
6-9	0.42	4.68	3.84
9-12	0.42	3.51	5.19
12-15	0.00	0.31	6.19
15-18	0.42	0.00	0.00
TOTAL	1.70	9.44	18.79
July 8			
0-3	0.20	0.00	2.23
3-6	0.42	0.00	8.33
6-9	0.85	0.00	9.41
9-12	0.53	0.00	8.59
12-15	0.00	0.00	0.00
15-18	0.00	0.00	0.00
TOTAL	2.01	0.00	28.56
July 22			
0-3	3.73	0.61	22.08
3-6	35.15	0.14	5.79
6-9	27.42	0.05	5.64
9-12	37.56	0.02	5.79
12-15	33.07	0.02	4.55
15-18	2.91	0.01	0.00
TOTAL	169.84	1.76	43.86

APPENDIX 1.5 cont'd: Photosynthetic flagellate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989 (Photosynthetic flagellates = *Dictyocha speculum*, *Heterosigma akashiwo*, *Eutreptiella* spp., and a Prasinophyte sp.).

Depth (m)	Region I	Region II	Region III
August 10			
0-3	4.59	19.67	6.68
3-6	7.29	20.61	16.42
6-9	6.78	20.61	19.66
9-12	5.51	0.00	6.63
12-15	7.02	3.64	0.66
15-18	2.55	7.23	1.33
TOTAL	33.74	71.75	51.38
August 26			
0-3	7.89	145.02	26.97
3-6	8.39	34.25	21.26
6-9	7.62	15.21	12.70
9-12	7.72	6.02	4.30
12-15	8.16	1.40	1.09
15-18	5.96	0.69	0.28
TOTAL	45.75	202.59	66.60
September 8			
0-3	2.32	0.00	3.00
3-6	1.66	5.85	7.10
6-9	2.54	2.70	1.00
9-12	8.11	0.89	0.17
12-15	0.50	0.20	0.39
15-18	6.00	0.10	0.25
TOTAL	21.11	9.74	11.90
September 25			
0-3	11.67	11.07	7.07
3-6	9.03	4.72	1.87
6-9	12.51	5.39	1.01
9-12	8.53	1.15	0.41
12-15	7.29	2.45	0.11
15-18	10.36	1.83	0.06
TOTAL	59.38	26.62	10.52

APPENDIX 1.6: Ciliate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
June 9			
0-3	5.96	80.08	34.15
3-6	7.68	37.56	4.47
6-9	4.77	23.22	0.00
9-12	6.38	14.24	0.00
12-15	1.73	8.36	0.19
15-18	1.00	101.48	0.14
TOTAL	27.52	264.94	38.95
June 25			
0-3	2.55	80.42	1.73
3-6	12.60	26.07	22.65
6-9	8.66	32.61	3.48
9-12	2.35	14.96	13.78
12-15	1.59	2.75	0.00
15-18	3.08	1.50	11.77
TOTAL	30.83	158.31	53.41
July 8			
0-3	12.02	0.00	24.29
3-6	2.66	0.00	246.05
6-9	9.69	26.82	43.85
9-12	14.00	14.78	37.59
12-15	13.23	4.71	24.79
15-18	2.34	3.96	92.75
TOTAL	53.95	50.27	469.33
July 22			
0-3	4.50	28.22	113.69
3-6	0 0-3	4.50	28.22 113.69
3-6	0.00	28.58	92.14
6-9	2.88	26.82	121.08
9-12	0.00	14.78	26.53
12-15	0.00	4.71	21.57
15-18	0.00	3.96	0.00
TOTAL	7.38	107.07	375.00

APPENDIX 1.6 cont'd: Ciliate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989.

