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SIZE-DISTRIBUTION OF PLANKTONIC BIOMASS AND METABOLIC ACTIVITY IN THE PELAGIC SYSTEM

by

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To Lily, Magdalena and Isaura

¡ Qué descansada vida
la del que huye el mundanal ruido,
y sigue la escondida
senda, por donde han ido
los pocos sabios que en el mundo han sido !

Un no rompido sueño,
un día puro, alegre, libre quiero;
no quiero ver el ceño
vanamente severo
del que la sangre sube o el dinero.

Del monte en la ladera
por mi mano plantado tengo un huerto,
que con la primavera,
de bella flor cubierto,
ya muestra en esperanza el fruto cierto.

A mí una pobrecilla
mesa, de amable paz bien abastada,
me baste; y la vajilla,
de fino oro labrada,
sea de quien la mar no teme airada.

Y mientras miserable-
mente se estan los otros abrasando
con sed insaciable
del no durable mando,
tendido yo a la sombra esté cantando.

A la sombra tendido,
de yedra y lauro eterno coronado,
puesto el atento oído
al son dulce, acordado,
del plectro sabiamente meneado.

(Extracted from "Vida Retirada", Fray Luis de León, 1528-1591)

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ABSTRACT

The study of the distribution of biomass by size is a holistic approach to analyzing the structure of the pelagic ecosystem. This approach has been applied to the study of ecosystems energetics, pollution and fisheries. The main objectives of this thesis are: first, to examine the patterns of variation in the size-distribution of pelagic biomass in different kinds of ecosystems; and second, to determine if there is any regularity in the distribution of metabolic activity by size at the community level of organization in the pelagic system. The answer to these issues have important implications for understanding and modelling fluxes of energy and matter in the oceanic ecosystem.

Normalized biomass size-spectra (NBS-spectra) covering a size-range from bacteria to zooplankton were constructed from plankton collected in Sargasso Sea, New England Seamounts area (Northwest Atlantic), Georges Bank, Northeast Channel, Gulf of Maine and Scotian Shelf. It is concluded that the planktonic biomass size-distribution at all stations sampled can be described by linear NBS-spectra. These results support the hypothesis that there is a regularity in the distribution of pelagic biomass by size. The NBS-spectrum in offshore waters presents a slope close to -1.0 when expressed in biovolume units and -1.1 when expressed in carbon units. Therefore, biovolume is roughly the same at all size classes (Sheldon's "linear biomass hypothesis"), however biomass expressed as carbon content slightly decreases with increasing size (Platt and Denman's model). In the highly productive Georges Bank, biomass increases considerably with body size in the zooplankton size-range. In Georges Bank, biomass size-diversity and evenness are highest in mixed waters, less in frontal waters and lowest in stratified waters.

At several stations in the Northwest Atlantic metabolic activity of size fractions was determine using the ETS technique. The metabolic activity in the pelagic system (from bacteria to zooplankton) decreases as a power function of body size with an exponent of -0.22. Consequently, the slope of the normalized metabolic size spectrum (NMS-spectrum) is -1.22. At all stations the NMS-spectrum has a more negative slope than the NBS-spectrum, indicating that the smallest organisms play even a more important role than the larger ones from a metabolic point than from a biomass point of view. These results, along with an analysis of other published data, suggest that the linearity of the NMS-spectrum and the numerical value of its slope (-1.2) may be characteristics of the pelagic ecosystem.

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GENERAL INTRODUCTION

A major issue in ecology today is how to deal with ecosystem complexity. Ecological systems, contrary to mechanical systems, are far too complex to be specified in complete detail (Platt 1981). A holistic alternative is to identify macroscopic properties that are diagnostic of ecosystem function (Platt et. al. 1981).

The study of the distribution of biomass by size is an ataxonomic approach to study the flow of energy and matter in the pelagic ecosystem (Platt 1985). In this formulation, every individual in the system is assigned to one of a series of size-classes. The high degree of aggregation of such an approach reduces the complexity of the system to a manageable level. The biomass size-distribution approach (BSD-aproach) in pelagic ecosystems is based on observational data (e.g. Sheldon et al. 1972, 1973, Platt et al. 1984, Rodriguez and Mullin 1986a) and on the size-dependence of most aspects of energy and material flow of an organism (Peters 1983a). For example, respiration (Hemmingsen 1960, Banse 1976, 1979, 1982), production (Banse and Mosher 1980, Bamstedt and Skjoldal 1980), ingestion (Ikeda 1977, Nival and Nival 1976, Cammen 1980, Capriulo 1982), and growth (Fenchel 1974, Blueweiss et al. 1978, Baldock et al. 1980, Taylor and Shuter 1981) are size-dependent processes.

Furthermore, it is known that several size-dependent processes can alter community structure. Size-selective predation can be a primary organizing force in some communities (Brooks and Dodson 1965, Hall et al. 1976, Vanni 1986). There is also evidence that the size structure of the grazers can influence the size structure of the phytoplankton community (Carpenter and Kitchell 1984, Bergquist et al. 1985). Cell size is recognized as an important element in competitive interactions and in seasonal or trophic succession patterns among phytoplankton (e. g. Parson and Takahashi 1973,

Margalef 1978, Smayda 1980, Sournia 1981). Indeed, body-size differences are an important means by which species avoid direct overlap in resource use (Schoener 1974, Werner and Gilliam 1984).

Although the roots of the BSD-approach can be traced back to Elton (1927; for a historical perspective see Platt 1985), Sheldon et al. (1972, 1973) provided new impetus by publishing a set of particle size-spectra from oceanic areas. Sheldon et al. (1972), based on their field observations, proposed the "linear biomass hypothesis" which states that in the pelagic system, there is "the tendency for roughly similar amounts of particulate material to occur in logarithmically equal size ranges" (Sheldon et al. 1972). Sheldon et al. (1972) explained the observed pattern as a result of the inverse relationship between doubling time and particle size. In other words, "this hypothesis states that under equilibrium conditions the biomass of predator and prey is similar and growth and predation are in balance" (Sheldon et al. 1986).

The regularities in pelagic size-structure observed by Sheldon et al. (1972, 1973) led to the development of theoretical models to explain and quantify the regularities (Kerr 1974, Sheldon et al. 1977, Platt and Denman 1977, 1978, Silvert and Platt 1978, 1980, Borgmann 1982, 1983, 1987, Dickie et al. 1987a, Boudreau and Dickie 1989, Boudreau et al. 1991).

Platt and Denman (1977, 1978) developed a theoretical model of the distribution of biomass by size in the pelagic system which predicted, contrary to the linear biomass hypothesis, that biomass decreases as a power function of body size with an exponent equal to - 0.22. This model which is independent of the trophic level formalism, assumes a continuous flux of energy from organisms of small size to those of larger size. The flux of energy is estimated as the biomass in the size class divided by its turnover rate. The

loss of energy from the flux is considered to be mostly due to respiration. The loss of energy to the decomposer food chain is considered constant throughout the size spectrum and in the calculation of the theoretical slope of a steady state system this term is considered negligible.

Since the late 1970's, the BSD-approach has found application in several fields such as fisheries research and pollution studies. In fisheries, the BSD-approach has been applied to predict fish production from phytoplankton standing stock (Moloney and Field 1985), and from primary and zooplankton production (Sheldon et al. 1977, Borgmann et al. 1984). The BSD-approach has formed the basis of models to estimate fish mortality rates (Peterson and Wrobleski 1984) and to analyze multispecies fisheries (Pope et al. 1988, Murawski and Idoine 1989). Also, models to estimate production of multispecific fisheries based on size-structure and the allometric relation of the production to biomass ratio have been developed (Dickie et al. 1987 a,b, Boudreau and Dickie 1989, Boudreau and Dickie 1992). In pollution studies, the BSD-approach has been used to model the flow of contaminants up the food web (Thomann 1979, 1981, Griesbach et al. 1982, Borgmann and Whittle 1983, Vezina 1986).

The potential applications of the BSD-approach, as well as its usefulness in the study of the basic fluxes of matter and energy, have triggered a considerable interest in expanding the data base on the size-structure of pelagic ecosystems. Accordingly, biomass size-distribution studies have been conducted in freshwater (e.g. Peters 1983b, 1985, Sprules et al. 1983, Sprules and Knoechel 1984, Sprules and Munawar 1986, Sprules et al. 1988, Echevarría et al. 1990, Rodriguez et al. 1990, Sprules et al. 1991, Ahrens and Peters 1991a) and marine (e.g. Sheldon et al. 1972, 1973, Beers et al. 1982, Rodriguez and Mullin 1986 a, b, Rodriguez et al. 1987, Warwick and Joint 1987, Jimenez et al. 1987, 1989, Witek and Krajewska-Soltys 1989) ecosystems.

In spite of the increase of descriptive studies of the size-structure of pelagic systems, there are several areas that need further attention. In the context of descriptive studies, there is a remarkable scarcity of observations for the oligotrophic ocean. The description of the biomass distribution in the deep ocean is particularly significant because most of the models of biomass size-distribution (e.g. Platt and Denmann 1977, 1978) are based on the assumption of equilibrium or steady state. Therefore, the oligotrophic ocean is an optimum setting for the testing of model predictions. Similarly, systems very far from the steady state are also of great interest. The other area needing further development is the relationship between biomass size-distribution and ecosystem processes such as respiration and production. The distribution of biomass by size, despite its linkage to the energetics of the system, is essentially a measure of ecosystem structure. The simultaneous study of size-structure and processes such as respiration should permit a better understanding of the relationship between structure and function in the ecosystem.

Consequently, the main objectives of this thesis are: 1) to examine the patterns of variation in the size-distribution of pelagic biomass in different kinds of ecosystems; and 2) to determine if there is any regularity in the distribution of metabolic activity by size at the community level of organization in the pelagic system. The answer to these issues have important implications for understanding and modelling the fluxes of energy and matter in the oceanic ecosystem.

In Chapter I, the patterns of the normalized biomass size-spectra from the Sargasso Sea and the New England Seamounts Area are analyzed. My results support the hypothesis that the biomass size distribution can be described by linear NBS-spectra and it is a conservative property of the oligotrophic ocean.

Chapter II deals with the distribution of biomass by size in Georges Bank, a highly dynamic and productive system. The planktonic biomass size distribution of this system can also be described by linear NBS-spectra. Although the parameters of the bacterio- to microplankton NBS-spectra are similar to those found in the oligotrophic ocean, an important change in the parameters of the NBS-spectrum at the zooplankton size-range was detected. Zooplankton biomass increases considerably with body size, which is a characteristic of Georges Bank in contrast to oceanic systems. Biomass-size diversity and evenness are highest in mixed waters, less in frontal waters and lowest in stratified waters.

Chapter III is a study of the size distribution of metabolic activity and biomass in the planktonic community at several stations in the Northwest Atlantic. At these sites, the metabolic activity of plankton by size can be represented by a linear normalized metabolic size-spectrum (NMS-spectrum). The linearity of the NMS-spectrum and the numerical value of its slope (-1.2) may be characteristic of the pelagic ecosystem. This finding is also supported by analysis of previously published data.

CHAPTER 1

PATTERNS OF BIOMASS SIZE-SPECTRA FROM OLIGOTROPHIC WATERS OF THE NORTHWEST ATLANTIC

ABSTRACT

The study of the distribution of biomass by size provides an ataxonomic approach for analyzing the structure of the pelagic ecosystem. However, empirical data regarding planktonic size-structure in offshore areas are scarce. Here, I report the results of a study of the planktonic biomass size-distribution at several stations located within two regions (Sargasso Sea and New England Seamounts Area) of the Northwest Atlantic. The biomass size-spectra covered a body-size range from bacteria to mesozooplankton and a depth range from the surface to 400 m. It is shown that the slope of the normalized biomass size-spectrum (NBS-spectrum) varies depending on whether volume or carbon units are used. The transformation from volume to carbon units makes the slope of the NBS-spectrum approximately 0.15 units more negative. The distribution of normalized-biomass by size was linear (plotted on a log-log scale) at all stations. The slopes of the NBS-spectra (volume scale) ranged from -0.96 to -1.01. There were no significant differences among the slopes of the NBS-spectra within either of the two areas studied. In addition, no significant differences were detected between the stations in the Sargasso Sea and those located in the New England Seamounts area. Apart from a tendency towards a decrease in the intercept of the normalized-biomass axis of the size-spectra in deeper waters, the NBS-spectra were also very similar through depth. The results of this study support the hypothesis that the planktonic size-structure of offshore systems is a conservative property.

INTRODUCTION

The study of the distribution of biomass by size in the pelagic system has been an important step in the search for generalizations in aquatic ecology. Regularities in the size-structure of communities have been observed in offshore systems (e.g. Sheldon et al. 1972, Beers et al. 1982, Platt et al. 1984, Rodriguez and Mullin 1986 a, b; Witek and Krajewska-Soltys 1989), lakes (e.g. Sprules et al. 1983, Sprules and Knoechel 1984; Sprules and Munawar 1986; Echevarría et al. 1990) and benthic communities (e.g Schwinghamer 1981, Warwick 1984, Schwinghamer 1985). In addition, theoretical research attempting to explain these regularities and/or to develop practical applications from them (e.g. fisheries predictions, toxicology studies) have been developed (e.g. Kerr 1974, Sheldon et al 1977, Platt and Denman 1977, 1978; Thomann 1979; Tseytlin 1981b; Peterson and Wroblewski 1984, Platt 1985, Silvert and Platt 1978, 1980; Borgmann 1982, 1983, 1987; Dickie et al. 1987a,b; Denman et al. 1989, Boudreau et al. 1991).

In spite of the growing body of evidence supporting the hypothesis that biomass is not distributed randomly among size classes in the pelagic system (Sheldon et al. 1972, Platt and Denman 1977, 1978), our knowledge of the size-structure of planktonic communities in offshore systems is still only rudimentary. Scarcity of empirical data in oligotrophic areas limits our capacity to test the generality of this hypothesis which, if validated, would be useful in modelling fluxes of energy and matter in the oceanic ecosystem.

In this paper, I describe biomass size-spectra from several stations located in the Sargasso Sea and in the New England Seamounts Area. The spectra cover a body size (volume scale) range of almost 14 orders of magnitude (from bacteria to

mesozooplankton) and a depth range from the surface to 400 m. Biomass size-spectra covering simultaneously such size and depth ranges have not been reported previously for the oligotrophic ocean. The main goal of this study is to test if the predictions of the size-spectrum theory as described by Platt and Denman (1977, 1978) hold for these selected oligotrophic areas of the Northwest Atlantic. The predictions are: (1) the distribution of normalized-biomass by size can be described by a linear relationship when plotted on a log-log scale, and (2) the slope of the normalized biomass-spectra is close to -1.2 .

MATERIALS AND METHODS

The sampling was conducted during two cruises on board the CSS Hudson (Department of Fisheries and Oceans, Canada). The first cruise (PLASMA cruise) took place in June-July 1987 in the New England Seamounts Area (NESA) of the Northwest Atlantic. The second cruise took place in the Sargasso Sea during September 1988. The station locations are described in Table 1.1 and shown in Figure 1.1.

Image Analysis

The sizing of organisms was carried out using an image analyzer, similar to that described by Campana (1987), with the following components modifications: (a) Newvicon Video Camera and (b) Oculus 300 (Coreco Inc.) frame grabber video digitizer board.

Bacterioplankton biomass

In the Sargasso Sea, all sampling depths were chosen based on the CTD data and the fluorescence profile obtained with an *in situ* fluorometer (Aquatracka, Chelsea Instruments, U. K.). Generally 18 depths were sampled in each bacterioplankton profile.

In the NESA two kinds of sampling strategies were applied. From the surface to the 100 meter depth, samples were usually taken every 5 meters. On the other hand, sampling depths from 100 m to 400 m were selected in the same manner as during the Sargasso Sea cruise.

Water samples were collected with 30-liter and 5-liter Niskin bottles and fixed with pre-filtered formaldehyde (0.2 μm pore size Nucleopore filters) to a final

TABLE 1.1.- Location of the stations.

Station Name	Location Lat (N)	Long (W)	Date	Day/Night
New England Seamounts Area				
Nashville	34° 47.60'	56° 36.41'	20/06/87	N
Indigo	34° 40.30'	54° 15.00'	22/06/87	N
Yakutat	34° 39.73'	50° 51.29'	28/06/87	N
Purple 10	31° 58.70'	55° 39.00'	01/07/87	D
Purple 11	31° 57.56'	55° 38.40'	02/07/87	N
Sargasso Sea				
SS11	35° 55.08'	64° 20.51'	11/09/88	N
SS12	35° 56.04'	64° 47.62'	13/09/88	N
SS13	36° 02.17'	65° 09.27'	16/09/88	N
SS14	36° 09.29'	65° 49.87'	19/09/88	N

Figure 1.1- Locations of sampling stations. Sargasso Sea stations : S1 = Sar11; S2 = Sar12; S3 = Sar13; S4 = Sar14. New England Seamounts Area: N1 = Indigo; N2 = Nashville; N3 = Yakutat; N4 = Purple 10; N5 = Purple 11.

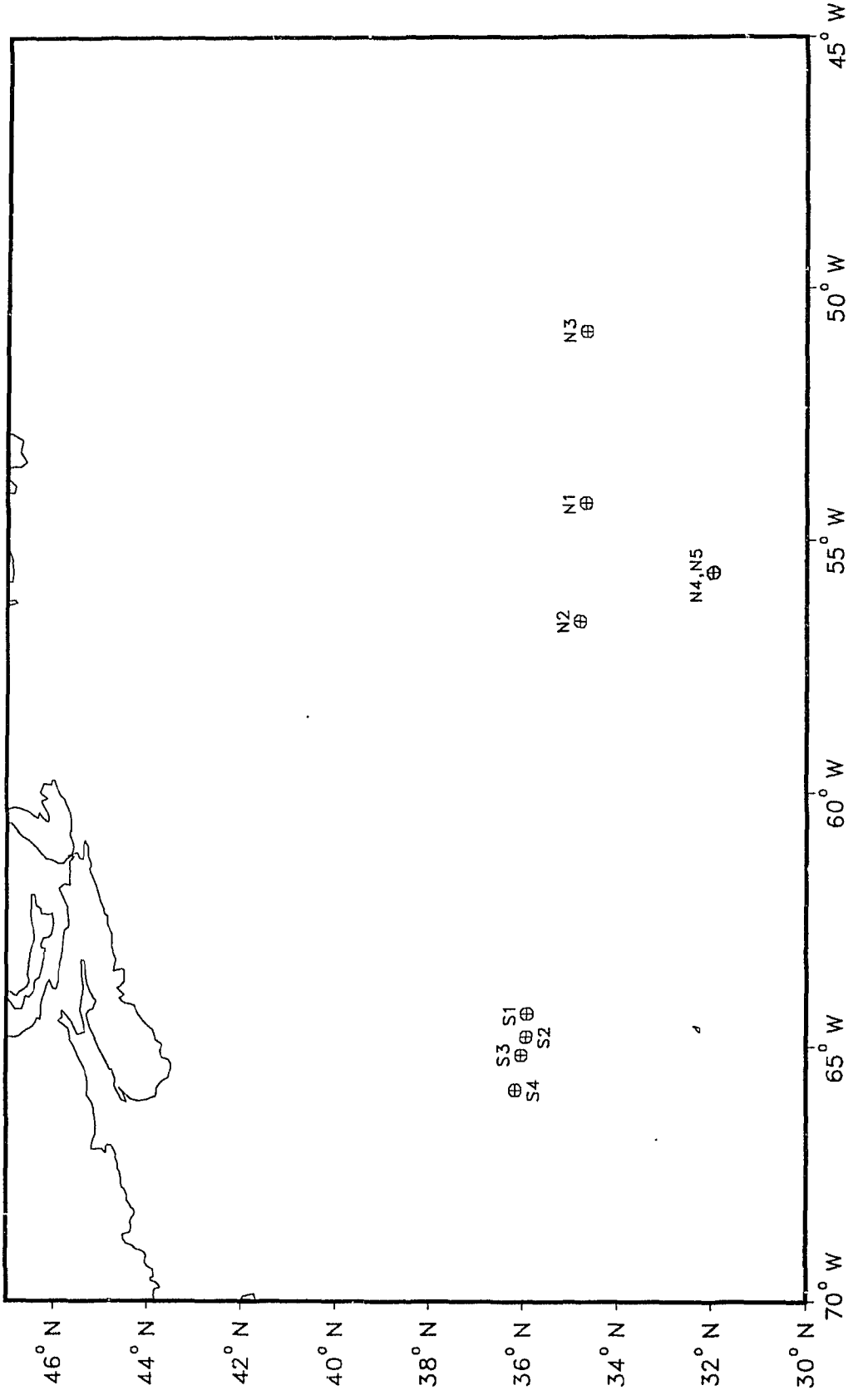

46° N
44° N
42° N
40° N
38° N
36° N
34° N
32° N
30° N
70° W
65° W
60° W
55° W
50° W
45° W
N1
N2
N3
N4,N5
S1
S2
S3
S4

Figure 1.1

concentration of 2%. The samples then were stored at 4°C in the dark until further analysis. In the laboratory, cells were stained with DAPI according to Porter and Feig (1980) and filtered onto 0.2 μm pore size black Nucleopore filters using a vacuum at a pressure of less than 100 mm Hg. The counting was performed with a Leitz Orthoplan epifluorescence microscope under 1000X magnification. Three slides per depth, with five to ten fields per slide, were counted using an ocular grid reticule. For the size determination, pictures (Kodak Ektachrome, P800/1600, slides) of randomly selected fields were taken. The slides were projected to a final magnification of 1500X. The images of the slide projection were captured with a video camera, and then digitized and processed with an image analyzer. The number of cells measured varied with picture quality ranging from 15 to 200, but generally around 60 bacteria were measured at each depth. Cell volume was calculated using the following formula:

$$V = (\pi / 4) W^2 (L - W/3) \qquad (1)$$

where L is the length of major axis, and W is the length of minor axis.

To convert the bacterial biovolume to biomass a conversion factor of 0.380 g C cm^{-3} (Lee and Furham 1987) was used.

Nano- and Microplankton Biomass

At each station, water from surface to 400 m was taken with 30 liter Niskin bottles. The depths to be sampled were chosen according to the heterogeneity of the fluorescence and density (σ_t) profiles obtained usually less than an hour before sampling. Generally 18 different depths were sampled at each station.

From the water obtained, an aliquot (500 ml) was taken to quantify microplankton sufficiently small to pass a 35 μm mesh netting. In addition, 20 liters were passed

through a 35 μm mesh using reverse filtration to concentrate the microplankters larger than 35 μm. The samples were fixed with formaldehyde-seawater solution to a final concentration of 2% and buffered with sodium borate.

To diminish the time spent in sample analysis, composite samples were made. The water column was divided in the following four strata : Mixed layer, Thermocline, Stratum I, and Stratum II. The division of the water column was based on the CTD data. Below the thermocline the water column was divided in half, into Strata I and II. Table 1.2 shows the depths of each of the strata at every station. The composite samples were made by mixing measured quantities of each of the samples according to the depth coverage of each of them.

An aliquot of 100 or 50 ml of each integrated sample (concentrated and unconcentrated) was sedimented using the Uthermol technique (Lund et al. 1958) for 48-72 hours. To improve the image and to facilitate the separation between living and non-living matter, the samples in the settling chambers were stained with bengal rose. Subsequently, the organisms were observed under 125X, 200X, 500X and 1250X magnifications. The sizing and counting of organisms was carried out using image analysis. An ocular micrometer and a Newporton Graticule (May 1965) were also used for direct sizing and counting. Approximately 200 organisms were sized at each magnification. The volume of the organisms was estimated assuming basic geometrical shapes and also guided by the recommendations of the Baltic Marine Environment Protection Commission (1983). Biovolumes were converted to carbon using the equation

TABLE 1.2. Vertical strata used in the division of the water column for the bacterio- to microplankton spectra.

Station	Depth range (m)			
Name	Mixed Layer	Thermocline	Stratum I	Stratum II
New England Seamounts Area				
Nashville	0 - 26	26 - 67	67 - 233.5	233.5 - 400
Indigo	0 - 26	26 - 75	75 - 237.5	237.5 - 400
Yakutat	0 - 23	23 - 90	90 - 245.0	245.0 - 400
Purple 10	0 - 15	15 - 106	106 - 253.0	253.0 - 400
Purple 11	0 - 17	17 - 90	90 - 245.0	245.0 - 400
Sargasso Sea				
SS11	0 - 48	48 - 150	150 - 275.0	275.0 - 400
SS12	0 - 48	48 - 103	103 - 251.5	251.5 - 400
SS13	0 - 45	45 - 114	114 - 257.0	257.0 - 400
SS14	0 - 56	56 - 175	175 - 287.5	287.5 - 400

of Strathmann (1967)

$$\log C = -0.460 + 0.866 \log V \qquad (2)$$

where C is cell carbon (pg) and V is cell volume (μm^3).

Zooplankton biomass

During the cruise to the NESA, collections were made with 55-cm or 73-cm diameter ring nets (mesh size 75 μm; vertical tows), and 62-cm diameter bongo nets (mesh size 253 μm and 505 μm; oblique tows). In the Sargasso Sea, the vertical collections were carried out with 72-cm diameter ring nets (mesh size 75 μm; vertical tows) and with Bongo nets specially designed (Bedford Institute of Oceanography) for vertical towing (61-cm diameter, mesh size 253 μm). Oblique tows were carried out with regular Bongo nets (61-cm diameter, mesh size 253 μm). All nets were equipped with flowmeters.

In the NESA, the catch from each side of the bongo was generally split with a plankton splitter. The zooplankton was size fractionated using sieves of 8000, 4000, 2000, 1000, 505, 253, and 153 μm mesh. In the Sargasso Sea, the catch from one of bongo sides was fixed with formaldehyde (final concentration 4% formaldehyde-seawater solution) and the catch from the other side of the Bongo was used to estimate zooplankton biomass. The zooplankton was size fractionated using sieves of 8000, 4000, 2000, 1000, 500, 250, 125, and 74 μm mesh.

Zooplankton size fractions were then filtered onto pre-weighed, pre-combusted (450 °C) glass fiber filters (Reeve Angel 934 AH). The zooplankters were quickly rinsed with distilled water. The filters were then dried for 36 hrs in an oven at 60°C and kept in

desiccators until further analysis. The size-fractions were weighed, on the land, in an electronic balance. The carbon content of the zooplankton size-fractions was determined using a Perkin Elmer 240-B CHN Elemental Analyzer.

To convert zooplankton biomass to biovolume the following equation from Wiebe (1988) was used:

$$\log F = -1.842 + 0.865 \log D \qquad (3)$$

where F is displacement volume (cc m^{-3}), and D is dry weight (mg m^{-3}).

To change the scale from length to weight as carbon, the following regression was used (Rodriguez and Mullin 1986):

$$\log T = 2.23 \log G - 5.58 \quad (r^2 = 0.98) \qquad (4)$$

where T is organism size (μg C) and G is the geometric mean (μm) of the mesh size retaining the organism and the next largest mesh size.

Preservation effect

It is known that fixatives can cause shrinkage or even loss of certain species (e.g. Hewes et al. 1984, Hobro and Willen 1977, Sukhanova and Ratkova 1977, Hallfors et al. 1979). However, since the information published on the subject is very controversial and there is no correction factor suitable for the wide range of organisms covered in this study, I did not attempt to make any corrections due to the effect of fixation. Therefore, my estimates of bacterio-, nano-, and microplankton biomass might be underestimated.

Biomass size-spectra construction and statistical considerations

To analyze the size-distribution of biomass, the spectra were normalized and plotted on a log-log scale as described by Platt and Denman (1977, 1978). This normalization is required since the width of the size classes varies through the size-spectra. In brief, the procedure consists in taking the variable of interest *m(s)* in the size class characterized by the weight or volume *(s)* and dividing it by the width of the size class, Δs. Thus the normalized version of the variable m is equal to :

$$M(s) = m(s) / \Delta s \qquad (5)$$

Regression analysis was carried out using least-squares (Model I) regression. For biomass size distribution data, where the independent variable (i.e. body size) is not under the control of the investigator and is subjected to error, Model II (i.e. both variables show random variation) would be more appropriate (Laws and Archie 1981). However, I have decided to use Model I because it allows the testing of differences between regression lines and also made easier the comparison with other published spectra. Furthermore, if the correlation coefficient is high ($r > 0.95$), as in most of the cases in this study, it will make very little difference which regression model is used (Laws and Archie 1981, Prothero 1986).

Prior to the comparison of regression lines the necessary assumption of homogeneity of variance was tested using Bartlett's test. After passing the Barlett's test, an F test for multiple comparisons among slopes and elevations, as described by Zar (1984), was used in comparing linear regression equations. In addition, a *t*-Test was used to test if the slopes of the normalized biomass size-spectrum were significantly different from -1 (Sokal and Rohlf 1981).

RESULTS

Although the samples are from two different seasons and regions, the normalized biomass size-spectra (NBS-spectra) from all the stations studied are very similar (see figure 1.2 and 1.3). A linear NBS-spectrum seems to be appropriate to describe the distribution of biomass by size at all stations. There is a slight trend in some of the residuals, but I believe that they are mainly associated with interfaces between the different methodologies used. The most conspicuous deviation from a linear NBS-spectrum occurs at the boundary between bacterioplankton and nanoplankton, that is to say between the techniques used in epifluorescence and inverted microscopy. It seems that the Uthermol technique does not work well with very small cells due to problems in achieving complete sedimentation of cells (e.g. Reid 1983, Hewes et al. 1984), and also to the difficulty in distinguishing between plankters and detrital particles (Paerl 1978). In addition, an unknown proportion of small fragile cells is completely destroyed by fixation procedures (e.g. Hewes et al. 1984, Hobro and Willen 1977). Therefore, it is very likely that the biomass of the three smallest size classes of the nanoplankton size range (i.e. lower limit of the size classes: 0.98, 2.76, 7.81 μm^3 respectively) is underestimated throughout this study. It is also likely that the smallest size-class in the bacterioplankton size range (i.e. 0.0042-0.048 μm^3) is underestimated due to the resolution of light microscopy and/or the efficiency of the filters used. Organisms close to 0.2 µm, which are likely to be overlooked in this study, can be very numerous. Indeed, it is known that in oligotrophic waters the concentration of viruses (size range between 0.002-0.2 µm) can be of the order of 2×10^6 virus ml^{-1} (Suttle et al. 1990). Therefore, the linearity of the NBS-spectra below 0.4 µm continues to be an open question.

An alternative explanation to account for the appearance of deviations from the linearity of the NBS-spectra, and for changes in the spectral slope within the spectra, is the occurrence of abrupt changes in the scaling coefficient α of the allometric

Figure 1.2.- Normalized biomass size-spectra in volume units from the stations in the New England Seamounts Area. Size range: 4.2×10^{-3} to 2.7×10^{11} μm^3 (from bacteria to mesozooplankton). Depth range: 0 to 400 m.

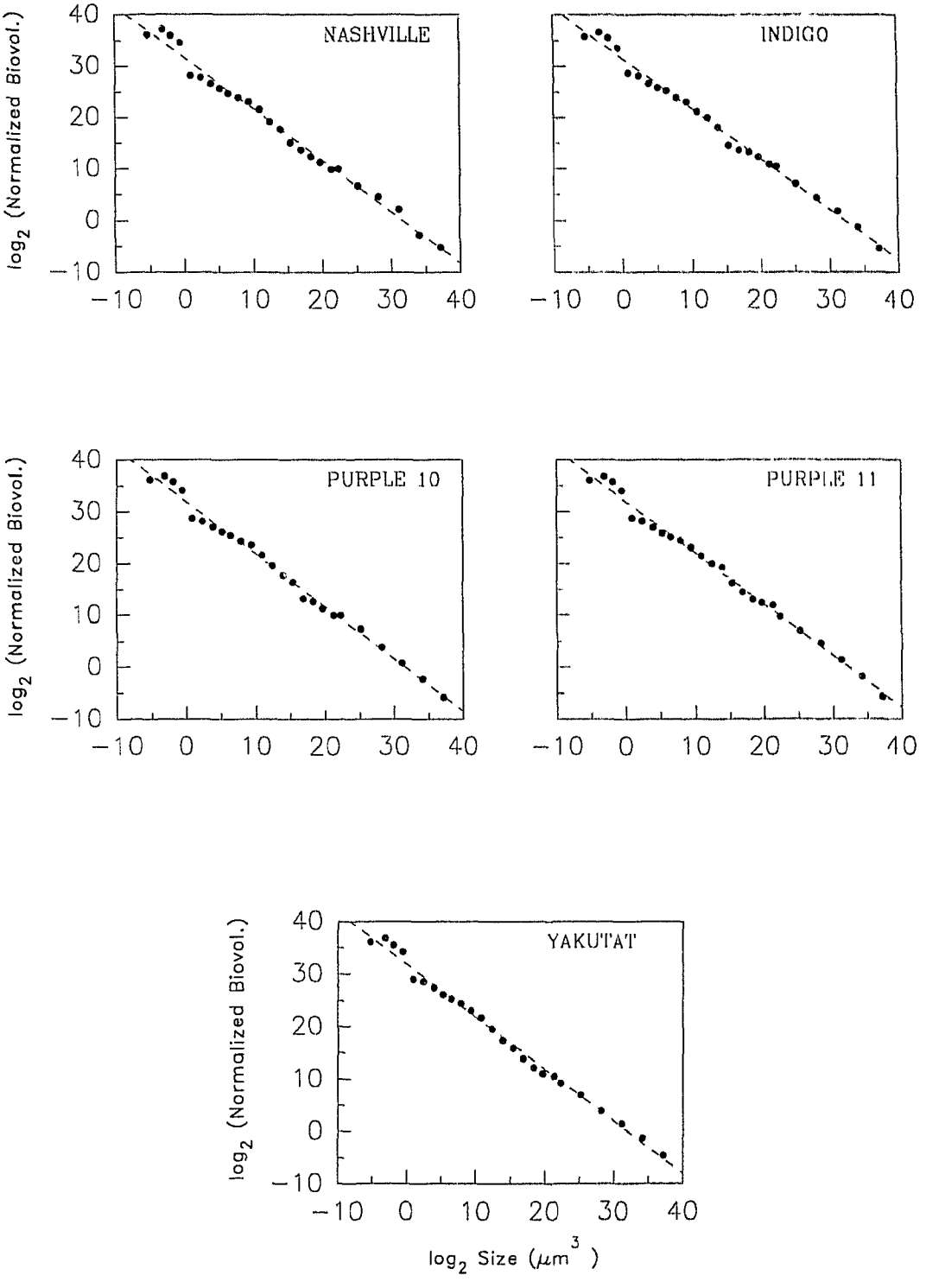

NASHVILLE
INDIGO
PURPLE 10
PURPLE 11
YAKUTAT
log2 (Normalized Biovol.)
log2 Size (μm3)
40
30
20
10
0
−10
−10
0
10
20
30
40

Figure 1.2

Figure 1.3.- Normalized biomass size-spectra in volume units from the stations in the Sargasso Sea. Size range: 4.2×10^{-3} to 2.7×10^{11} μm^3 (from bacteria to mesozooplankton). Depth range: 0 to 400 m. Note that station Sar 11 only covers from 4.2×10^{-3} to 5.0×10^{5} μm^3.

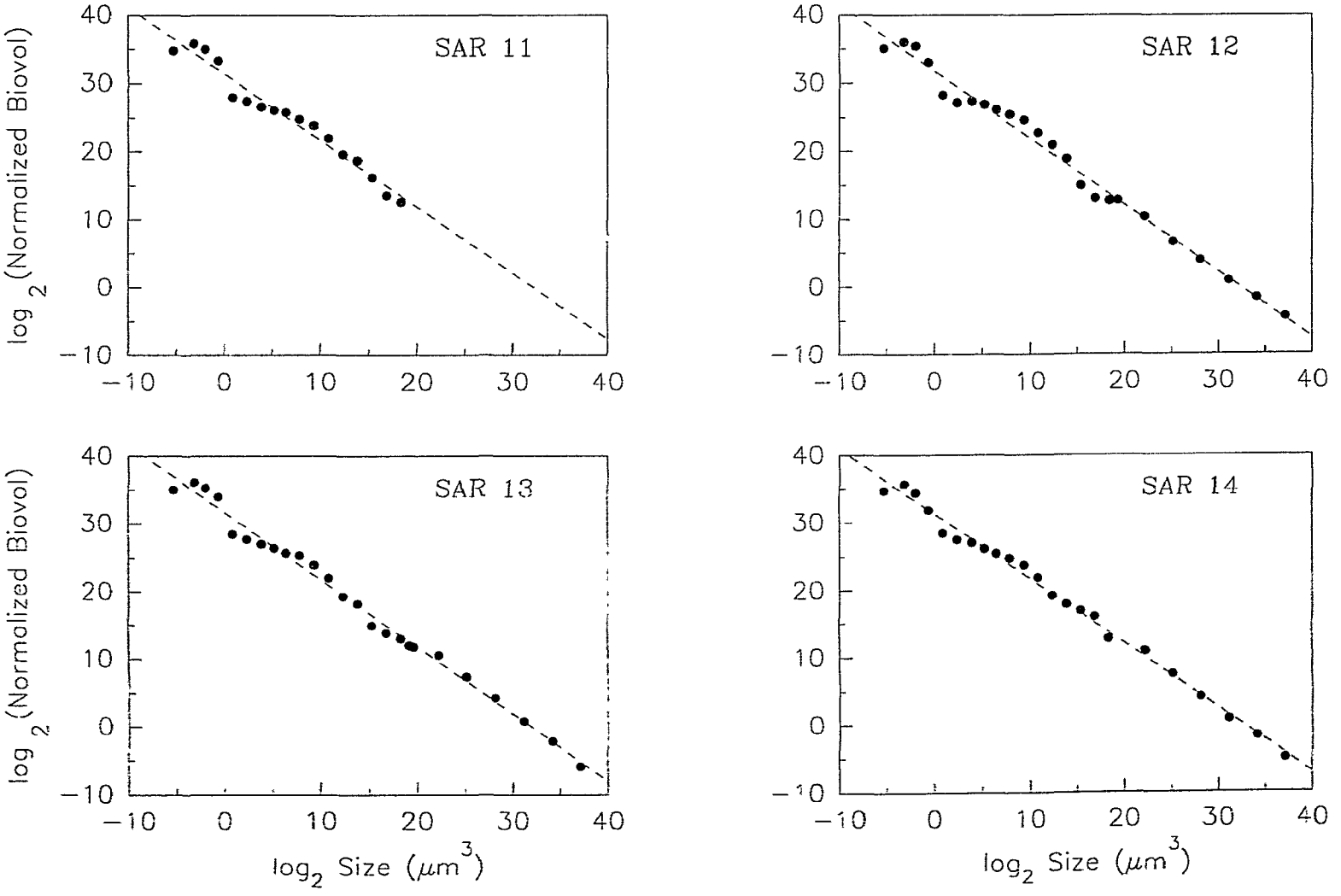

SAR 11
SAR 12
SAR 13
SAR 14
log 2 (Normalized Biovol)
log2 Size (μm3)
40
30
20
10
0
−10
−10
0
10
20
30
40

Figure 1.3

relationship between specific respiration and size (Platt 1985). It is known that unicellular, heterothermic and homothermic organisms have characteristic values of α (Fenchel 1974). Therefore, if different parts of the biomass size-spectrum were composed of mostly one type of organisms (e.g. unicellulars) abrupt changes would occur at the boundary where a new value of α takes over (Platt 1985).

In spite of the methodological problems involved in the construction of biomass spectra, the different methods used do not seem to alter the basic linearity of the NBS-spectra (Figures 1.2 and 1.3). Table 1.3 shows the regression parameters for the whole size-spectrum studied, viz. from bacteria to mesozooplankton, and covering a depth range from surface to 400 m. The slopes of the NBS-spectra among the stations in the NESA, as well as among those in the Sargasso Sea, are not significantly different ($P < 0.01$). Moreover, there are no significant differences in the slope of the NBS-spectra between the stations located in the Sargasso Sea and those located in the NESA ($P < 0.01$).

The level of primary productivity, chlorophyll and nutrients present in the stations studied (see Table 1.4) are within the range of values expected for the Sargasso Sea, as well as for the oceanic Northwest Atlantic (e.g. Menzel and Ryther 1960, Glover et al. 1985, Bidigare et al. 1990, Prezelin and Glover 1991, Irwin et al. 1991). Even though there are some differences among stations, and also between the Sargasso Sea and the NESA, in general they can be considered as typical representatives of offshore oligotrophic areas.

The bacterio- to microplankton NBS-spectra are also remarkably similar through depth (figures 1.4 and 1.5). Table 1.5 and Table 1.6 show the regression parameters of the NBS-spectra from each of the vertical strata studied. It has been suggested that the intercept of the normalized-biomass axis is an indicator of the total biomass in the system

TABLE 1.3. Regression parameters for the normalized biomass size-spectra from the New England Seamounts Area and the Sargasso Sea (Model: $\log_2 Y = \log_2 a + b \log_2 X$). Size range: 4.2×10^{-3} - 2.7×10^{11} μm^3 (from bacteria to mesozooplankton). Depth range covered 400 m. Unnormalized biovolume expressed in $\mu m^3\ m^{-3}$.

Station Name	Slope	$\log_2 a$	r^2	N	Std. Err. X Coeff.	Std. Err. Y Est.
New England Seamounts Area						
Nashville	-0.981	31.608	0.992	25	0.018	1.077
Indigo	-0.998	31.664	0.988	25	0.022	1.303
Yakutat	-0.997	31.808	0.992	25	0.017	1.033
Purple 10	-1.010	31.917	0.992	25	0.018	1.084
Purple 11	-0.991	31.937	0.993	25	0.018	1.052
Combined NESA	-0.996	31.787	0.991	125	0.008	1.090
Sargasso Sea						
Sargasso 11*	-0.976	31.443	0.965	17	0.048	1.393
Sargasso 12	-0.983	31.754	0.987	24	0.023	1.374
Sargasso 13	-0.995	31.747	0.990	25	0.020	1.183
Sargasso 14	-0.961	31.314	0.993	23	0.017	0.991
Combined Sargasso Sea	-0.979	31.563	0.989	89	0.011	1.205
All Stations this study	-0.989	31.690	0.990	214	0.007	1.137

* Note: only covers a size range from 4.2×10^{-3} to 4.99×10^5 μm^3.

TABLE 1.4. Primary productivity and other related measurements in the stations studied. The values are weighted averages from surface to 150 m. Primary production in the New England Seamounts Area and the Sargasso Sea only cover from 0 - 100 m. PP = primary production (mg C m^{-3} day^{-1}); CHL = chlorophyll concentration (mg m^{-3}); SiO_3 = silicate concentration (mg at m^{-3}); PO_4 = phosphate concentration (mg at m^{-3}); NO_3 = nitrate concentration (mg at m^{-3}); POC = particulate organic carbon (mg m^{-3}); PON = particulate organic nitrogen (mg m^{-3}). Data from Irwin et al. (1989, 1990).

Station Name	PP	CHL	$Si O_3$	PO_4	NO_3	POC	PON
New England Seamounts Area							
Nashville	1.056	0.25	0.31	0.12	1.31	92.20	9.40
Indigo	1.152	0.26	0.68	0.12	1.18	88.20	13.18
Yakutat	0.864	0.25	0.96	0.11	1.00	89.17	9.37
Purple 10	0.648	0.17	1.21	0.13	0.44	91.48	15.55
Purple 11	1.104	0.18	0.66	0.12	0.45	85.17	12.98
Sargasso Sea							
Sargasso 11	2.184	0.35	0.44	0.08	0.58	48.47	6.23
Sargasso 12	2.868	0.25	0.42	0.04	0.48	48.50	4.77
Sargasso 13	3.444	0.33	0.42	0.10	0.56	49.17	5.70
Sargasso 14	2.700	0.29	0.45	0.07	0.49	41.70	4.17

Figure 1.4.- Normalized biomass size-spectra in volume units for each σ^e the depth strata at each station in the New England Seamounts Area. Size range: 4.2×10^{-3} to 5.0×10^5 μm^3 (from bacteria to microplankton). Depth range: 0 to 400 m.

Symbols: O Mixed layer; ∇ Thermocline; □ Stratum I; Δ Stratum II.

Regression lines : —— Mixed layer; - - - - - Thermocline; ---------- Stratum I; ····· Stratum II.