Depth (m)	Region I	Region II	Region III
August 10			
0-3	7.27	67.14	120.36
3-6	12.56	20.26	81.80
6-9	7.41	21.24	25.38
9-12	4.61	22.09	19.21
12-15	9.79	23.04	0.00
15-18	2.34	21.45	0.00
TOTAL	43.98	153.13	246.75
August 26			
0-3	2.96	47.28	22.13
3-6	8.62	33.50	50.56
6-9	9.49	9.07	0.43
9-12	4.02	7.82	4.12
12-15	4.10	3.67	0.41
15-18	9.32	3.00	0.00
TOTAL	38.51	104.34	77.64
September 8			
0-3	25.36	0.00	37.60
3-6	22.00	51.98	23.54
6-9	7.17	29.18	2.29
9-12	104.45	7.67	11.77
12-15	79.15	4.05	6.08
15-18	40.11	2.60	0.38
TOTAL	278.24	95.49	81.67
September 25			
0-3	2.11	41.12	22.21
3-6	51.01	29.15	2.42
6-9	95.31	2.56	2.59
9-12	4.22	9.98	0.00
12-15	12.15	9.37	0.00
15-18	1.53	4.33	11.96
TOTAL	166.34	96.51	39.18

APPENDIX 1.7: Photosynthetic ciliate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989 (Photosynthetic ciliate = *Mesodinium rubrum*).

Depth (m)	Region I	Region II	Region III
June 9			
0-3	4.86	156.42	0.69
3-6	2.78	43.37	0.00
6-9	0.00	13.01	0.00
9-12	9.03	5.78	6.94
12-15	0.00	1.45	0.69
15-18	1.39	0.00	0.00
TOTAL	16.66	218.58	7.64
June 25			
0-3	9.72	23.85	0.00
3-6	0.00	15.61	0.00
6-9	4.17	34.53	6.94
9-12	1.07	3.84	0.00
12-15	1.07	3.84	0.00
15-18	2.78	7.67	0.00
TOTAL	18.79	89.35	6.94
July 8			
0-3	8.33	0.00	0.00
3-6	4.17	0.00	15.27
6-9	5.55	18.42	11.11
9-12	1.39	0.00	4.17
12-15	2.78	0.00	0.00
15-18	0.00	0.00	0.00
TOTAL	22.22	18.42	30.55
July 22			
0-3	0.00	46.04	0.00
3-6	0.00	40.29	9.72
6-9	0.00	18.42	11.11
9-12	0.00	0.00	2.78
12-15	0.00	0.00	1.39
15-18	0.00	0.00	0.00
TOTAL	0.00	104.74	24.99

APPENDIX 1.7 cont'd: Photosynthetic ciliate biomass ($\mu gC \cdot L^{-1}$) at each depth interval in regions I, II, and III between June and September in 1989 (Photosynthetic ciliate = *Mesodinium rubrum*).

Depth (m)	Region I	Region II	Region III
August 10			
0-3	0.00	49.88	0.00
3-6	0.00	49.88	5.55
6-9	2.08	49.88	4.17
9-12	0.69	0.00	24.99
12-15	0.69	1.45	1.39
15-18	0.69	5.25	0.00
TOTAL	4.17	156.33	36.10
August 26			
0-3	1.39	0.00	0.00
3-6	0.00	3.84	1.39
6-9	0.00	2.89	48.60
9-12	0.00	0.00	2.78
12-15	0.00	0.00	0.00
15-18	0.00	0.00	0.00
TOTAL	1.39	6.74	52.76
September 8			
0-3	0.69	0.00	0.00
3-6	0.00	8.65	27.77
6-9	0.69	26.86	0.00
9-12	4.86	7.67	0.00
12-15	0.00	0.00	0.00
15-18	3.47	0.00	0.00
TOTAL	9.72	43.18	27.77
September 25			
0-3	0.00	4.12	458.59
3-6	0.00	7.42	19.44
6-9	0.00	7.67	1.39
9-12	0.00	0.90	0.00
12-15	0.00	1.36	0.00
15-18	0.00	0.00	0.00
TOTAL	0.00	21.47	479.42