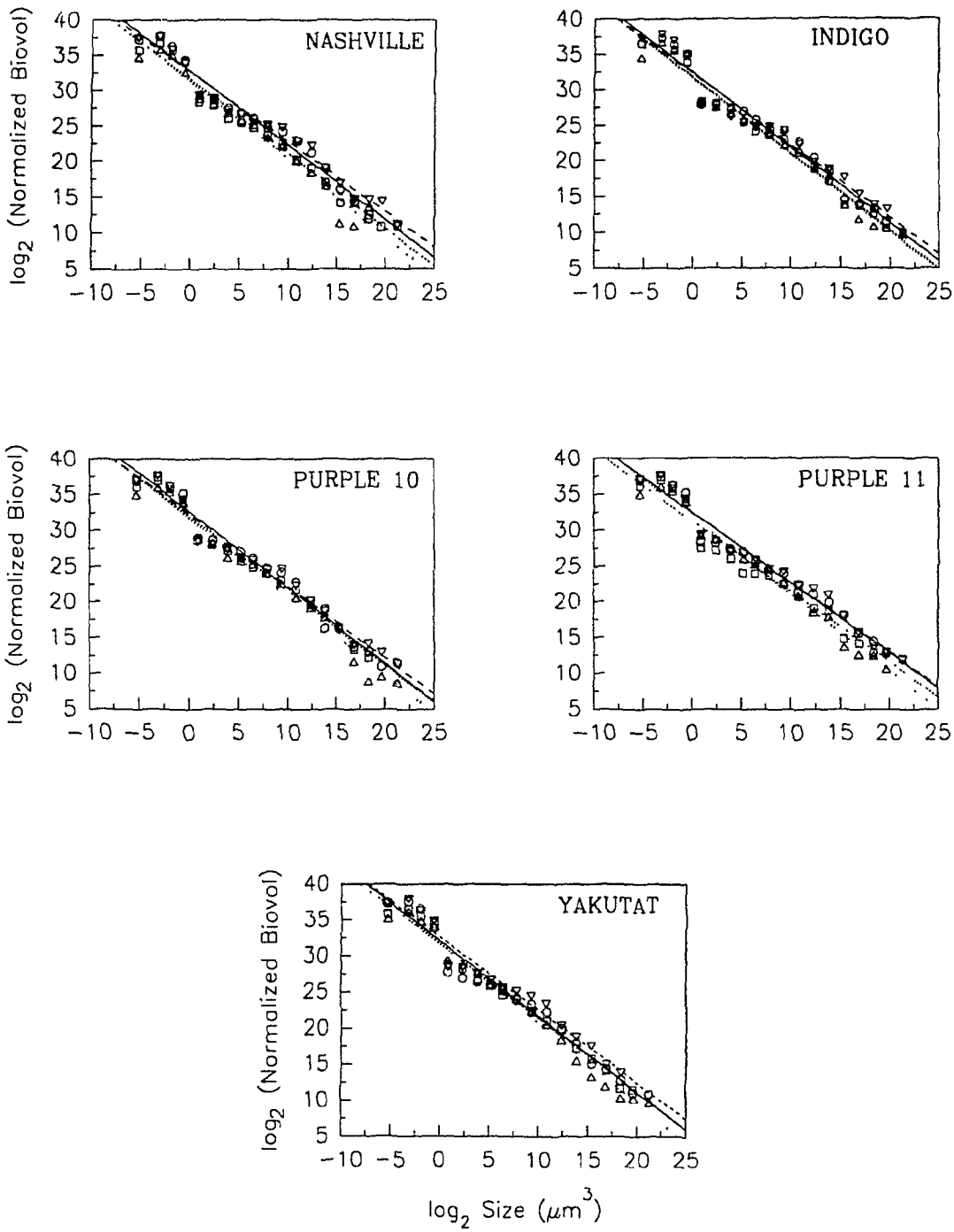

NASHVILLE
INDIGO
PURPLE 10
PURPLE 11
YAKUTAT
log2 (Normalized Biovol)
log2 Size (μm3)
40
35
30
25
20
15
10
5
−10 −5 0 5 10 15 20 25

Figure 1.4

Figure 1.5.- Normalized biomass size-spectra in volume units for each of the depth strata at each station in the Sargasso Sea Size range: 4.2×10^{-3} to 5.0×10^{5} μm^3 (from bacteria to microplankton). Depth range: 0 to 400 m.

Symbols: O Mixed layer; ∇ Thermocline; □ Stratum I; Δ Stratum II.

Regression lines : —— Mixed layer; - - - - - Thermocline; ---------- Stratum I; · ····· Stratum II.

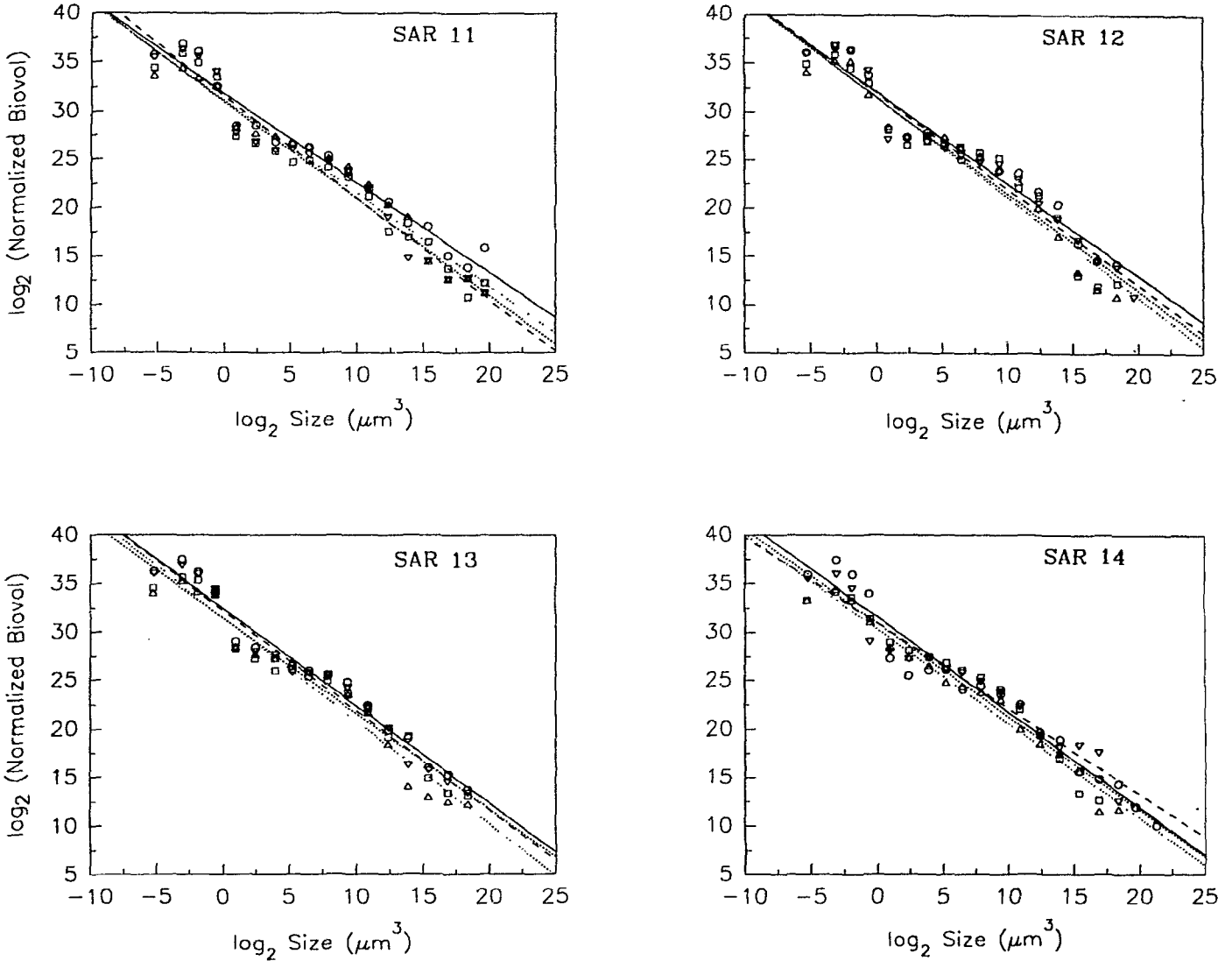

SAR 11
SAR 12
SAR 13
SAR 14
log2 (Normalized Biovol)
log2 Size (μm3)
40
35
30
25
20
15
10
5
−10
−5
0
5
10
15
20
25

Figure 1.5

TABLE 1.5. Regression parameters for the microplankton NBS-spectra in volume units from the New England Seamounts Area (Model: $\log_2 Y = \log_2 A + b \log_2 X$). Size range : 4.2×10^3 - 4.99×10^5 μm^3. ML = Mixed Layer ; TC = Thermocline ; S-I = Stratum I ; S-II = Stratum II. Unnormalized biovolume expressed in $\mu m^3\ m^{-3}$.

Station	Stratum	Slope	Intercept	r^2	N	Std. Err. Slope	Std. Err. Y Est.
Nashville	ML	-1.042	32.716	0.970	17	0.047	1.379
Nashville	TC	-0.987	32.637	0.970	17	0.045	1.307
Nashville	S-I	-1.071	31.679	0.975	17	0.044	1.290
Nashville	S-II	-1.086	31.282	0.965	17	0.053	1.543
Indigo	ML	-1.051	32.425	0.959	17	0.056	1.631
Indigo	TC	-1.011	32.316	0.947	17	0.061	1.797
Indigo	S-I	-1.084	31.839	0.975	17	0.044	1.301
Indigo	S-II	-1.101	31.713	0.960	17	0.057	1.688
Yakutat	ML	-1.059	32.210	0.960	17	0.055	1.630
Yakutat	TC	-1.011	32.701	0.965	17	0.049	1.442
Yakutat	S-I	-1.050	31.779	0.981	17	0.037	1.102
Yakutat	S-II	-1.137	31.950	0.980	17	0.042	1.225
Purple 10	ML	-1.074	32.735	0.971	17	0.048	1.398
Purple 10	TC	-1.024	32.434	0.966	17	0.049	1.435
Purple 10	S-I	-1.044	32.042	0.974	17	0.043	1.274
Purple 10	S-II	-1.087	31.709	0.964	17	0.054	1.593
Purple 11	ML	-0.974	32.481	0.965	17	0.048	1.407
Purple 11	TC	-0.972	32.561	0.967	17	0.046	1.352
Purple 11	S-I	-1.030	31.455	0.958	17	0.055	1.624
Purple 11	S-II	-1.072	31.820	0.978	17	0.042	1.222

TABLE 1.6. Regression parameters for the microplankton NBS-spectra in volume units from the Sargasso Sea (Model: $\log_2 Y = \log_2 A + b \log_2 X$). Size range : 4.20×10^{-3} - 4.99×10^{5} μm^3. ML = Mixed Layer ; TC = Thermocline ; S-I = Stratum I; S-II = Stratum II. Unnormalized biovolume expressed in $\mu m^3\ m^{-3}$.

Station	Stratum	Slope	Intercept	r^2	N	Std. Err. X Coeff.	Std. Err. Y Est.
SS11	ML	-0.959	31.911	0.971	17	0.043	1.249
SS11	TC	-1.059	31.569	0.954	17	0.060	1.754
SS11	S-I	-1.014	30.994	0.957	17	0.057	1.628
SS11	S-II	-0.946	31.086	0.953	17	0.054	1.575
SS12	ML	-0.954	32.109	0.952	17	0.055	1.613
SS12	TC	-0.971	31.901	0.948	17	0.059	1.712
SS12	S-I	-1.004	31.563	0.932	17	0.070	2.042
SS12	S-II	-1.038	31.551	0.946	17	0.064	1.875
SS13	ML	-1.003	32.425	0.969	17	0.046	1.342
SS13	TC	-1.027	32.174	0.964	17	0.051	1.497
SS13	S-I	-0.983	31.418	0.958	17	0.053	1.557
SS13	S-II	-1.061	31.442	0.953	17	0.061	1.776
SS14	ML	-0.970	31.521	0.937	17	0.065	1.891
SS14	TC	-0.884	30.937	0.952	17	0.051	1.496
SS14	S-I	-0.965	30.992	0.949	17	0.060	1.591
SS14	S-II	-0.975	30.317	0.976	17	0.040	1.160

(Sprules and Munawar 1986; Gasol et al. 1991). In fact I observed that there is a tendency towards a decrease in the intercept of the normalized-biomass axis of the spectra in deep waters. This is a consequence of the fact that more biomass is present in the mixed layer and thermocline strata than in the deep strata. The slopes of the NBS-spectra do not vary greatly with depth and there is a slight tendency to have more negative slopes with increasing depth. This similarity in the shape of the size-spectra through depth has been observed in offshore zones of tropical oceans (Sheldon 1972, Tseytlin 1981a).

An important issue in the construction of biomass size-spectra is the way in which biomass is measured and/or expressed. In this study, depending on the size range of organisms, I have measured biomass as biovolume (bacterio-, nano-, and microplankton), dry weight (micro- and zooplankton) and carbon content (micro- and zooplankton). From the standpoint of energy flux studies carbon content is probably the most appropriate measurement of biomass. Since the carbon content of many organisms is size dependent (e.g phytoplankton), the slope of the biomass spectrum would vary depending on whether volume or carbon units are used. Table 1.7 and figures 1.6 and 1.7 show the biomass NBS-spectra constructed in this study expressed in carbon units. It can be seen that the slopes of the NBS-spectra are more negative when described in carbon units than when described in volume units (Table 1.3). This variation of the slope has been noted in a microbial size-spectrum from the North Sea (Geider 1988). The slopes of the NBS-spectra in biovolume units are not significantly different from -1.0 (t-Test, $P < 0.01$), and therefore in agreement with the Linear Biomass Hypothesis (Sheldon et al. 1972). By contrast, the slopes of the NBS-spectra in carbon units are significantly different from -1.0 (t-Test, $P < 0.01$). The slopes of the NBS-spectra, in carbon units, from this study are in close agreement with Platt and Denman's model and with the findings of Platt et al. (1984) and Rodriguez and Mullin (1986) for the North Pacific Central Gyre.

TABLE 1.7. Regression parameters for the normalized biomass size-spectra in carbon units from the New England Seamounts Area and the Sargasso Sea (Model: $\log_2 Y = \log_2$ Intercept + $\log_2 X$). Size range : 1.6×10^{-9} - 1.33×10^{3} µg C ind^{-1} (from bacteria to mesozooplankton). For the calculations biomass was expressed in µg C m^{-3}. Normalized biomass (m^{-3}). Depth range covered 400 m.

Station	Slope	$\log_2$ Intercept	r^2	N	Std. Err. Slope	Std. Err. Y Est.
New England Seamount Area						
Nashville	-1.145	7.084	0.993	25	0.020	1.039
Indigo	-1.156	6.837	0.989	25	0.025	1.271
Yakutat	-1.156	7.013	0.992	25	0.021	1.085
Purple 10	-1.175	6.735	0.991	25	0.022	1.148
Purple 11	-1.151	7.253	0.992	25	0.021	1.079
Combined NESA	-1.156	6.984	0.991	125	0.0097	1.102
Sargasso Sea						
Sargasso 11*	-1.091	7.916	0.968	17	0.049	1.377
Sargasso 12	-1.125	7.497	0.985	24	0.029	1.493
Sargasso 13	-1.141	7.158	0.989	25	0.025	1.279
Sargasso 14	-1.091	7.808	0.993	23	0.019	0.970
Combined Sargasso Sea	-1.117	7.508	0.987	89	0.0136	1.266
All stations this study	-1.141	7.182	0.989	214	0.008	1.185

* Note: only covers a size range from 1.6×10^{-9} to 6.15×10^{-2} µg C ind^{-1}.

Figure 1.6.- Normalized biomass size-spectra in carbon units from the stations in the New England Seamounts Area. Size range: 1.6×10^{-9} to 1.33×10^{3} µg C ind^{-1} (from bacteria to mesozooplankton). Depth range: 0 to 400 m.

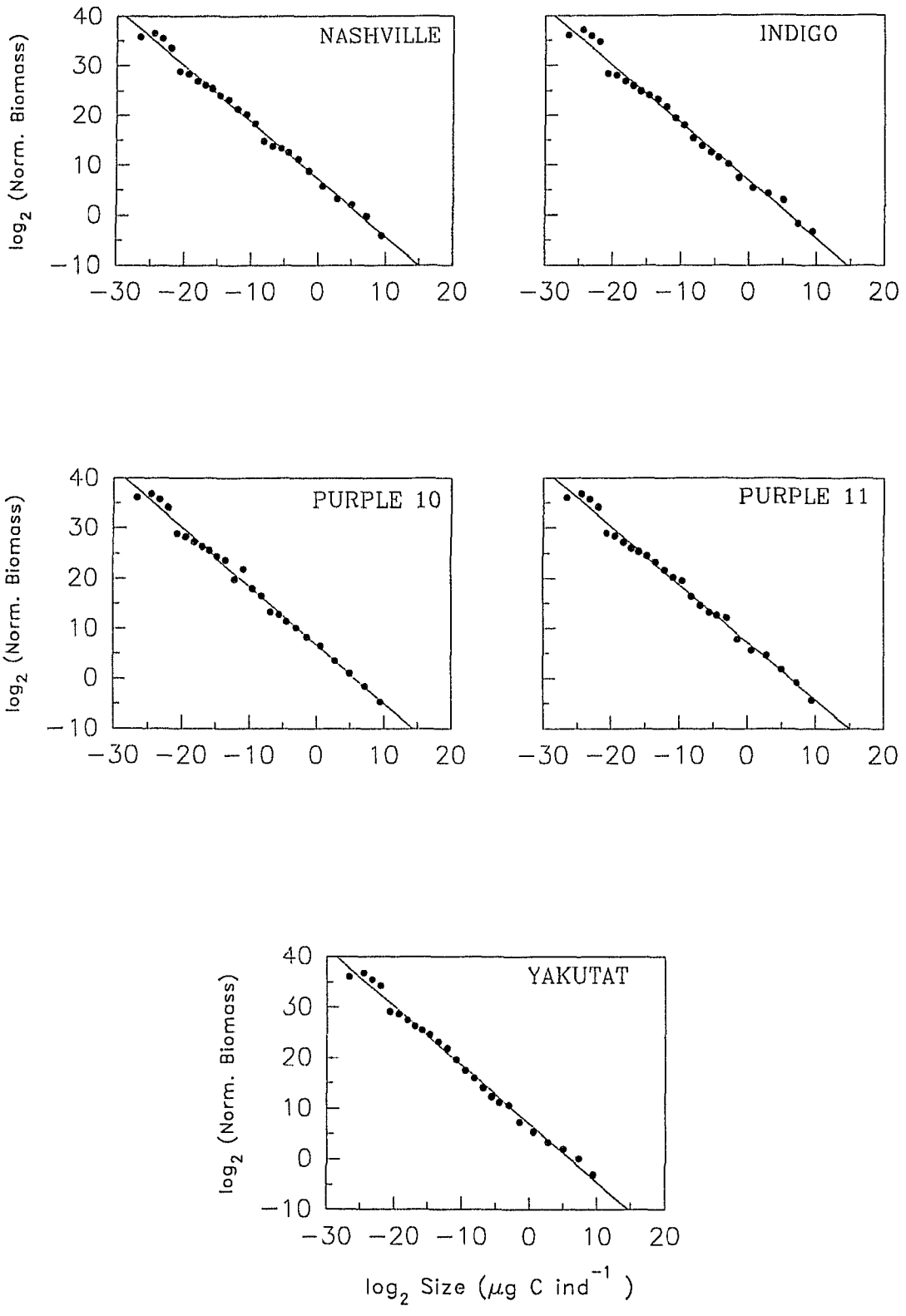

NASHVILLE
INDIGO
PURPLE 10
PURPLE 11
YAKUTAT
log2 (Norm. Biomass)
log2 Size (μg C ind-1)
40
30
20
10
0
−10
−30 −20 −10 0 10 20

Figure 1.6

Figure 1.7.- Normalized biomass size-spectra in carbon units from the stations in the Sargasso Sea. Size range: 1.6×10^{-9} to 1.33×10^{3} µg C ind^{-1} (from bacteria to mesozooplankton). Depth range: 0 to 400 m. Station Sar 11 only covers from 1.6×10^{-9} to 6.15×10^{-2} µg C ind^{-1}.

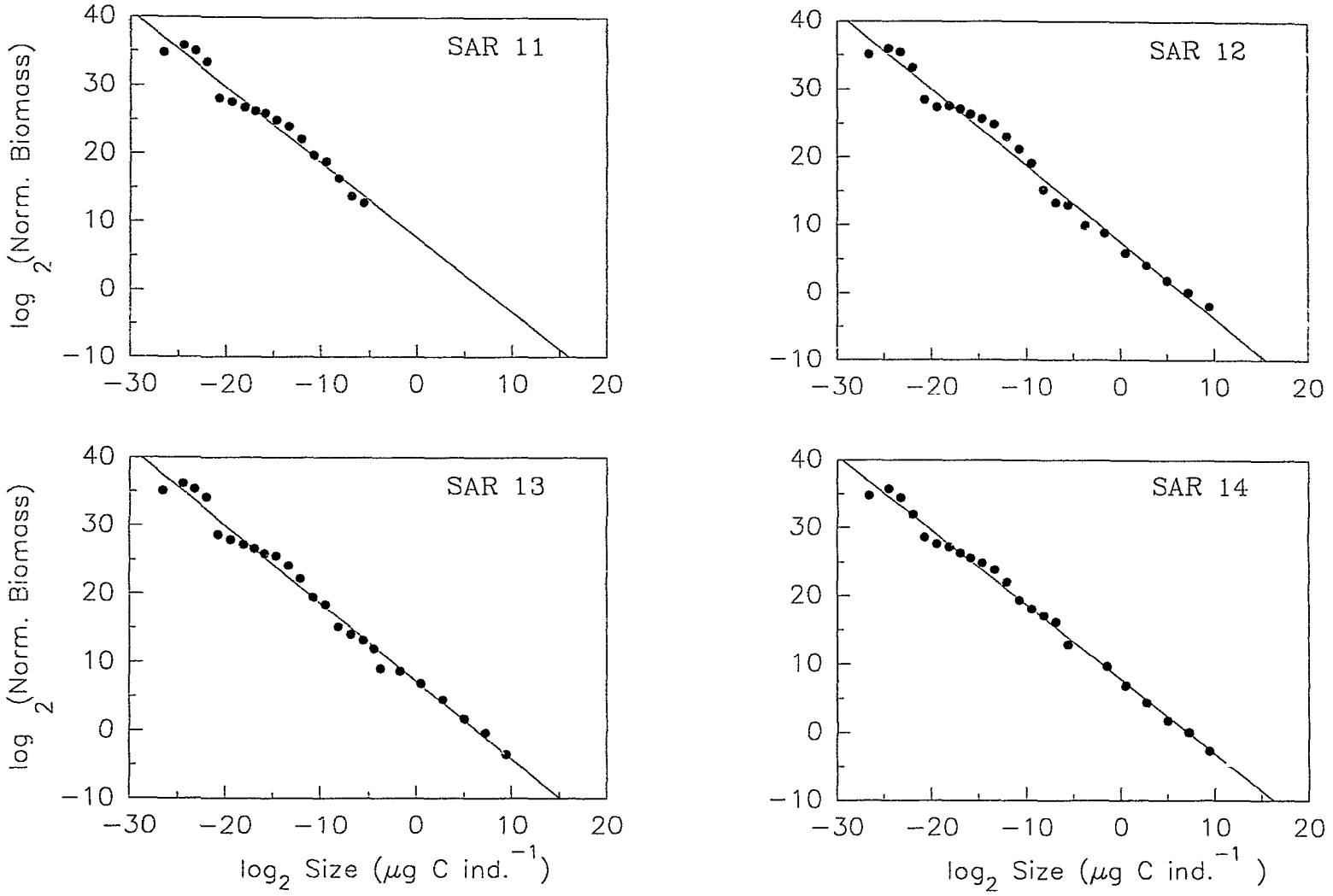

SAR 11
SAR 12
SAR 13
SAR 14
log 2 (Norm. Biomass)
log2 Size (μg C ind.-1)
40
30
20
10
0
−10
−30
−20
−10
0
10
20

Figure 1.7

DISCUSSION

My results support the hypothesis that the distribution of planktonic biomass by size in oceanic systems can be described by a linear NBS-spectra and is a conservative property of these systems. In fact, the slopes of the NBS-spectrum from the three major studies carried out in deep oceanic waters (Rodriguez and Mullin 1986a, Witek and Krajewska-Soltys 1986, this study) are very similar. The numerical values of the slopes of the NBS-spectra (as carbon) found in this study (see Table 1.6) are in agreement with the predictions of Platt and Denman's (1977, 1978) model. One of the assumptions of Platt and Denman's model is that the system must be in a steady-state, or at least, in a practical sense, the ecosystem has to be close to a steady-state. In oceanic, oligotrophic areas like the ones studied in this paper, the assumption of steady-state should not be far wrong. However, in other kinds of ecosystems, where the steady state assumption does not necessarily hold (e.g. coastal zone, lakes, lagoons etc), a linear NBS-spectrum is not always the most appropriate model (e.g. Sprules and Munawar 1986, Ahrens and Peters 1991a, Gasol et al. 1991).

The fact that the way in which biomass is expressed can alter the slope of the biomass size-spectra has important implications for the question about the numerical value of the theoretical slope for a steady state system. Sheldon et al. (1972), based on field observations, suggested the "linear biomass hypothesis" which, in simple terms, states that in the pelagic system there is roughly the same biomass at all size classes and, consequently, the slope of the unnormalized spectrum is 0, and that of the normalized spectrum is -1. Alternatively, Platt and Denman (1977, 1978) proposed their model based on the size-dependance of growth and metabolism which postulates that in the steady state the total biomass in any given size class decreases in a regular manner with increasing size. Platt and Denman (1977, 1978) suggested a slope of -0.22 for the

unnormalized biomass size-spectrum and -1.22 for the NBS-spectrum. However, since the transformation from volume to carbon units makes the slope of the spectrum approximately 0.15 units more negative (compare table 1.3 with Table 1.7), the two proposed theoretical values for the slope are very close when biomass is expressed in the same units (i.e. approx. -1.16 for the flat Sheldon spectrum converted into carbon units and -1.22 Platt and Denman's model). Both theoretical and empirical considerations limit our ability to discriminate between these two proposed slopes.

First, consider the uncertainty associated with the selection of parameters for the calculation of the slope in Platt and Denman's model. Platt and Denman (1977, 1978) used the following expression to estimate the slope of the NBS-spectrum :

$$b = -(1 - x + \alpha A + q) \qquad (6)$$

where b is the slope of the NBS-spectrum; x is the exponent for the weight dependence of turnover time ; α is a proportionality constant for the biomass-scaled turnover time ; A is a proportionality constant for biomass-scaled metabolic rate ; and q is an exponent for feeding efficiency.

The parameter α is the most critical one from an ecosystem structure point of view (Platt 1985). From Fenchel's (1974) data, Platt and Denman (1978) estimated that the product αA has a value of 0.5 for heterotherms and 0.1 for unicells. To estimate the theoretical slope they used an αA of 0.5, which for planktonic studies, where there is an important contribution from unicellular organisms to total biomass, should be considered as an upper limit. The lower limit, given by an αA of 0.1 , i.e. the hypothetical case where all organisms are unicells, would yield a slope of -0.82. Consequently Platt and Denman's model produces a range of slopes from -0.82 to -1.23 for the NBS-spectrum. This range of values is wide enough to include in it Sheldon's flat spectrum.

Second, the sensitivity of our current methods for the estimation of biomass and size makes it almost impossible to discern between two empirical slopes as close as only 0.06 units as in the case of Sheldon's -1.16 (carbon units) and Platt and Denman's -1.22.

Resolving the question about the theoretical value of the slope for a steady state system is important in establishing a point of reference that can be useful in evaluating, by comparison, other ecosystems. It is also useful, in the generation of hypotheses to explain the deviation from this idealized pattern, and in modelling fluxes in the pelagic system. However, since there is no evidence for the existence of a fixed ratio of unicells, heterotherms, and homotherms in the pelagic system, it is possible for systems in steady state to have slightly different slopes. It is important to emphasize that the cornerstone of the size-spectrum theory is the regularity and the linearity of the NBS-spectrum in close-to-steady-state systems, and not the numerical value of the slope.

My finding of a difference of -0.15 units between the slope of a NBS-spectrum expressed as carbon and one expressed as volume depends on the conversion factors used. Ideally, the carbon content of all size classes should be obtained experimentally. In practice, however, it is very difficult to do so especially at the smallest size classes. In this study I have experimentally obtained the carbon content from the size class 64 μm up to 8000 μm by direct measurement. Below this size range I have used conversion factors from the literature. Despite the fact that the use of conversion factors has an unknown level of uncertainty, I think that as an approximation they work reasonably well. However, the value - 0.15 has to be taken just as a first approximation.

Dickie et al. (1987a) analyzed the distribution of specific production by size in ecosystems. They identified two kinds of slopes in the relationship between log-specific

production and log-body size. First, a unique primary slope reflecting the size dependence of metabolism. This primary slope is uniform, low and negative (approx. -0.18). Second, a collection of secondary slopes, which represent an ecological scaling of production related to rapid changes of log annual-specific-production with log body-size within groups of organisms with similar production efficiencies. These secondary slopes are steeper than the primary slope. Boudreau et al. (1991) have pointed out that such ecological scaling would produce dome-like patterns in the biomass size-spectra. In fact, dome-like patterns have been observed in several ecosystems (e.g. Rodriguez et al. 1990, Sprules and Munawar 1986, Sprules et al. 1988, 1991). However, oligotrophic oceanic systems present NBS-spectra which can be properly described by a straight line (e.g. Rodriguez and Mullin 1986a, this study). The linearity of the NBS-spectra in oligotrophic oceanic waters would indicate the dominance of the metabolic scaling over the ecological scaling in these areas.

The complete absence or scarcity of conspicuous dome-like patterns in the biomass size-distribution in some pelagic ecosystems can also be explained in trophodynamic terms by several not mutually exclusive hypotheses. First, if the food web in a particular system is unstructured (*sensu* Isaacs 1972, 1973), and consequently *"each moiety of food material merely passes through an infinite series of steps and conversions (with associated losses), partly and successively converted into living material, and partly and successively into non-living but recoverable material"* (Isaacs 1973) the domes, if any, will tend to be minor. Second, the dome-like patterns will also be less conspicuous in systems with a more structured food web but where there is a large range of prey/predator body-size ratios (Thiebaux and Dickie 1992). Indeed, the assumption of a constant prey/predator ratio for the pelagic ecosystem is erroneous as shown by Longhurst (1989, 1991). Third, if the trophic positions (i.e. groups of organisms having a common production efficiency, Boudreau and Dickie 1992) are not sufficiently

characterized by different size ranges, the domes will not be conspicuous in the biomass size-spectra.

The theory proposed by Dickie et al. (1987a), Boudreau et al. (1991) and Boudreau and Dickie (1992) represents a significant advance in the study of the size-structure of the pelagic ecosystem. However, a degree of caution must be exercised when interpreting dome-like patterns in the biomass size-spectra. Not all observed dome-like patterns are produced by the secondary scaling described by Dickie et al. (1987a). In fact, dome-like patterns may result from mere methodological artifacts. In addition, some observed dome-like patterns in pelagic systems could be the by-product of the propagation of a peak of biomass or energy (Silvert and Platt 1978, 1980) through the size-spectrum. Waves of energy changing the shape of the biomass spectrum have been observed both in coastal (Rodriguez et al. 1987, Jimenez et al. 1989) and oceanic waters (Rodriguez and Mullin 1986b).

Finally, I would like to comment on the testing of size-spectrum theory using data collected with electronic counters, which do not discriminate between living and non-living matter. Size-spectrum theory is clearly a theory applicable only to living matter. Its theoretical bases are related to the size dependence of many ecophysiological variables and to prey-predator relationships. The whole particle size spectrum (i. e. living and non-living matter) responds to a different set of phenomena and questions which do not necessarily have ecological relevance. The contribution of non-living matter to marine size-spectra can be considerable, even in oligotrophic waters, as I have noticed in some of my samples. It is expected that in the near future improvements in techniques related to flowcytometry (e.g. Olson et al. 1985, Robertson and Button 1989, Dubelaar et al. 1989, Boucher et al. 1991) will allow the automated construction of living-matter size-spectra in the microbial size range. Until then, microscopical observation appears to be

the only reliable method for constructing biomass size-spectra. Another methodological avenue where more effort should be focused is the development of chemical methods for the estimation of biomass suitable for working with such diverse range of organisms.

Biomass size-distribution as an ecosystem property

Ecology has been criticized as not having a strong set of general theories (e.g. Cragg 1966, Lawton 1974, Peters 1976). In fact, it is even difficult to find consensus among ecologists regarding which ecological concepts are the most important and what is the meaning of some of those key concepts (e.g. McIntosh 1982, Cherret 1989). It is in this context of lack of generalizations that size-spectrum theory can play an important role. Despite the fact that the size-spectrum approach is rooted in the well-accepted concepts of the pyramids of biomass and numbers (Cousins 1985, Platt 1985) and that research in this field can be traced back to the first half of the century (e.g. Elton 1927, Ghilarov 1944) it is still far from being widely accepted. The theory has been criticized both on methodological and on conceptual grounds. The most common concerns are related to the time-space framework to be used in both designing and interpreting the results, the sensitivity of the NBS-spectrum, and the utility of this generalization for fisheries applications. Size-spectrum theory is far from being a finished product and these logical concerns must be an important aspect of future research in this field. However, the empirical and theoretical evidence obtained until now suggests that there is a basic regularity in the distribution of biomass by size in pelagic systems. This regularity is represented by the slope of the NBS-spectrum (Platt and Denman 1978) and it is also expressed in the primary slope of the relationship between log-specific production and log body mass (Dickie et al. 1987a). This basic pattern should be regarded as an ecological generalization. However, ecologists seem to be reluctant to accept generalizations. In the words of Murray (1986; Pages 149, 157) :

" We should note further that Newton's equations did not provide answers to every question we might ask about a moving object.... Why should we be more demanding of ecological and evolutionary theories? Theory serves to organize our thoughts and perceptions and aids us in designing our research to be more effective. A good theory not only elucidates the relationship between the important parameters of a system but provides clues to the causes of perturbations that introduce discrepancies between the predicted and the real world"..."As long as ecologists refuse to recognize their generalizations, principles, and laws as such, ecology will never have them".

Furthermore, the development of the size-spectrum theory has been an interesting and solid interaction between inductive and deductive thought. Elton's (1927) general principles on the organization of marine food webs as well as the "linear biomass hypothesis" of Sheldon et al. (1972) are examples of inductive thought. It is in the theoretical work of Kerr (1974) and Platt and Denman (1977, 1977) that a more deductive approach is seen. More recent theoretical work can also be included within this category (e.g. Thomann 1979, 1981; Silvert and Platt 1978, 1980, Borgmann 1982, 1983, 1987, Dickie et al. 1987a, Boudreau et al. 1991). The deductive approach is exemplified by the work of Platt and Denman (1977,1978) where, from a set of allometric principles, they predicted a particular shape and slope for an idealized biomass size-spectrum for an oceanic, close-to-steady state, system. It is not common in ecology to find theories which clearly state predictions to be falsified (*sensu* Popper 1959) by observation. A few years after Platt and Denman's theory was published, Platt et al. (1984) and Rodriguez and Mullin (1986), using data from the North Pacific Central Gyre, were able to validate it by finding a close agreement between observation and Platt and Denman's predictions. It is possible that other competitive theories may explain the regularities we observe in the biomass size-distribution or, even that the generalization of a regular biomass size-

distribution in the oceanic system might be falsified in the future, but until then we have a generalization to work with and an explanation of why it is so.

CHAPTER 2

PLANKTONIC BIOMASS SIZE-SPECTRA AND BIOMASS SIZE-DIVERSITY ACROSS THE TIDAL FRONT OF GEORGES BANK.

ABSTRACT

A study of the planktonic biomass size-distribution across the tidal front of Georges Bank was carried out in late summer. Normalized biomass size-spectra (NBS-spectra) and biomass-size diversity and evenness were used to analyze the patterns in the biomass size-distribution. The total planktonic biomass in the waters above and surrounding the bank ranges from 74 to 199 mg C m^{-3}, the highest values occurring in mixed waters with the lowest biomass in stratified waters. The same horizontal trend was detected in the distribution of bacterio- and microplankton total biomass. However, no pattern was found in the horizontal distribution of zooplankton biomass among the different zones studied. The planktonic biomass size-distribution from Georges Bank and vicinity can be described by linear NBS-spectra. The slopes of the NBS-spectra, from bacteria to zooplankton, indicate that biomass (as biovolume) slightly increases with body size. However, the bacterio- to microplankton NBS-spectra indicate that biomass in this size-range remains more or less constant with an increase in body size, but that the zooplankton biomass increases considerably with body size. These trends in the planktonic biomass size-distribution seem to be a distinct characteristic of Georges Bank in comparison with the oligotrophic ocean. Biomass-size diversity and evenness are highest in mixed waters, decreasing in frontal waters and presenting the lowest values in stratified waters. Biomass-size diversity and evenness indices are useful complementary tools in biomass size-distribution studies.

INTRODUCTION

Georges Bank presents one of the highest rates of fish production of the world (Grosslein et al. 1980, Cohen and Grosslein 1987). Although the complete dynamics and factors involved in maintaining this high productivity are not fully understood, it is known that the tidal frontal system surrounding the bank plays a major role (Loder and Platt 1985). The frontal system presents characteristics of both a tidal mixing front (e. g. Simpson et al. 1978) and a stratified shelf break with strong tidal advection (Pingree et al. 1983). The frontal zone clearly separates the mixed waters (central Georges Bank) from the stratified waters from spring to fall. During winter, however, Georges Bank and its surrounding areas are vertically well-mixed, at least up to 100 m depth, and the exchange between Georges Bank and the surrounding areas is large (Flagg 1987). During the spring to fall months the frontal system helps to maintain the flux of nutrients (Loder and Platt 1985, Horne et al. 1989), which seems to be a key element in maintaining phytoplankton and zooplankton production as well as for the survival of the early life stages of fish (Loder et al. 1992).

From a biological point of view, several horizontal patterns have been found in Georges Bank. Primary production and phytoplankton biomass are high in both mixed and frontal areas and decline with increasing stratification across the front (Cohen et al. 1982, Flagg et al. 1982, O'Reilly and Busch 1984, Ulloa 1986, O'Reilly et al. 1987, Horne et al. 1989). Bacterial density (Hobbie et al. 1987) and total zooplankton biomass (Kane and Green 1990) are also highest in shallowest water and decrease as water deepens. However, in relation to other biological variables, the front seems to act as a barrier rather than just an intermediate zone between the well mixed and stratified waters. The zooplankton species composition across the Bank is clearly influenced by the frontal system (Perry et al. 1992) and several zooplankton species seem to be retained on the

Bank (Clarke et al. 1943, Davies 1984, Lough and Trites 1988). It has also been suggested that the distribution of zooplankton across the frontal zone presents size-dependent differences related to the physical processes (Perry et al. 1992, Loder et al. 1992). Furthermore, it seems that the size-distribution of primary producers is dissimilar between shallow and deep waters on Georges Bank (O'Reilly et al. 1987).

The highly dynamical physical and biological characteristics of Georges Bank, as well as the horizontal patterns described above, make this ecosystem an interesting study case from a biomass size-distribution point of view. The biomass size-distribution of oceanic ecosystems seems to be a remarkably stable property of the pelagic ecosystem (Platt and Denman 1978, Platt et al. 1984, Rodriguez and Mullin 1986 a, b, see also Chapter 1). In oligotrophic oceanic areas, normalized-biomass decreases as a power function of body size. However in coastal areas and in lakes the biomass size-distribution of the planktonic community varies considerably presenting patterns which differ from the power function observed between normalized-biomass and body-size in oceanic areas (e.g. Sprules and Munawar 1986, Jimenez et al 1989, Rodriguez et al. 1987, 1990, Ahrens and Peters 1991a, Sprules et al. 1991).

In this paper I study the biomass size-distribution of the planktonic community, from bacteria to zooplankton, across the tidal front in Georges Bank. The main objectives of this study are, first, to test if the biomass size-distribution in this highly productive and dynamic system can be described by a linear normalized biomass size-spectrum (*sensu* Platt and Denman 1977,1978), and, second, to determine if there are distinct characteristics in the biomass size-distribution of the planktonic community across the front in Georges Bank.

MATERIALS AND METHODS

The study was carried out onboard the CSS Hudson during 15-31 August 1988 across the tidal front on the North East side of Georges Bank. The location of the sampling stations is shown in Figure 2.1 and described in Table 2.1.

Sampling

Sampling depths for the bacterio-, nano- and microplankton were chosen according to the heterogeneity of the fluorescence and density (σ_t) profiles obtained usually less than an hour before sampling. The fluorescence and density profiles were obtained with an *in situ* fluorometer (Aquatracka, Chelsea Instruments, U. K.) and with a CTD respectively. When possible, the sampling covered the whole water column (see Table 2.1). At deep stations samples were taken up to 300 meters. The water samples were taken with 30 liters Niskin oceanographic bottles.

The zooplankton collections were made with a 72-cm diameter ring nets (mesh size 64 μm; vertical tows), and with Bongo nets specially designed (Bedford Institute of Oceanography) for vertical towing (61-cm diameter, mesh size 253 μm). Oblique tows were carried out with regular Bongo nets (61-cm diameter, mesh size 253 μm). All nets were equipped with flowmeters.

Bacterioplankton biomass

The samples were fixed with pre-filtered formaldehyde (0.2 μm pore size Nucleopore filters) to a final concentration of 2%, and then stored at 4°C in the dark until further analysis. In the laboratory, cells numbers were estimated using the DAPI epifluorescence direct counting technique (Porter and Feig 1980) after collection on 0.2 μm pore size black Nucleopore filters (vacuum pressure < 100 mm Hg). The counting

Figure 2.1.- Locations of sampling stations.

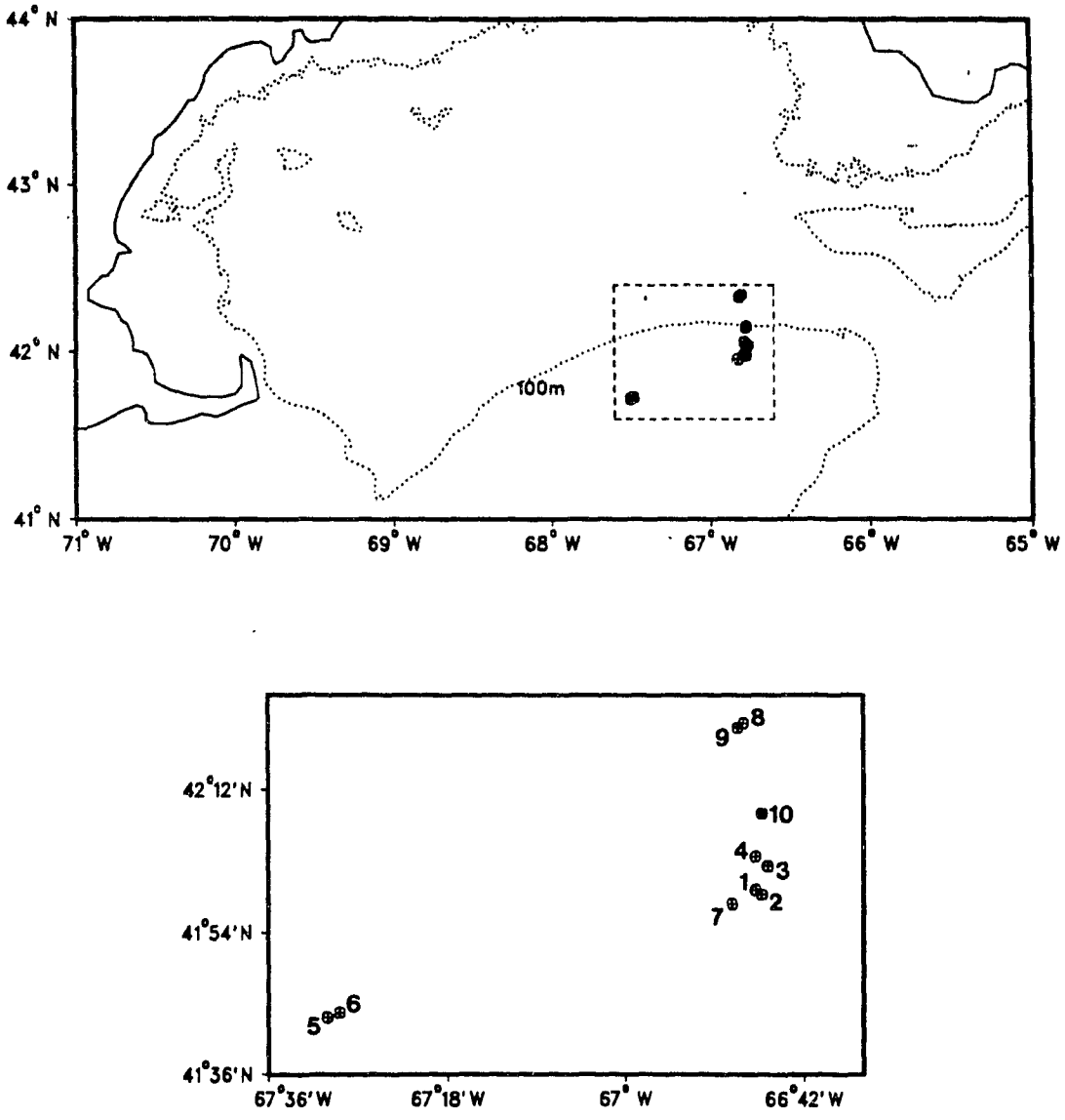

44° N
43° N
42° N
41° N
71° W
70° W
69° W
68° W
67° W
66° W
65° W
100m
42°12'N
41°54'N
41°36'N
67°36'W
67°18'W
67° W
66°42'W
1
2
3
4
5
6
7
8
9
10

Figure 2.1

TABLE 2.1.- Location of the stations sampled.

Station Name	Location Lat (N)	Location Long (W)	Date	Day/Night	Sampling Coverage (m)	Number of Depths Sampled*
GB1	41° 59.37'	66° 46.90'	17/08/88	N	0 - 60	8
GB2	41° 58.80'	66° 46.40'	18/08/88	N	0 - 60	8
GB3	42° 02.60'	66° 45.70'	20/08/88	N	0 - 60	8
GB4	42° 04.10'	66° 46.50'	21/08/88	N	0 - 60	8
GB5	41° 43.23'	67° 29.86'	22/08/88	N	0 - 37	6
GB6	41° 43.72'	67° 28.98'	23/08/88	N	0 - 40	6
GB7	41° 53.72'	66° 49.12'	26/08/88	N	0 - 51	7
GB8	42° 20.24'	66° 48.41'	27/08/88	N	0 - 320	12
GB9	42° 19.87'	66° 48.59'	28/08/88	N	0 - 300	12
GB10	42° 08.80'	66° 46.40'	29/08/88	N	0 - 80	6

* Bacterio-, nano and microplankton sampling. Zooplankton sampling was carried with integrated tows of the vertical column.

was performed with a Leitz Orthoplan epifluorescence microscope under 1000X magnification. Three slides per depth, with five to ten fields per slide, were counted using an ocular grid reticule. For the size determination, photographs (Kodak Ektachrome, P800/1600, slides) of randomly selected fields were taken. The slides were projected to a final magnification of 1500X. The enlarged images were captured with a video camera, and then digitized and processed with an image analyzer (see below). The number of cells measured varied with picture quality ranging from 28 to 246, but with an average of 142 bacteria measured at each depth (approx. 900 to 1650 bacteria measured per profile). Cell volume was calculated using the following formula:

$$V = (\pi / 4) W^2 (L - W / 3) \qquad (1)$$

where L is the length of major axis, and W is the length of minor axis. Bacterial carbon biomass was calculated using a conversion factor of 0.380 g C cm^{-3} (Lee and Furham 1987).

After calculating the total bacterial biomass in each depth sampled, the data were integrated into strata according to the same criteria used for the nano- and microplankton biomass as described below (see also Table 2.2).

Nano- and Microplankton Biomass

Immediately after sampling, an aliquot (500 ml) was taken to quantify microplankton sufficiently small to pass a 35 µm mesh netting. In addition, 20 liters were passed through a 35 µm mesh using reverse filtration to concentrate the microplankters larger than 35 µm. The samples were fixed with formaldehyde-seawater solution to a final concentration of 2% and buffered with sodium borate.

TABLE 2.2. Vertical strata used in the construction of the bacterio- to microplankton biomass size-spectra.

Station		Depth range (m)			
Name	$\Delta\sigma_t$	Mixed Layer	Thermocline	Stratum I	Stratum II
GB1	1.925	0 - 11	11 - 25	25 - 60	------
GB2	1.084	0 - 12	12 - 18	18 - 60	------
GB3	2.700	0 - 16	16 - 32	32 - 60	------
GB4	1.586	0 - 12	12 - 24	24 - 60	------
GB5	0.001	0 - 35	------	------	------
GB6	0.001	0 - 40	------	------	------
GB7	0.537	0 - 51	------	------	------
GB8	2.177	0 - 20	20 - 72	72 - 190	190 - 320
GB9	2.555	0 - 27	27 - 65	65 - 145	145 - 300
GB10	2.928	0 - 18	18 - 34	34 - 80	------

To reduce the time spent in sample analysis, composite samples were made. The water column was divided in the following four strata: Mixed layer, Thermocline, Stratum I, and Stratum II. The division of the water column was based on the CTD data. Below the thermocline the water column was divided in half, into Strata I and II. Table 2.2 shows the depths of each of the strata at every station. The composite samples were made by mixing measured quantities of each of the samples according to the depth coverage of each of them.

Cells counts and sizing were made on settled 100 or 50 ml subsamples of each integrated sample (concentrated and unconcentrated). The subsamples were allowed to sediment for 48-72 hours (Uthermol technique, Lund et al. 1958). To enhance image contrast and to facilitate the separation between living and non-living matter, Bengal Rose stain was added to the samples in the settling chambers. Subsequently, the organisms were observed with an inverted microscope using 125X, 200X, 500X and 1250X magnifications. The sizing and counting of organisms was carried out using image analysis. An ocular micrometer and a Newporton Graticule (May 1965) were also used for direct sizing and counting. Approximately 200 organisms were sized at each magnification. The volume of the organisms was estimated assuming basic geometrical shapes and also guided by the recommendations of the Baltic Marine Environment Protection Commission (1983). The conversion from volume to carbon units was carried out using the equations of Strathmann (1967).

Image Analysis

The sizing of organisms was carried out using an image analyzer, similar to that described by Campana (1987), with the following components modifications: (a) Newvicon Video Camera and (b) Oculus 300 (Coreco Inc.) framegrabber video digitizer board.

Zooplankton biomass

The catch from one side of the bongo net was fixed with formaldehyde (final concentration 4% formaldehyde-seawater solution) for taxonomical analysis. The catch from the other side of the Bongo was immediately size-fractionated to estimate zooplankton biomass. The sieves used had the following dimensions : 8000, 4000, 2000, 1000, 500, 250, 125, and 64 μm mesh.

Zooplankton size-fractions were then filtered onto pre-weighed, pre-combusted (450 °C) glass fiber filters (Reeve Angel 934 AH). The zooplankters were quickly rinsed with distilled water. The filters were then dried for 36 hrs in an oven at 60°C and kept in desiccators until further analysis. The size-fractions were weighed on an electronic balance in the laboratory. The carbon content of the zooplankton size-fractions was determined using a Perkin Elmer 240-B CHN Elemental Analyzer.

To convert zooplankton biomass to biovolume the following equation from Wiebe (1988) was used:

$$\log F = -1.842 + 0.865 \log D \qquad (3)$$

where F is displacement volume ($cm^3\ m^{-3}$), and D is dry weight ($mg\ m^{-3}$). To change the scale from length to carbon the equation of Rodriguez and Mullin (1986b) was used.

Definition of frontal, mixed and stratified waters.

Due to the physical characteristics of Georges Bank, the geographical location of the stations or the bathymetry of the bank, by themselves, are not sufficient to classify the different kinds of waters (i.e. mixed, frontal and stratified waters) present in the bank and

vicinity. Therefore, I have used the criteria suggested by Horne et al. (1989) for Georges Bank. Frontal waters are defined as those where the vertical density difference ($\Delta\sigma_t$) between surface and 50 meters depth is between 0.2 and 1.5 σ_t units. Mixed waters and stratified waters correspond to those where the $\Delta\sigma_t$ between surface and 50 meters is less than 0.2 and higher than 1.5 σ_t units respectively.

Biomass size-spectra construction and statistical considerations

The biomass size spectra were normalized and plotted on a log-log (base 2) scale as described by Platt and Denman (1977, 1978). This normalization is required since the size range spanned by each of the size-classes varies through the size-spectra. Therefore, the biomass *m(s)* in the size class characterized by the weight or volume *(s)* is divided by the width of the size class, Δs. Thus the normalized version of the variable *m* is equal to :

$$M(s) = m(s) / \Delta s \qquad (4)$$

Regression analysis was carried out using least-squares (Model I) regression. For the data of the current study, where the independent variable is not under the control of the investigator and is subject to error, Model II (i.e. both variables show random variation) would be more appropriate (Laws and Archie 1981). However, Model I was chosen because it permits the testing of differences between regression lines and also made easier the comparison with other published spectra. Furthermore, if the correlation coefficient is high ($r > 0.95$), as in most of the cases in this study, it will make very little difference which regression model is used (Laws and Archie 1981, Prothero 1986).

Prior to the comparison of regression lines the necessary assumption of homogeneity of variance was tested using Bartlett's test. After passing Barlett's test, an *F*

test for multiple comparisons among slopes and elevations, as described by Zar (1984), was used in comparing linear regression equations. In addition, a *t*-Test was used to test if the slopes of the normalized biomass size-spectrum were significantly different from -1 (Sokal and Rohlf 1981).

Biomass-size diversity and evenness indices

Since the use of biomass-size diversity indices for analyzing biomass size-distribution data is not widespread, I will recall some fundamental concepts regarding species diversity indices emphasizing its relevance for biomass-size diversity studies.

The concept of species diversity is essentially composed of two elements which are species richness and equitability or evenness (Peet 1974). Species richness is the number of species in the sample. Evenness is a description of the shape of the histogram which is maximum when all species are equal and the greater the disparities among the different species abundances, the smaller the evenness (Pielou 1969). Therefore, different species diversity indices can be classified as Species-richness indices, Heterogeneity indices and Equitability indices depending on which of the two components of diversity is emphasized (Peet 1974). Since in the study of biomass-size diversity the organisms are lumped into an arbitrary number of size-classes the concept of "size-class richness" is irrelevant. However, for comparative purposes the number of size-classes used to aggregate the organisms is still an important element. The heterogeneity indices take into account both the distribution of individuals among the species (evenness) and the number of species present in the sample (Peet 1974, Pielou 1969).

The use of diversity indices in analyzing marine particle size-spectrum was first introduced by Parsons (1969). In the current study, the following species diversity and evenness indices were modified to make them suitable to biomass size-distribution

studies: Shannon-Wiener's index of diversity (Margalef 1957), Simpson's index of diversity (Simpson 1949), Pielou's index of evenness (Pielou 1966b, 1967) and Heip's index of evenness (Heip 1974, Heip and Engels 1974). Simpson's and Shannon-Wiener's Indices are heterogeneity indices. Simpson's Index measures the probability that two randomly chosen individuals will be of the same species (Peet 1974). This index is considered to be a dominance index since it measures how individuals in a sample are concentrated into a few species (Whittaker 1965, Colinvaux 1986). Simpson's index varies inversely with diversity (Peet 1974). The equitability or evenness indices, like those of Pielou *(J)* and Heip *(E)* indices, are independent of species richness and measure the relative evenness of the numerical importance of a species in a sample. Basically, these evenness indices compare the measured diversity of the community with the maximum theoretical diversity value it can achieve.

Table 2.3 shows the biomass-size diversity and evenness indices and their analogous species based indices. The biomass-size diversity and evenness indices are calculated using the original biomass (biovolume) data (*viz.* without logarithmic transformations).

Following the same line of reasoning of Pielou (1966a), biomass-size diversity can be defined as the amount of uncertainty which exists regarding the size-class to which a unit of biomass selected at random belongs. The greater the uncertainty, the greater is the diversity (Pielou 1966a). The biomass-size diversity index γ (analogous to Shannon's species diversity index) will have its minimum value ($\gamma = 0$) when all biomass in the sample belongs to only one size-class. The γ index will be maximum when the biomass is equally distributed among the size classes in the sample. In this particular case the γ index will be equal to the natural logarithm of the number of size classes.

TABLE 2.3. Biomass-size diversity and evenness indices used in the analysis of the biomass size-distribution in each station.

Index	Formula	Reference	BSD Index
Shannon-Wiener	$H' = - \Sigma\ (ni/N) \ln (ni/N)$	(Margalef 1957)	$\gamma = - \Sigma\ (bi/B) \ln (bi/B)$
Simpson	$\lambda = \Sigma\ [(ni\ (ni-1)] / [N(N-1)]$	(Simpson 1949)	$\Omega = \Sigma\ [(bi(bi-1)] / [B(B-1)]$
Pielou	$J' = H' / \ln S$	(Pielou 1966, 1967)	$\varphi = \gamma / \ln C$
Heip	$E = (e^{H'} - 1) / (S - 1)$	(Heip 1974)	$\xi = (e^{\gamma} - 1) / (C - 1)$

Symbols: BSD = Biomass size-distribution, *ni* = number of individuals of the *i*th species, *N* = number of individuals in the sample, *S* = number of species in the sample, *bi* = biomass of the *i*th class, *B* = total biomass in the sample, *C* = number of size classes.

On the other hand, the biomass-diversity index Ω (analogous to Simpson's species diversity index) behaves in such a way that the biomass diversity of the sample is lower when the probability that two units of biomass randomly chosen belong to the same size-class is higher. Biomass size-diversity is minimal when Ω is maximal and consequently equal 1.

The species evenness indices are dependent on species number and to calculate the index it is necessary to known the total number of species in the community, information that in practice is almost impossible to obtain (Peet 1974). Since the total number of size classes is known, the measurement of biomass-size evenness has a major advantage in comparisons to its species evenness counterpart.

It is important to note that all biomass-size diversity and biomass-size evenness indices used in this study are dimensionless, and consequently, independent of the biomass units used.

RESULTS

The total biomass concentration of the planktonic community (from bacteria to mesozooplankton) in Georges Bank and vicinity ranged from 74 to 199 mg C m^{-3}. Highest biomass concentrations occur in mixed waters (central Bank). Biomass concentrations decrease through the front and reach their lowest values in stratified waters (see Figure 2.2). However, biomass concentration was highly variable in stratified waters with some stations (Stations GB9 and GB1) presenting biomass levels equivalent to those stations located at the front. It is interesting to note that when total biomass is expressed as biovolume the horizontal pattern described is less conspicuous. It seems that the use of biovolume and its conversion factors overestimate the contribution of zooplankton to the total biomass.

The planktonic biomass size-distribution in Georges Bank can be described by linear normalized-biomass size-spectra (NBS-spectra). The bacterio- to microplankton NBS-spectra by depth in each of the stations studied are shown in Figures 2.3 and 2.4. The parameters of the NBS-spectra are described in Tables 2.4 and 2.5. It is clear from Figures 2.3 and 2.4 that the size-classes 0.98, 2.76 and 7.81 μm^3 (lower limit), the smallest size classes determined by the Uthermol technique, present a biomass level much lower than the expected from the NBS-spectrum slope. As discussed in Chapter 1, these size-classes are likely to be underestimated. Incomplete sedimentation of cells, uncertainty in resolving between detrital particles and plankters, and losses due to fixation procedures are among the causes of this underestimation (for a discussion see Chapter 1). Therefore, the parameters of the NBS-spectra omitting these size-classes are also given throughout this study (for the parameters of the bacterio- to microplankton NBS-spectra see Table 2.5).

Figure 2.2.- Total biomass (from bacteria to zooplankton) across the $\Delta\sigma_t$ gradient in Georges Bank.

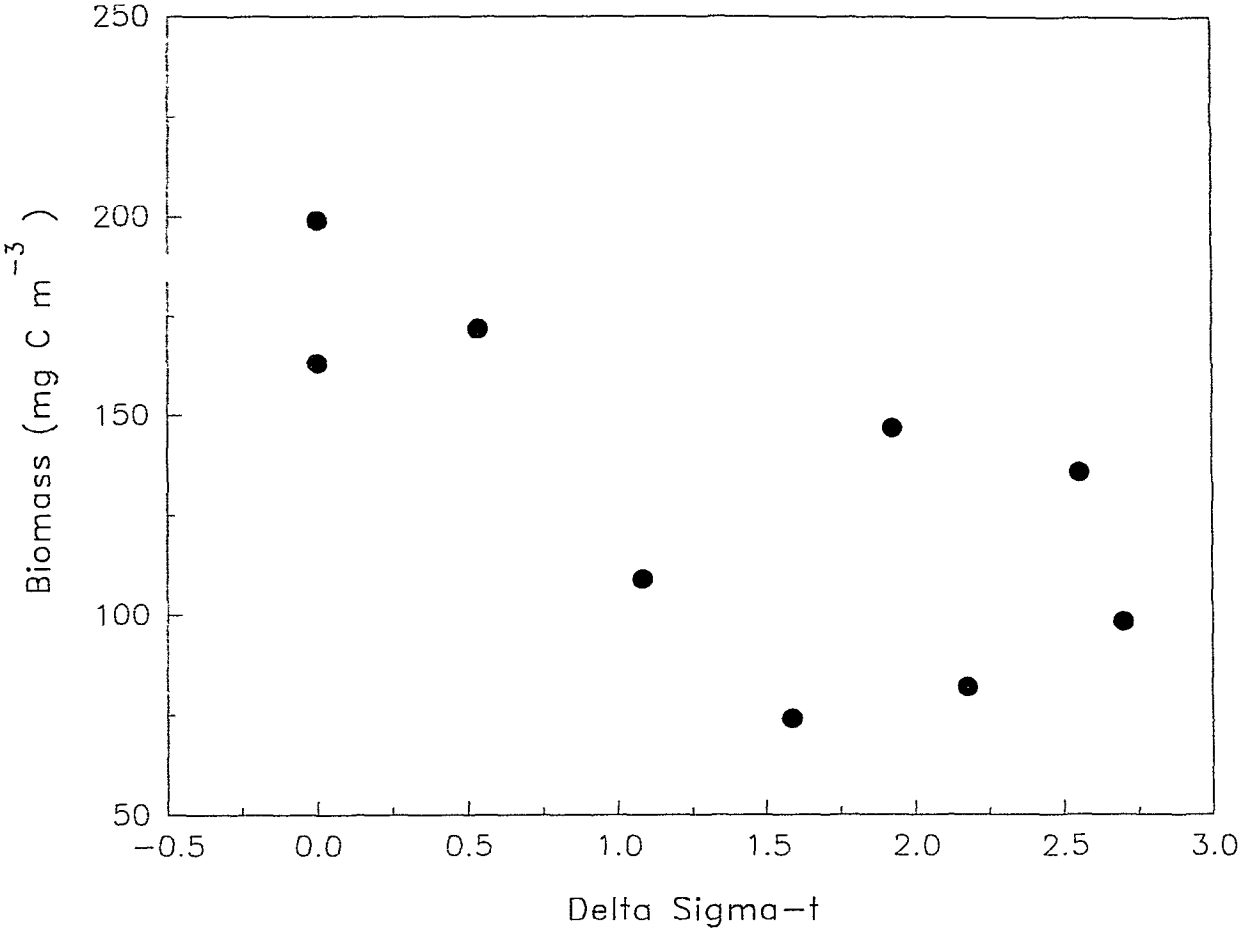

250
200
150
100
50
Biomass (mg C m^{-3})
−0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Delta Sigma−t

Figure 2.2

Figure 2.3.- Normalized biomass size-spectra in volume units for each of the depth strata. Stations are located in stratified waters (S) in Georges Bank and vicinity. Size range: 4.2×10^{-3} to 5.0×10^{5} μm^3 (from bacteria to microplankton). Symbols: O Mixed layer; ∇ Thermocline; □ Stratum I; Δ Stratum II.

Regression lines : - - - - Mixed layer; ····· Thermocline; -- -- -- Stratum I; ------ Stratum II.

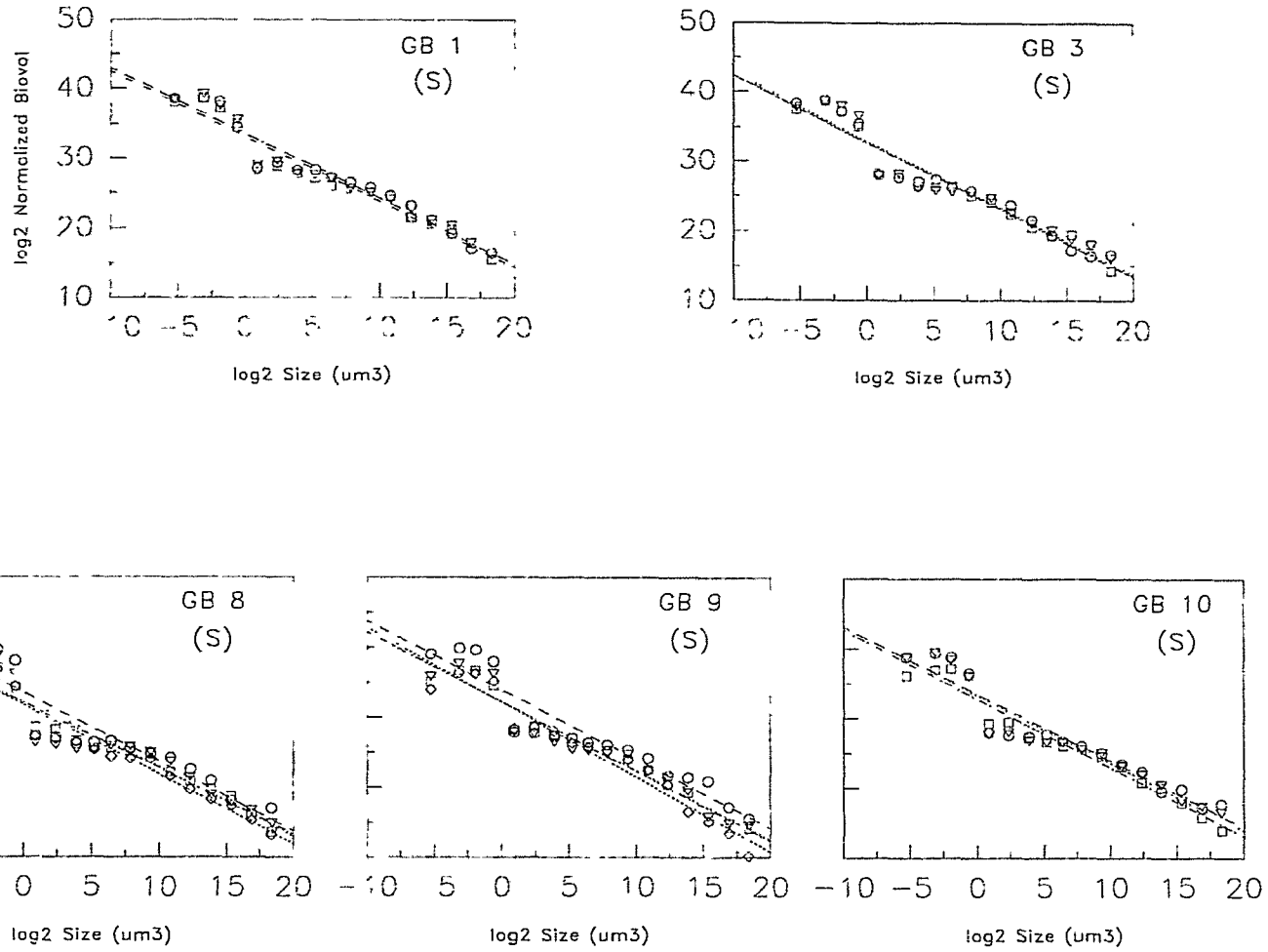

GB 1
(S)
GB 3
(S)
GB 8
(S)
GB 9
(S)
GB 10
(S)
log2 Normalized Biovol
log2 Size (um3)
50
40
30
20
10
−10 −5 0 5 10 15 20

Figure 2.3

Figure 2.4.- Normalized biomass size-spectra in volume units for each of the depth strata at station located in frontal (F) and mixed (M) in Georges Bank and vicinity. Size range: 4.2×10^{-3} to 5.0×10^{5} μm^3 (from bacteria to microplankton). Symbols: O Mixed layer; ∇ Thermocline; □ Stratum I; Δ Stratum II.

Regression lines : - · · - - Mixed layer; ····· Thermocline; -- -- -- Stratum I; ------ Stratum II.

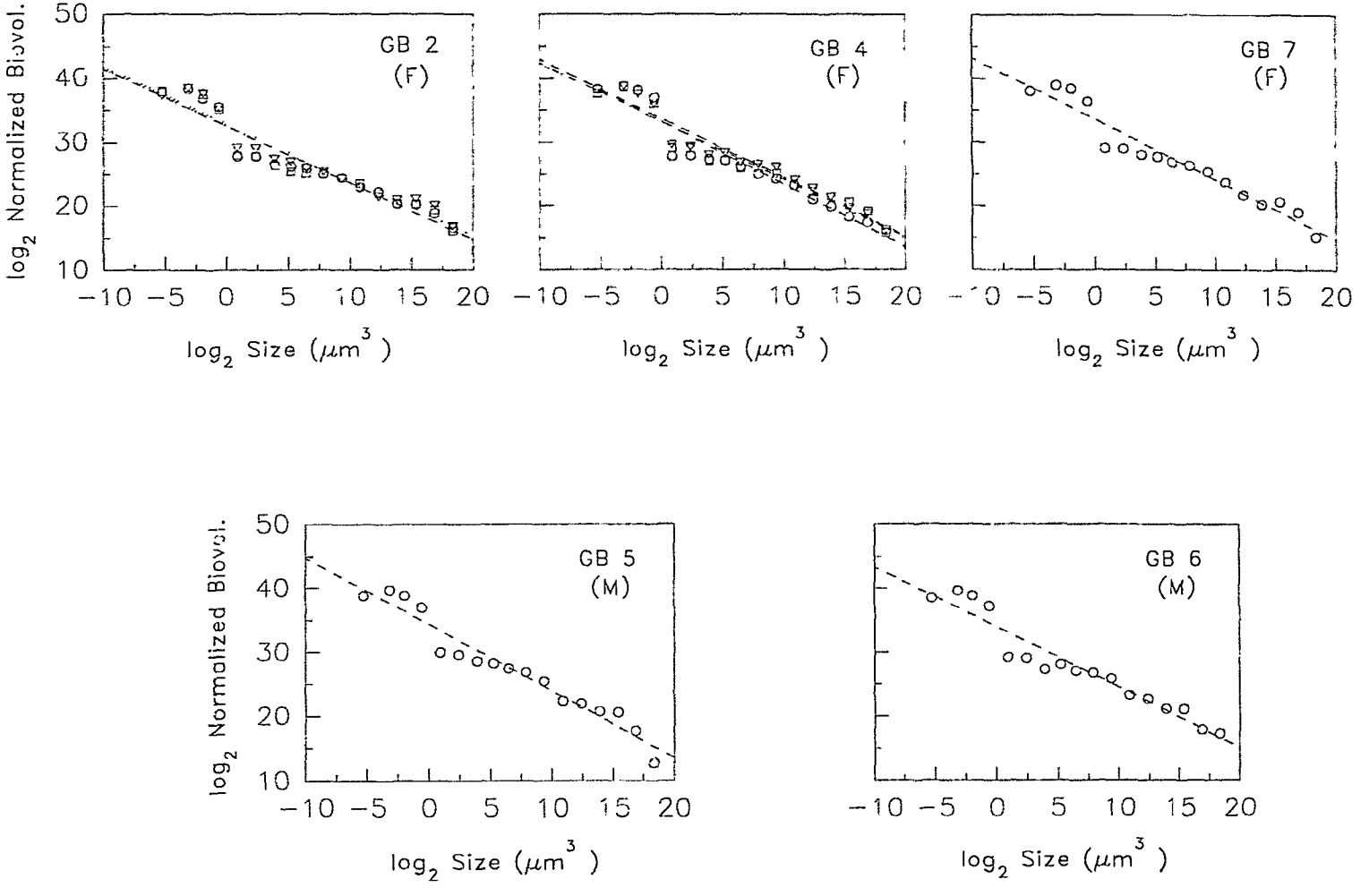

log2 Normalized Biovol.
50
40
30
20
10
−10 −5 0 5 10 15 20
log2 Size (μm3)
GB 2
(F)
GB 4
(F)
GB 7
(F)
GB 5
(M)
GB 6
(M)

Figure 2.4

TABLE 2.4. Regression parameters for the bacterio- to microplankton NBS-spectra in Georges Bank. (Model: $\log_2$ Normalized Biovolume = $\log_2$ a + b $\log_2$ Size (μm^3). Size range : 4.2 x 10^{-3} - 4.99 x 10^5 μm^3. ML = Mixed Layer ; TC = Thermocline ; S-I = Stratum I ; S-II = Stratum II; TOT = whole water column. Unnormalized biovolume expressed in μm^3 m^{-3}.

Station Name	Stratum	Slope	Biomass (Biovolume) size-spectra $\log_2$ a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	ML	-0.929	33.547	0.946	17	0.057	1.672
GB1	TC	-0.932	33.539	0.950	17	0.055	1.612
GB1	S-I	-0.930	33.105	0.947	17	0.056	1.653
GB2	ML	-0.887	32.555	0.919	17	0.068	1.982
GB2	TC	-0.882	32.961	0.931	17	0.062	1.818
GB2	S-I	-0.893	32.591	0.909	17	0.073	2.130
GB3	ML	-0.974	33.029	0.938	17	0.064	1.884
GB3	TC	-0.954	32.892	0.917	17	0.074	2.157
GB3	S-I	-0.962	32.723	0.939	17	0.063	1.848
GB4	ML	-0.984	33.186	0.930	17	0.070	2.042
GB4	TC	-0.922	33.654	0.953	17	0.052	1.535
GB4	S-I	-0.911	33.212	0.933	17	0.063	1.841
GB5	TOT	-1.039	34.336	0.949	17	0.062	1.811
GB6	TOT	-0.941	33.908	0.927	17	0.068	1.995

(CONTINUES NEXT PAGE)

TABLE 2.4 (continued)

GB7	TOT	-0.952	33.685	0.940	17	0.062	1.810
GB8	ML	-0.988	33.509	0.883	17	0.093	2.711
GB8	TC	-0.981	32.660	0.882	17	0.093	2.707
GB8	S-I	-0.937	32.055	0.947	17	0.057	1.660
GB8	S-II	-0.990	31.735	0.946	17	0.061	1.781
GB9	ML	-0.986	33.903	0.899	17	0.085	2.495
GB9	TC	-0.983	32.206	0.938	17	0.065	1.910
GB9	S-I	-0.995	32.211	0.958	17	0.053	1.561
GB9	S-II	-1.066	32.132	0.949	17	0.063	1.848
GB10	ML	-0.952	33.522	0.917	17	0.074	2.166
GB10	TC	-0.969	33.321	0.922	17	0.073	2.121
GB10	S-I	-0.982	32.805	0.961	17	0.051	1.490

TABLE 2.5. Regression parameters for the microplankton NBS-spectra in Georges Bank, withouth the three smallest size classes determined with the Uthermol technique (i.e. lower limit of the size classes : 0.98, 2.76, and 7.81 μm^3). Model: $\log_2$ Normalized Biomass = $\log_2$ a + b $\log_2$ Size (μm^3). Size range : 4.2×10^{-3} - 4.99×10^5 μm^3. ML = Mixed Layer ; TC = Thermocline ; S-I = Stratum I ; S-II = Stratum II; TOT = whole water column. Unnormalized biovolume expressed in $\mu m^3\ m^{-3}$.

Station Name	Stratum	Slope	Biomass (Biovolume) size-spectra $\log_2$ a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	ML	-0.986	34.542	0.987	14	0.033	0.914
GB1	TC	-0.983	34.445	0.983	14	0.037	0.983
GB1	S-I	-0.982	34.024	0.981	14	0.040	1.111
GB2	ML	-0.950	33.684	0.972	14	0.047	1.307
GB2	TC	-0.929	33.795	0.960	14	0.055	1.540
GB2	S-I	-0.955	33.708	0.959	14	0.057	1.598
GB3	ML	-1.039	34.182	0.985	14	0.037	1.041
GB3	TC	-1.018	34.065	0.967	14	0.054	1.523
GB3	S-I	-1.019	33.743	0.976	14	0.046	1.285
GB4	ML	-1.051	34.376	0.979	14	0.045	1.257
GB4	TC	-0.973	34.562	0.936	14	0.033	0.936
GB4	S-I	-0.964	34.180	0.970	14	0.049	1.363
GB5	TOT	-1.090	35.244	0.975	14	0.050	1.415

(CONTINUES NEXT PAGE)

TABLE 2.5 (continued)

GB6	TOT	-1.004	35.057	0.975	14	0.046	1.291
GB7	TOT	-1.008	34.671	0.976	14	0.045	1.276
GB8	ML	-1.075	35.087	0.962	14	0.062	1.731
GB8	TC	-1.072	34.301	0.968	14	0.056	1.568
GB8	S-I	-0.978	32.793	0.968	14	0.051	1.436
GB8	S-II	-1.043	32.672	0.977	14	0.046	1.299
GB9	ML	-1.067	35.343	0.966	14	0.057	1.605
GB9	TC	-1.034	33.119	0.966	14	0.056	1.566
GB9	S-I	-1.032	32.854	0.973	14	0.049	1.366
GB9	S-II	-1.096	32.610	0.958	14	0.066	1.854
GB10	ML	-1.026	34.824	0.977	14	0.045	1.258
GB10	TC	-1.040	34.592	0.979	14	0.044	1.238
GB10	S-I	-1.017	33.442	0.976	14	0.046	1.295

The intercept on the ordinate of the NBS-spectra of the bacterio- to microplankton size-range decreases with depth in stations located in stratified waters. This pattern is an indication that the total bacterio- to microplankton biomass diminishes with depth at these stations. No clear patterns emerge from the depth distribution of slopes or intercepts of the bacterio- to microplankton NBS-spectra from frontal waters suggesting more or less similar biomass levels through the water column. This is consistent with the high degree of physical mixing that takes place on Georges Bank.

The NBS-spectra of the total planktonic community (from bacteria to zooplankton) integrated for the whole water column are shown in Figures 2.5 and 2.6. The parameters of the NBS-spectra are described in Tables 2.6 to 2.9. The slopes of the NBS-spectra (biovolume units; Table 2.6) range from -0.875 to -0.949 and, therefore, the slopes of the unnormalized biomass size-spectra range between 0.125 and 0.051. Station GB10 has not been included in this comparison because of its narrower size-range coverage. The slopes of the NBS spectra are approximately 0.10 units more negative when expressed in carbon units than when expressed in biovolume units (Tables 2.8 and 2.9).

The numerical value of the slopes of NBS-spectra in volume units indicates that in Georges Bank and vicinity biomass slightly increases with body size when plotted on a log-log scale. The slopes, with the exception of station GB 5, are significantly different to -1.0 (t-Test, $P < 0.05$). However, in carbon units biomass is roughly the same at all size classes (slopes not significantly different to -1.0, t-Test, $P < 0.05$). The presence of more positive slopes than those observed in oligotrophic oceanic systems (Rodriguez and Mullin 1986b, Witek and Krajewska-Soltys 1989, see also Chapter 1) seems to be a distinct characteristic of Georges Bank.

Figure 2.5.- Normalized biomass size-spectra in volume units from the stations located in stratified waters (S) in Georges Bank and vicinity. Size range: 4.2×10^{-3} to 2.7×10^{11} μm^3 (from bacteria to zooplankton).

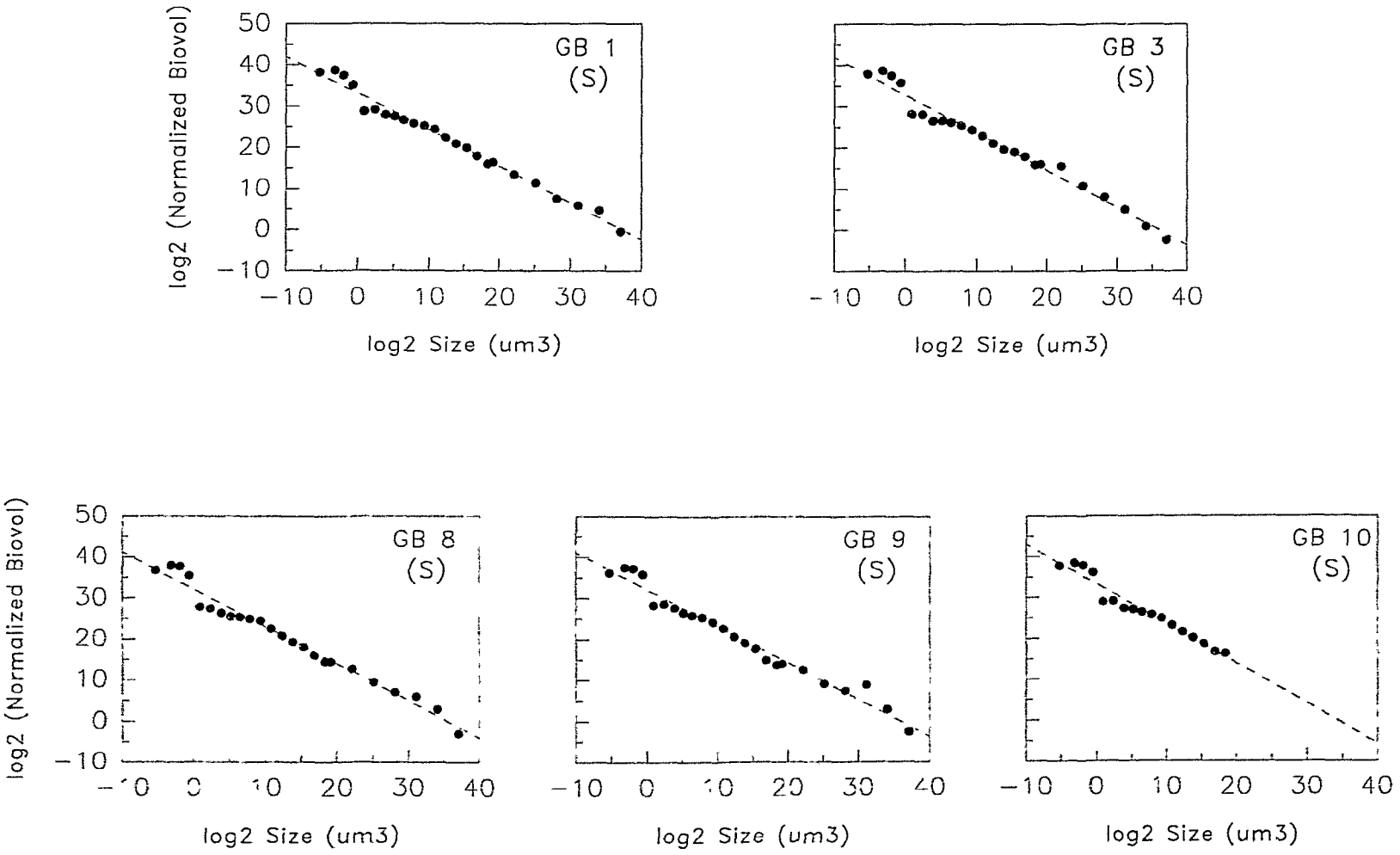

log2 (Normalized Biovol)
GB 1
(S)
GB 3
(S)
GB 8
(S)
GB 9
(S)
GB 10
(S)
log2 Size (um3)
50
40
30
20
10
0
−10
−10
0
10
20
30
40

Figure 2.5

Figure 2.6.- Normalized biomass size-spectra in volume units from the stations located in frontal waters (F) and mixed waters (M) in Georges Bank and vicinity. Size range: 4.2 x 10^{-3} to 2.7 x 10^{11} μm^3 (from bacteria to zooplankton).

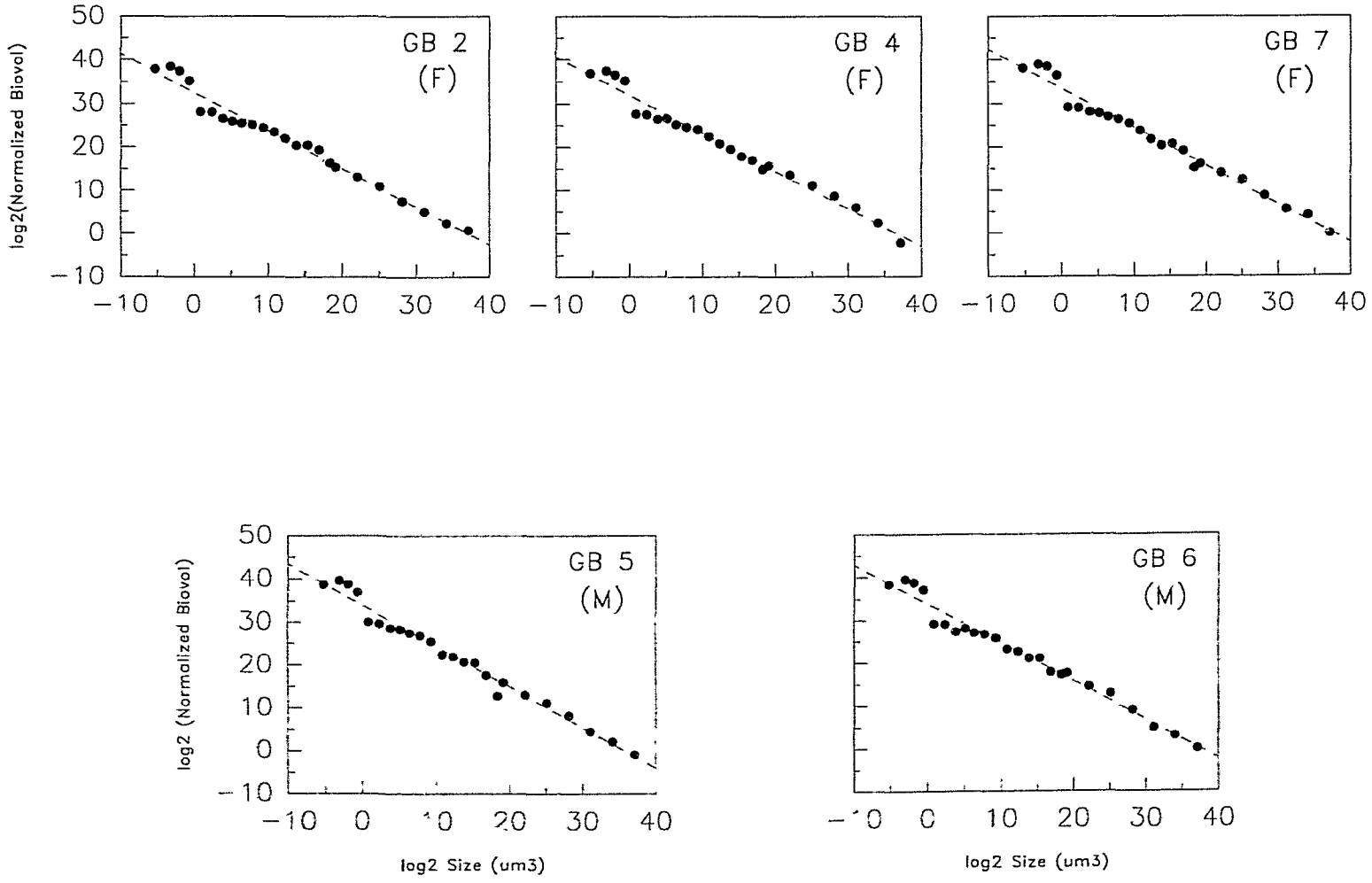

log2(Normalized Biovol)
GB 2
(F)
GB 4
(F)
GB 7
(F)
GB 5
(M)
GB 6
(M)
log2 (Normalized Biovol)
log2 Size (um3)
log2 Size (um3)

Figure 2.6

TABLE 2.6. Regression parameters for the NBS-spectra in Georges Bank. Data integrated for the whole water column. Model: $\log_2$ Normalized Biomass = $\log_2$ a + b $\log_2$ Size. Size range : 4.2×10^{-3} - 2.7×10^{11} μm^3 (from bacteria to zooplankton). Unnormalized biovolume expressed in $\mu m^3\ m^{-3}$.

Station Name	Slope	Biomass (Biovolume) size-spectra $\log_2$ a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	-0.886	33.131	0.983	24	0.025	1.443
GB2	-0.880	32.594	0.976	24	0.029	1.693
GB3	-0.912	32.814	0.976	24	0.030	1.777
GB4	-0.875	31.943	0.977	24	0.028	1.646
GB5	-0.949	33.946	0.981	24	0.028	1.645
GB6	-0.902	33.808	0.976	24	0.030	1.745
GB7	-0.895	33.437	0.980	24	0.027	1.598
GB8	-0.904	32.129	0.975	24	0.031	1.804
GB9	-0.897	32.145	0.972	24	0.032	1.878
GB10*	-0.972	33.264	0.972	17	0.058	1.682

* Only includes bacterio-, nano- and microplankton.

TABLE 2.7. Regression parameters for the NBS-spectra in Georges Bank, withouth the three smallest size classes from the uthermol technique. Data integrated for the whole water column. Model: $\log_2$ Normalized Biomass = $\log_2$ a + b $\log_2$ Size (μm^3). Size range : 4.2 x 10^{-3} - 2.7 x 10^{11} μm^3 (from bacteria to zooplankton). Unnormalized biovolume expressed in μm^3 m^{-3}.

Station Name	Slope	Biomass (Biovolume) size-spectra $\log_2$ a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	-0.916	33.906	0.992	21	0.019	1.048
GB2	-0.915	33.508	0.988	21	0.023	1.258
GB3	-0.949	33.777	0.988	21	0.024	1.316
GB4	-0.908	32.799	0.988	21	0.0231	1.268
GB5	-0.977	34.667	0.987	21	0.026	1.425
GB6	-0.940	34.798	0.990	21	0.022	1.226
GB7	-0.926	34.247	0.989	21	0.023	1.253
GB8	-0.937	32.997	0.984	21	0.027	1.485
GB9	-0.920	32.737	0.976	21	0.033	1.809
GB10*	-1.025	34.201	0.981	14	0.040	1.137

* Only includes fron bacterio- to microplankton.

TABLE 2.8. Regression parameters for the NBS-spectra in Georges Bank in carbon units. Data integrated for the whole water column. Model: $\log_2$ Normalized Biomass = $\log_2$ a + b $\log_2$ Size. Size range : 1.60×10^{-9} - 1.33×10^{3} µg C (from bacteria to zooplankton). Unnormalized biomass expressed in µgC m^{-3}.

Station Name	Slope	Biomass (Biovolume) size-spectra $\log_2$ a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	-0.983	11.833	0.979	24	0.030	1.516
GB2	-0.979	11.369	0.971	24	0.036	1.788
GB3	-1.018	10.768	0.976	24	0.034	1.699
GB4	-0.972	10.869	0.975	24	0.033	1.646
GB5	-1.071	10.786	0.977	24	0.035	1.743
GB6	-1.027	11.675	0.975	24	0.035	1.751
GB7	-0.993	11.906	0.974	24	0.034	1.715
GB8	-1.006	10.330	0.967	24	0.039	1.967
GB9	-0.997	10.544	0.963	24	0.041	2.071
GB10*	-1.100	9.582	0.952	17	0.063	1.626

* Only includes bacterio-, nano- and microplankton.

TABLE 2.9. Regression parameters for the NBS-spectra in Georges Bank in carbon units, withouth the three smallest size classes from the uthermol technique. Data integrated for the whole water column. Model: $\log_2$ Normalized Biomass = $\log_2$ a + b $\log_2$ Size (µg C). Siz range : 1.60×10^{-9} - 1.33×10^{3} (from bacteria to zooplankton). Unnormalized biomass expressed in µg C m^{-3}.

Station Name	Slope	Biomass (Biovolume) size-spectra log a	r^2	N	Std. Err. Slope	Std. Err. Y Est
GB1	-1.014	11.859	0.987	21	0.027	1.268
GB2	-1.016	11.406	0.981	21	0.032	1.515
GB3	-1.057	10.807	0.987	21	0.028	1.325
GB4	-1.007	10.901	0.984	21	0.029	1.383
GB5	-1.100	10.811	0.981	21	0.034	1.630
GB6	-1.068	11.718	0.987	21	0.028	1.341
GB7	-1.026	11.935	0.982	21	0.032	1.518
GB8	-1.040	10.364	0.975	21	0.038	1.798
GB9	-1.020	10.559	0.965	21	0.044	2.088
GB10*	-1.154	9.280	0.980	14	0.047	1.168

* Only includes fron bacterio- to microplankton.

Figure 2.7 shows the variation of slopes and intercepts of the NBS-spectra across the front. The *F* test reveals that no significant differences occur among slopes or intercepts of the NBS-spectra at a level of significance of $P < 0.001$.

One difference between NBS-spectra from Georges Bank and those from oligotrophic oceanic areas (see Chapter 1) is the greater degree of scatter around the regression line observed in the zooplankton size-classes. This is particularly evident in stations GB4, GB8, and GB9 (see Figure 2.8). Table 2.10 describes the parameters of the zooplankton NBS-spectra. The slopes of the zooplankton NBS-spectra indicate that zooplankton biomass increases considerably between successive size-classes. Exceptions to this observation are the zooplankton size-spectra from stations GB6 and GB3 where zooplankton biomass remains constant or only slightly increases with body size. In contrast, the parameters of the bacterio- to microplankton NBS-spectra indicate that in this size-range biomass remains constant with an increase in body-size (Table 2.10).

A taxonomical analysis was performed on the zooplankton biomass-spectra from station GB7 and GB9. The objective was to obtain a general view of the variability of taxa through the zooplankton size-spectra and to determine if the most conspicuous peak of zooplankton biomass observed in this study (size-class 12.9 - 60.4 µg C Stn GB9) was produced by a high concentration of organisms belonging to only one taxon or to a combination of several taxa. Table 2.11 and 2.12 describe the taxonomic composition of the zooplankton size-spectra from these stations. The peak observed in the size class 12.9 to 60.4 µgC in station GB9 is dominated (99% numerical abundance) by *Calanus sp.* In fact *Calanus sp.* dominates numerically also in the two adjacent size classes with 66% and 80% of total abundance in the size class 2.75 - 12.9 µgC and size class 60.4 - 283.5 µg C respectively. In station GB 7, the peak of biomass in the size class 0.585 - 2.75 µg C is composed of copepods, 41% *Paracalanus sp.* and 27 % *Centropages sp.* The peak of

Figure 2.7.- Variation of the parameters of the NBS-spectrum (integrated water column, from bacteria to zooplankton) from each station across the front.

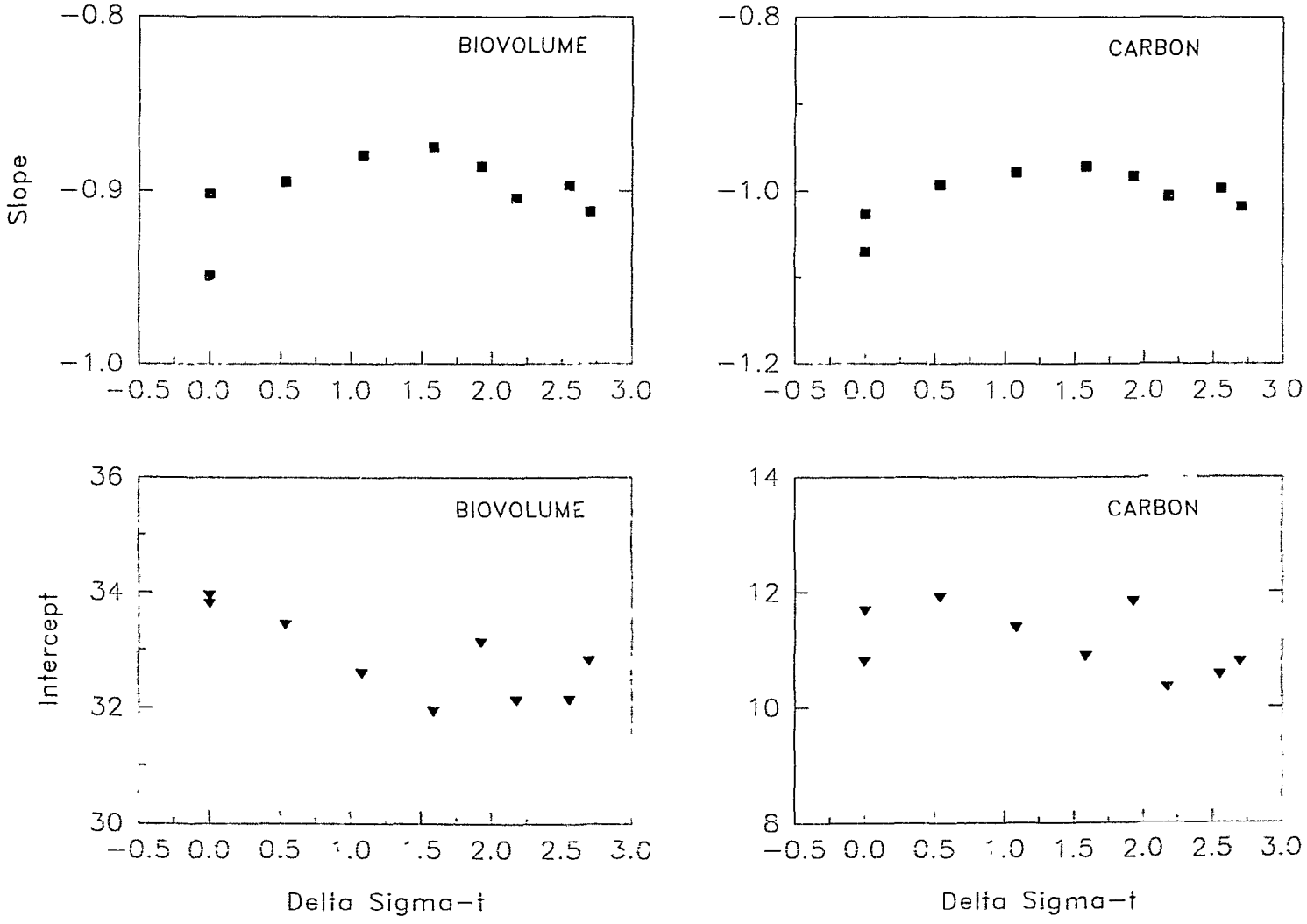

BIOVOLUME
CARBON
Slope
−0.8
−0.9
−1.0
−1.2
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
BIOVOLUME
CARBON
Intercept
36
34
32
30
14
12
10
8
Delta Sigma−t
Delta Sigma−t

Figure 2.7

Figure 2.8.- Zooplankton NBS-spectra in carbon units from each of the stations in Georges Bank and vicinity. (F) frontal waters; (M) mixed waters; (S) stratified waters.

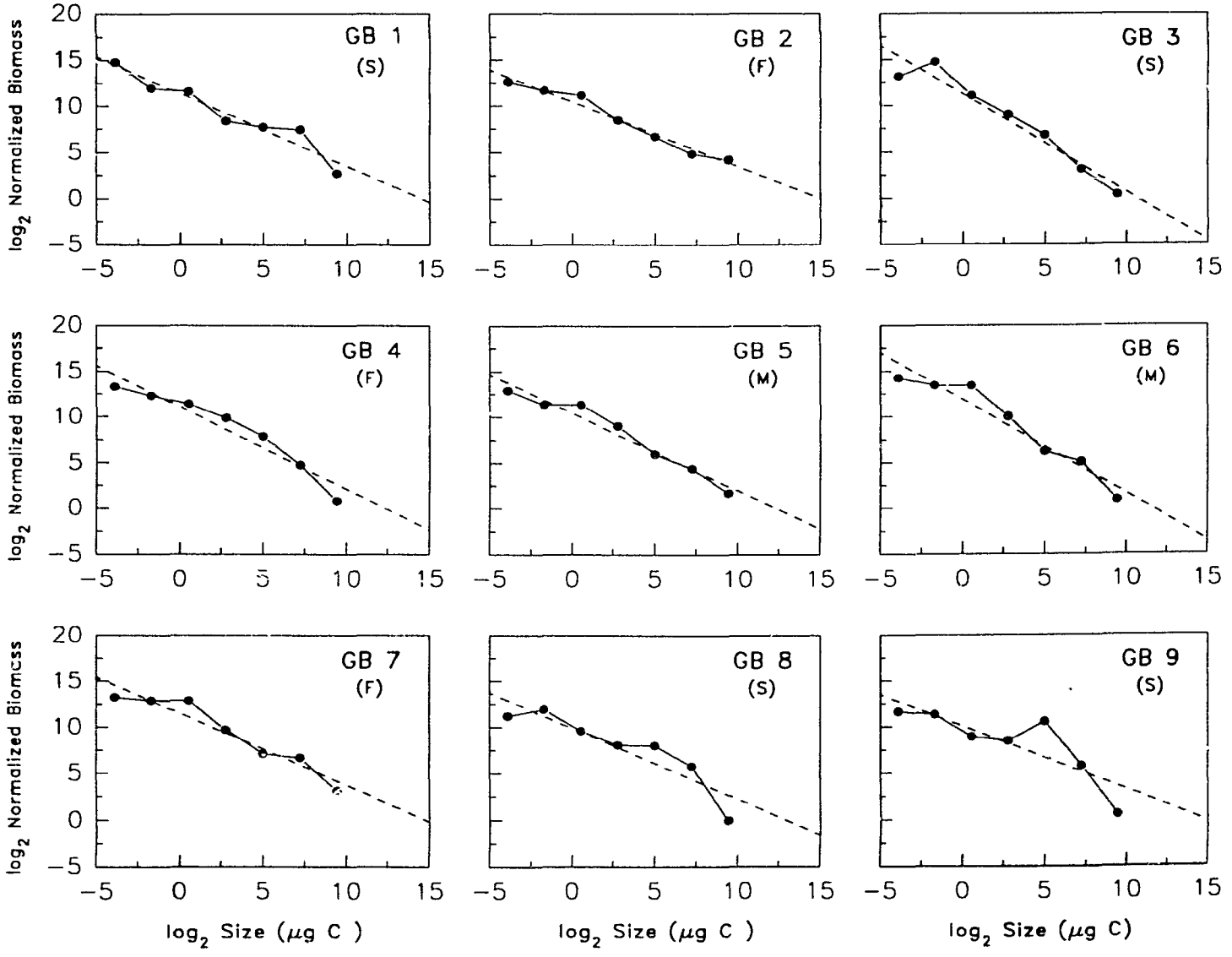

GB 1
(S)
GB 2
(F)
GB 3
(S)
GB 4
(F)
GB 5
(M)
GB 6
(M)
GB 7
(F)
GB 8
(S)
GB 9
(S)
log2 Normalized Biomass
log2 Size (μg C)
20
15
10
5
0
−5
−5
0
5
10
15

Figure 2.8

TABLE 2.10. Parameters of the NBS-spectra of the zooplankton in carbon units. Model: $\log_2$ Normalized biomass = $\log_2 a$ + b $\log_2$ Size (µg C). Bacterio- to microplankton size-range: 1.6×10^{-9} to 0.028 µg C. Zooplankton size-range: 0.028 to 1.33×10^{3} µg C. Unnormalized biomass expressed in µg C m^{-3}.

	Bacterio- to microplankton		Zooplankton	
Station	Slope	$\log_2 a$	Slope	$\log_2 a$
GB1	-1.106	10.387	-0.787	11.423
GB2	-1.070	10.636	-0.697	10.432
GB3	-1.145	9.259	-1.057	11.242
GB4	-1.132	8.765	-0.898	11.095
GB5	-1.228	8.715	-0.848	10.459
GB6	-1.130	10.643	-1.027	11.867
GB7	-1.135	10.160	-0.781	11.519
GB8	-1.165	8.347	-0.767	9.908
GB9	-1.185	7.868	-0.689	10.076

TABLE 2.11. Taxonomic analysis of zooplankton size-spectra from station GB 7. Values are given as percentages of total number of organisms in the size-fraction. Symbols: 1 = size fraction 0.028 - 0.125 µg C; 2 = size fraction 0.125 - 0.585 µg C; 3 = size fraction 0.585 - 2.746 µg C; 4= size fraction 2.746 - 12.882 µg C; 5 = size fraction 12.882 - 60.436 µg C; 6= size fraction 60.436 - 283.53 µg C; 7 = size fraction 283.526 - 1330.119 µg C. N = Total number of organisms classified.

	SIZE CLASS						
TAXONOMIC CATEGORY	1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
COPEPODA							
Calanoida							
Calanus sp.				1.72	4.32		
Pseudocalanus sp.		2.46	4.74	5.91	2.32		
Paracalanus sp.	0.44	14.38	40.52	27.34	24.25		
Clausocalanus sp.			1.72	2.46			
Centropages sp.		0.11	26.29	47.53	28.24		
Acartia sp.		1.05	3.02	5.42	2.66		
Temora sp.		0.35		0.74	0.332		
Pontella sp.					1.00		
Exoskeleton sp.		2.81	2.15	0.98	0.66		
Cyclopoida							
Oithona sp.	0.30	17.19	15.09	2.22	2.99		
Harpacticoida							
Microsetella sp.		0.35	0.43	0.25			
Macrosetella sp.					1.99		
Unid			0.21				

(CONTINUES NEXT PAGE)

TAXONOMIC CATEGORY	SIZE CLASS 1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
NAUPLII							
Cyclopoid	28.89	22.10			2.99		
Calanoid	10.67	14.39			0.66		
Harpacticoid	0.30						
AMPHIPODA							
Gammarus sp.					5.31	28.61	25.23
Cirolana sp.						0.26	
Unid				0.49	1.33	2.10	
DECAPODA							
Stomatopoda							
Crangon sp.				0.25	3.32	1.57	1.25
Juv Carngon						1.84	
damaged					0.66		
Euphausiacea							
unid Calyptopis					0.33		
Brachyura							
Megalopa						0.26	0.31
Zoea				0.25			0.31

(CONTINUES NEXT PAGE)

TAXONOMIC CATEGORY	SIZE CLASS 1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
MYSIDACEA							
Mysid				1.72	3.32	1.05	1.25
Damaged				0.25	3.32	0.79	0.31
CHAETOGNATA							
Saggita sp.		0.35		1.23	7.31	62.47	68.22
TUNICATA							
Thalacea							3.11
Larvacea		0.79		1.23	1.00	0.26	
MOLLUSCA							
Bivalvia Juv	2.07	3.16			0.33		
Gastropoda Juv	0.30	3.86	1.29				
Pteropoda (Thecosomata)							
Limacina sp.					1.00		
POLYCHAETA						0.26	
FISH LARVAE							
Merluccius Bilinearis						0.52	

(CONTINUES NEXT PAGE)

TAXONOMIC CATEGORY	SIZE CLASS 1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
EGGS							
Copepod egg masses	1.18						
Copepod individual	12.00						
Chaetognath			1.72				
PHYTOPLANKTON							
Ceratium	8.44	5.61	0.43		0.33		
Peridineum	0.30						
Dinophysis	33.93						
Foraminifera	1.18	0.35					

TABLE 2.12. Taxonomic analysis of zooplankton size-spectra from station GB 9. Values are given as percentages of total number of organisms in the size-fraction. Symbols: 1 = size fraction 0.028 - 0.125 µg C; 2 = size fraction 0.125 - 0.585 µg C; 3 = size fraction 0.585 - 2.746 µg C; 4= size fraction 2.746 - 12.882 µg C; 5 = size fraction 12.882 - 60.436 µg C; 6= size fraction 60.436 - 283.53 µg C; 7 = size fraction 283.526 - 1330.119 µg C. N = Total number of organisms classified.

	SIZE CLASS						
TAXONOMIC CATEGORY	1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
COPEPODA							
Calanoida							
Calanus sp.			0.87	65.76	99.42	80.38	26.78
Pseudocalanus sp.				1.17	0.29		
Paracalanus sp.		0.67	4.93	9.73			
Microcalanus sp.	0.24	4.35	0.87				
Clausocalanus sp.			0.58	1.17			
Euchaeta sp.				0.39		17.95	23.21
Metridia sp.						0.63	
Scolecithricella sp.				0.78			
Centropages sp.			2.90	8.17			
Acartia sp.				0.78			
Anomolocera sp.				0.39			
Exoskeleton sp.				6.61	0.29		
Unid Juv		4.68	3.48				
Cyclopoida							
Oithona sp.	0.24	6.02	16.23	1.17			

(CONTINUES NEXT PAGE)

TAXONOMIC CATEGORY	SIZE CLASS 1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
Harpacticoida							
Microsetella sp.	0.24	2.34	12.17				
Oncaea sp.			0.29				
NAUPLII							
Cyclopoid	17.07	17.05	7.54				
Calanoid	13.90	32.78	31.01				
Harpacticoid	1.95	2.67	3.48				
AMPHIPODA							
Parathemisto sp.				1.94		0.21	1.79
Unid Juv			2.03				
DECAPODA							
Stomatopoda							
Pasiphaea sp.							3.57
Euphausiacea							
Euphausia sp.							7.14
Metanauplius				0.39			
Thysanoessa sp.				0.21		0.83	3.57
Nematoscelis sp							30.36
Meganictyphanes sp.							1.79

(CONTINUES NEXT PAGE)

TAXONOMIC CATEGORY	SIZE CLASS 1 (N = 410)	2 (N = 299)	3 (N = 345)	4 (N = 257)	5 (N = 347)	6 (N = 479)	7 (N = 56)
CHAETOGNATA							
Eukrohnia sp.							1.79
MOLLUSCA							
Gymnosomata sp.				0.39			
ECHINODERMATA							
UNID Larvae	0.24						
EGGS							
Copepod egg masses	1.95		0.29				
Copepod individual	6.58	3.68					
Chaetognatha			0.29				
Euphausiid			0.29	0.78			
PHYTOPLANKTON							
Ceratium	41.71	23.08	11.30				
Peridineum	1.22						
Dinophysis	1.46		0.29				
Nitschia			0.29				
Radiolarians			0.29				
Foraminifera	6.58	5.00	0.29				
Centroid	5.85						
Unid Pennate	0.73	1.00					
UnId			0.29				

biomass detected in station GB7 (size class 60.4 - 283.5 μg C) is mainly composed of the chaetognath *Saggita* sp. (62 % numerical abundance). It is important to note, that in both stations analyzed taxonomically, phytoplankton cells are a considerable numerical component of the size-class 0.028 - 0.125 μg C . The importance of phytoplankton based upon numerical abundance, represent 44% and 58% of the organisms in this size class in stations GB7 and GB9 respectively. However, since from a biomass point of view the zooplankton dominate this size-class, the class has been considered as belonging to the zooplankton size-spectra.

It is interesting to note that in the zooplankton size-spectra, most genera (and probably species) are spread over more than one size-class (see Tables 2.11 and 2.12). Indeed, some genera are found in four different size classes. Although the efficiency of size-fractionation by sieving may be contributing to this pattern, it is evident that many species cover a wide range of size classes. This is an important fact to be taken into account when constructing models of the pelagic system based on body size where prey-predator relationships play an important role.

The distribution of bacterio-, micro- and zooplankton biomass across the $\Delta \sigma_t$ gradient is shown in Figure 2.9. The general pattern of the distribution of bacterioplankton and microplankton is a gradient with the highest biomass occurring in mixed waters (central bank). There is a general decrease in biomass with increased stratification across the front. In contrast, the zooplankton biomass does not present a clear trend across the front. Indeed, the highest biomass level of zooplankton was found in stratified waters (Stn GB1 and GB9). The range of variation among stations in total biomass of bacterio-, micro-, and zooplankton is 3.5 to 4.5 fold.

Figure 2.9.- Total bacterio-, micro-, and zooplankton biomass across the $\Delta\sigma_t$ gradient in Georges Bank. Size ranges: Bacterioplankton = 1.60 x 10^{-9} to 3.40 x 10^{-7} µg C; Microplankton = 3.40 x 10^{-7} to 0.028 µg C ; Zooplankton = 0.028 to 1330.119 µg C.

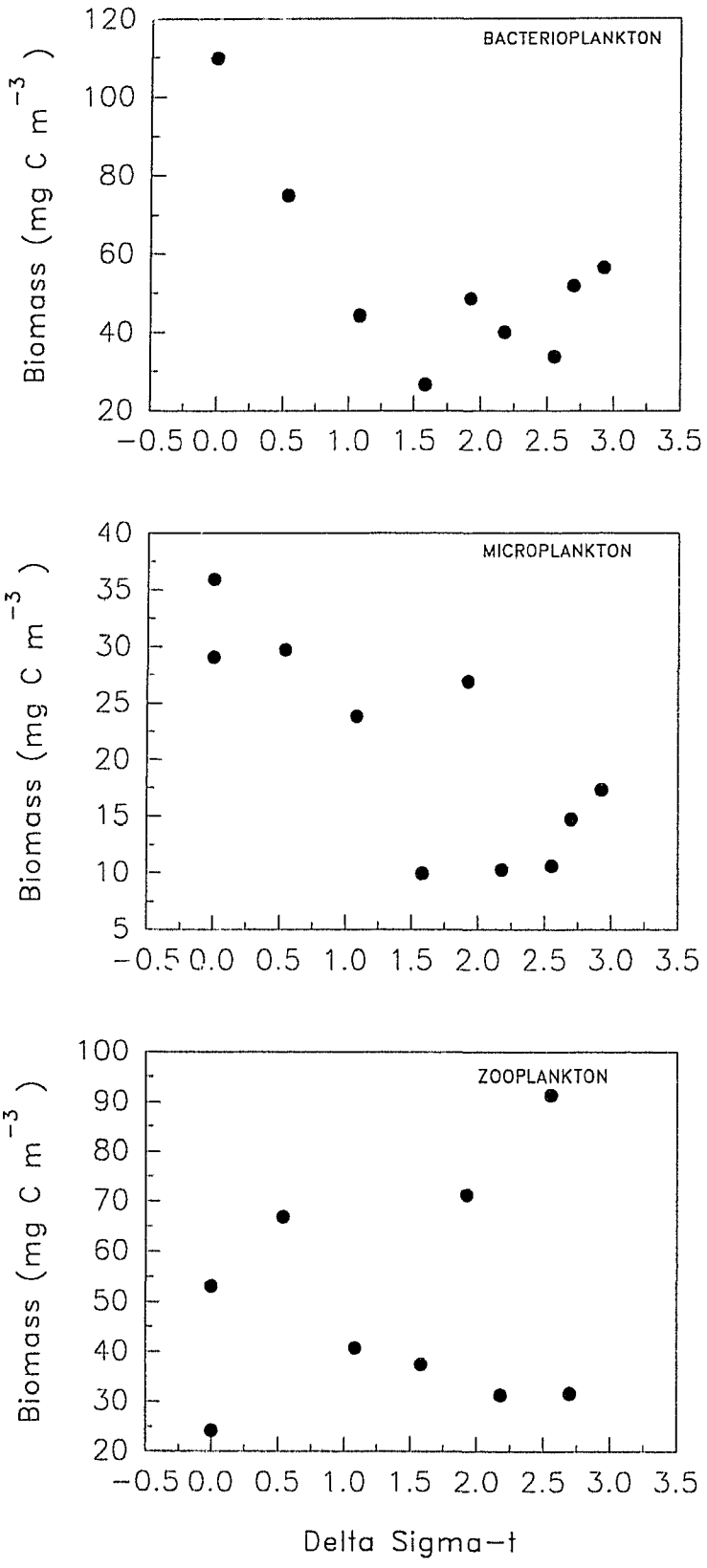

BACTERIOPLANKTON
Biomass (mg C m^{-3})
120
100
80
60
40
20
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
MICROPLANKTON
Biomass (mg C m^{-3})
40
35
30
25
20
15
10
5
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
ZOOPLANKTON
Biomass (mg C m^{-3})
100
90
80
70
60
50
40
30
20
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
Delta Sigma−t

Figure 2.9

Figure 2.10 shows the biomass ratios among bacterio-, nano- and zooplankton in each station across the $\Delta\sigma_t$ gradient. The bacteria to microplankton biomass-ratio is high both in mixed and stratified waters but low in frontal waters. The bacteria to zooplankton biomass ratio is very high in the central bank in comparison to frontal or stratified waters. Finally there is a decline in the microplankton to zooplankton biomass ratio from the mixed to stratified waters. The range of variation of the biomass ratios increased as the difference in size between the size-classes compared increased.

A general analysis of the distribution of biomass by size can also be achieved using biomass-size diversity and biomass-size evenness indices analogous to those used in describing species diversity. Table 2.13 describes the biomass-size diversity and evenness indices from each station. Figure 2.11 shows the vatiation of the diversity and evenness indices across the $\Delta\sigma_t$ gradient. It can be seen from the γ, φ and ξ indices that both biomass-size diversity and evenness are highest in mixed waters. Values decrease in frontal waters and present the lowest values in the stratified waters. Among the stations located in stratified waters, GB8 presents very high γ, φ and ξ indices.

The Ω index shows an opposite trend to the biomass-size diversity index γ, being lower in mixed waters and increasing toward more stratified waters. Such a result is consistent with the characteristics of Ω (see methods). The major peak observed in Ω corresponds to the biomass peak of *Calanus sp.* in Station GB 9. It is known that Simpson's index, the analogous species diversity index to Ω, is very sensitive to the abundance of the more plentiful categories in a sample (Hill 1973).

For the sake of comparison, the biomass-size diversity and evenness indices from two stations located in the oceanic oligotrophic ocean (New England Seamount area, see Chapter 1) have also been included in Table 2.13. In comparison to Georges Bank, the

Figure 2.10.-Biomass ratio among bacterio-, micro and zooplankton across the $\Delta\sigma_t$ gradient in Georges Bank. Size ranges: Bacterioplankton = 1.60 x 10^{-9} to 3.40 x 10^{-7} µg C; Microplankton = 3.40 x 10^{-7} to 0.028 µg C ; Zooplankton = 0.028 to 1330.119 µg C.

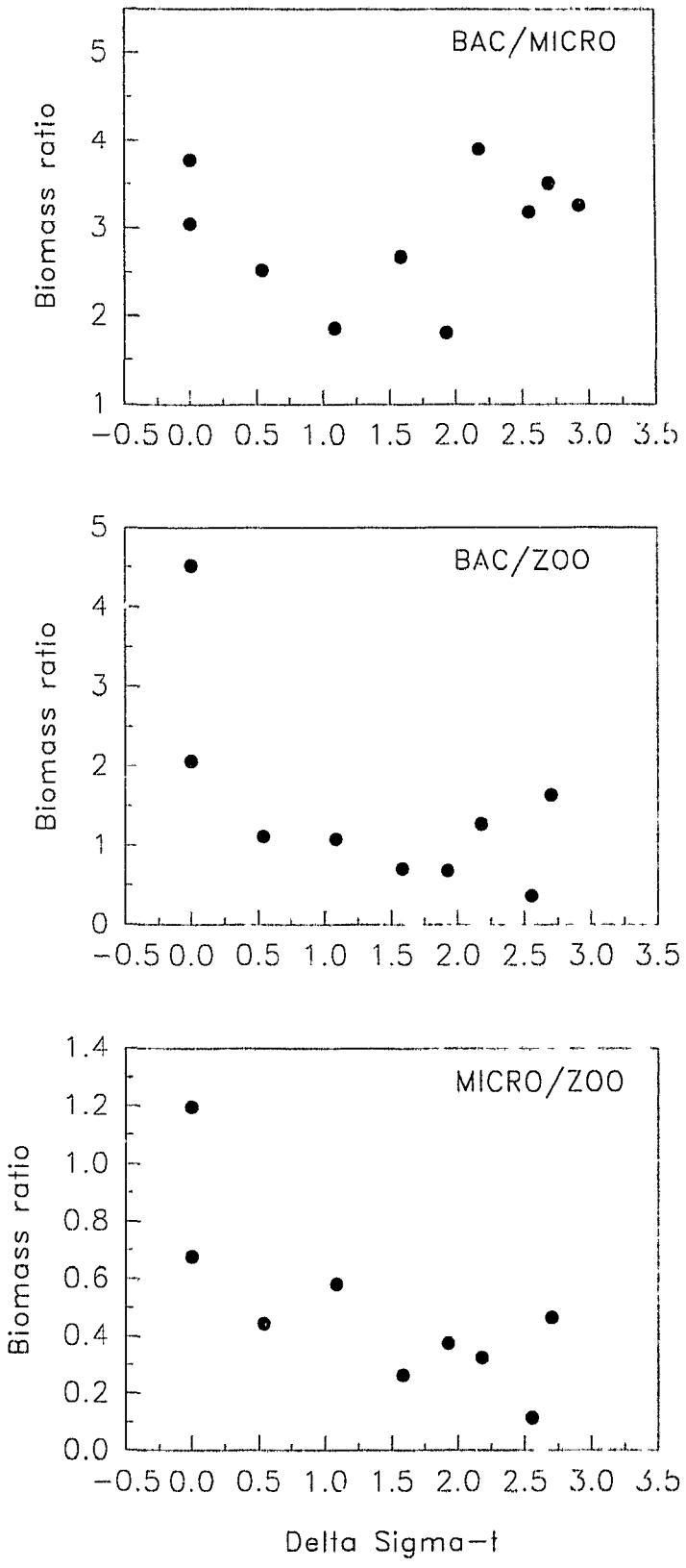

BAC/MICRO
Biomass ratio
5
4
3
2
1
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
BAC/ZOO
Biomass ratio
5
4
3
2
1
0
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
MICRO/ZOO
Biomass ratio
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
−0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
Delta Sigma−t

Figure 2.10

TABLE 2.13. Biomass-size diversity and evenness in different stations in Georges Bank. Data estimated from biomass (biovolume) data without logarithmic transformation.

Station	$\Delta\sigma_t$	γ	φ	Ω	ξ
GB 1	1.925	0.987	0.311	0.197	0.073
GB 2	1.084	2.474	0.779	0.130	0.473
GB 3	2.700	1.087	0.342	0.138	0.085
GB 4	1.586	1.034	0.325	0.131	0.079
GB 5	0.001	2.776	0.873	0.074	0.654
GB 6	0.001	2.631	0.828	0.093	0.561
GB 7	0.537	2.489	0.783	0.118	0.480
GB 8	2.177	2.295	0.722	0.162	0.388
GB 9	2.555	1.177	0.370	0.558	0.098
GB 10*	2.928	2.486	0.877	0.102	0.688
Open Ocean Stations**					
PURPLE 10		2.977	0.925	0.061	0.776
INDIGO		2.828	0.878	0.077	0.663

* Only includes from bacterio- to microplankton

** The location of these stations is described in Chapter 1.

Figure 2.11.- Biomass-size diversity and evenness in each of the station across the $\Delta\sigma_t$ gradient in Georges Bank. See Table 2.3 for a description of the different indexes used.

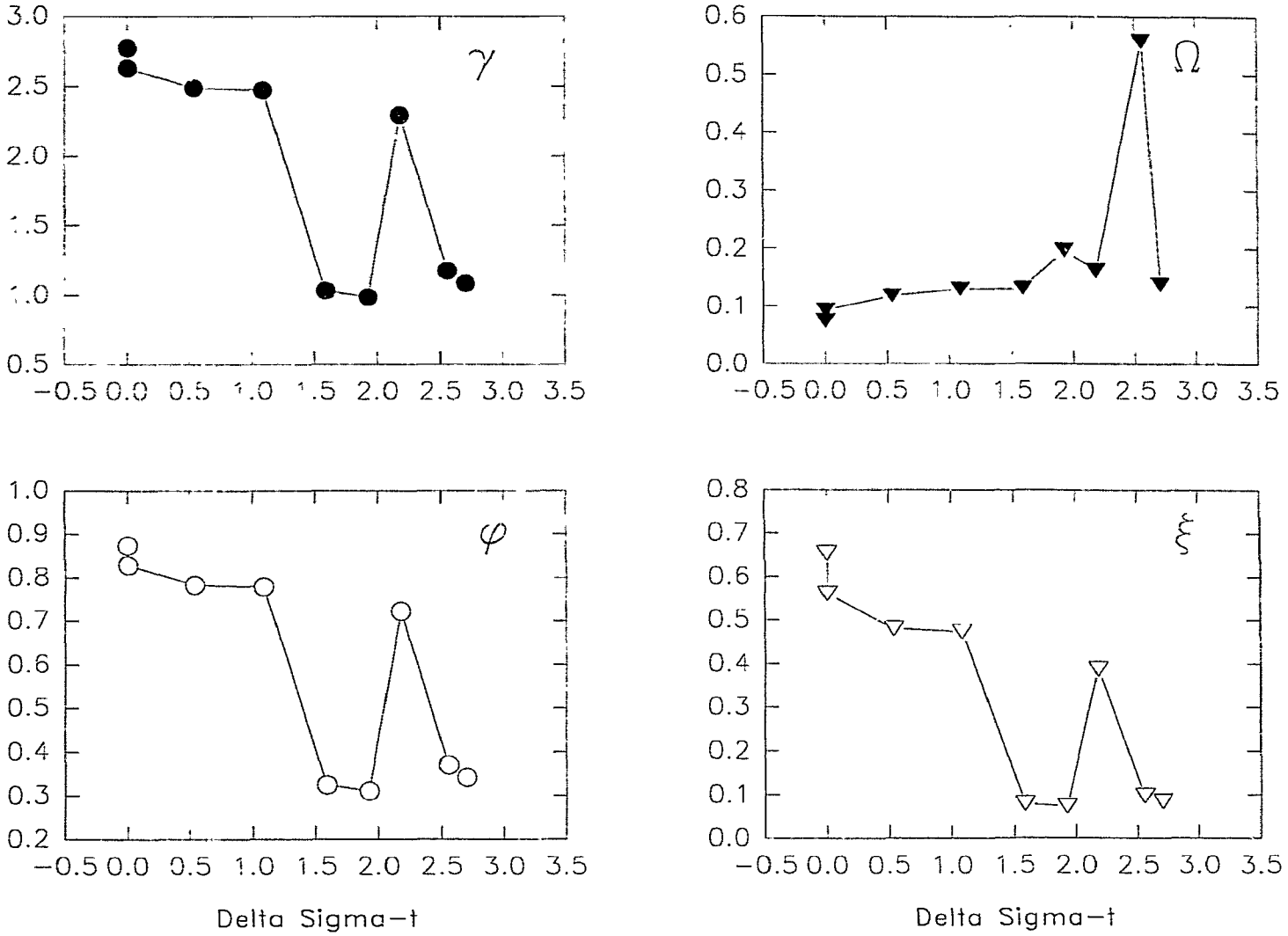


Figure 2.11

stations from the oligotrophic ocean show the highest diversity (γ), lowest dominance (Ω) and highest evenness (φ and ξ) in the biomass size-distribution.

Since diversity indices are highly correlated (e. g. Hicks 1980), it is not surprising that the same basic trends in the biomass-size diversity and evenness described for Georges Bank were found with the several indices used.

DISCUSSION

NBS-spectra in Georges Bank

The biomass size-distribution from the different locations in Georges Bank and surrounding waters can be described by a linear NBS-spectrum. In this regard the NBS-spectra from Georges Bank do not seem to present the conspicuous non-linear patterns observed in several coastal and lakes ecosystems (e.g. Sprules and Munawar 1986, Sprules et al. 1988, Jimenez et al 1989, Rodriguez et al. 1987, 1990, Hobson 1988, Echevarría et al. 1990, Ahrens and Peters 1991a, Gasol et al. 1991). However, because of the time-scale limitation of the current data, these results can not be extrapolated to other times of the year, especially during bloom situations.

In comparison to NBS-spectra from the oligotrophic ocean (see Chapter 1), the intercepts of Georges Bank NBS-spectra are much higher, indicating, as expected, higher biomass concentrations. Variability of the parameters of the NBS-spectra from Georges Bank through the year can be expected. As an indication of such variability, it can be pointed out that the intercept of a NBS-spectrum from a station located in Georges Bank sampled at the end of September 1990 (see Chapter 3) presented a much higher intercept (Normalized-biomass axis intercept = 34.49) than those of the NBS-spectra found in this study.

The slopes of the NBS-spectra of Georges Bank and vicinity are clearly more positive than those from oligotrophic areas. The zooplankton size-range presented even more positive slopes (see Table 2.10) than the whole NBS-spectra. The numerical values of the slopes of the NBS-spectra in Georges Bank (volume units) indicate that biomass increases with body size. This seems to be a clear difference between Georges Bank and the oligotrophic ocean (e.g. Rodriguez and Mullin 1986 a, b; see Chapter 1). The

zooplankton unnormalized biomass, increases with size presenting slopes from 0.057 to 0.311 (carbon units, Table 2.10).

It is important to note that there is a change in the slope of the NBS-spectrum at the zooplankton size-range. Indeed, the bacterio- to microplankton NBS-spectra (Table 2.10) have slopes close to those ones observed in oligotrophic areas. Sprules and Munawar (1986), comparing the parameters of the NBS-spectra from different Canadian lakes, noted that the variability in the zooplankton size-range is much higher than the one observed in the nano- and microplankton size range. Sprules and Munawar (1986) conclude that roughly equivalent abundance of nannoplankton produce higher abundance of zooplankton in more productive systems. Higher turnover rates in the microbial component of the trophic web in more productive areas would be responsible for the higher levels of zooplankton biomass observed (Sprules and Munawar 1986).

The considerable increase of biomass with size in the zooplankton size-range in most of the stations in Georges Bank (see Table 2.10) does not follow the predictions of the "linear biomass hypothesis" (Sheldon et al. 1972, Sheldon et al. 1977) nor the Platt and Denman's model (Platt and Denman 1977, 1978). The latter postulates that the total biomass in any given class decreases in a regular manner with increasing size. Nevertheless, in Chapter 1 I have shown that depending on the parameters used in obtaining the numerical solution of Platt and Denman's model, their model includes, as a particular case, Sheldon's flat spectrum. The slopes predicted by Platt and Denman range between -0.82 (when all organisms are unicells) and -1.23 (when all organisms are heterotherms). The slopes of the NBS- spectra from bacteria to zooplankton in Georges Bank are within the limits predicted by Platt and Denman's model. The slopes of some of the zooplankton NBS-spectra are as low as -0.697, clearly below the limits predicted by

Platt and Denman's model, specially if we take into consideration that most organisms in this size-range are heterotherms.

Zooplankton size-spectra presenting negative or "flat" slopes have been observed in most marine ecosystems such as a warm-core Gulf Stream Ring (Davis and Wiebe 1985), coastal waters (Villate 1991), the tropical ocean (Tseytlin 1981a), the Peruvian upwelling zone (Mackas et al. 1981), the slope waters off Northern Peru (Dickie 1981), the Adriatic Sea (Greze et al. 1986), the North Pacific Central Gyre (Rodriguez and Mullin 1986 b), and the Northwest Atlantic oligotrophic areas (Witek and Krajewska-Soltys 1989, see also Chapter 1). However, in other kinds of ecosystems such as lakes (Ahrens and Peters 1991a, Sprules et al. 1991) and a coastal lagoon (Lam Hoai and Grill 1991) unimodal distributions have been observed in the zooplankton size-range. It is important to remark that the shorter the size-range studied, the higher will be the probability of finding patterns far from linearity (e.g. Minns et al 1987).

The abrupt change in the numerical values of the slopes of the zooplankton-size range in comparison to those of the bacterio- to microplankton size-range observed in Georges Bank suggests that caution must be exercised when attempting to estimate fish stocks from the standing stock of smaller organisms. A consideration of the natural turnover rate of the organisms in the ecosystem seems to be fundamental if the model is going to have any validity. In addition, it is possible that the slope of bigger organisms than the ones considered in this study may be different than that of the zooplankton size-range. Ahrens and Peters (1991a), analyzing the predictions of fish biomass based on NBS-spectra suggest that is likely that biomass per size-class does not peak in the largest class but, on the contrary, possibly declines.

Most of the allometric models available for the planktonic ecosystem (e. g. Kerr 1974, Sheldon et al. 1972, 1977, Platt and Denman 1977, 1978, Silvert and Platt 1978, 1980, Borgmann 1982, 1987) require the system to be in a steady state. Georges Bank is a system unlikely to be in steady state, at least in the time framework of this study. It is interesting to note that, despite being far from steady-state, the distribution of biomass by size can still be described by a power function. The distance from steady-state seems to be reflected in the more positive slopes of the system and the higher degree of scatter around the regression line of the zooplankton size-range. Positive slopes of unnnormalized biomass spectra have been observed in several systems far from steady state (e.g. Hobson 1988, Gilabert et al. 1990).

Biomass-size diversity and evenness in Georges Bank

Although species diversity has been considered to be related to community stability, evolution and competition (e.g. Margalef 1963, 1977, 1980; Connel and Orias 1964, MacArthur 1965, Odum 1971) there is considerable controversy regarding the validity of these relationships. The debate is particularly strong regarding the relationship between diversity and stability (e. g. Odum 1975, Orians 1975, Kikkawa 1986). There is also extensive discussion regarding the concept of species diversity (e.g. Eberhardt 1969, Hurlbert 1971) and which is the most appropriate species diversity index (e.g. Peet 1974, Perkins 1983). Today, after decades of research, there is certain pessimism with respect to the possibility of generating a general theory of species diversity (Brown 1981). As a consequence, there is a scarcity of recent studies dealing with species diversity patterns in planktonic communities. However, despite the debatable aspects of the use of species diversity indices for studying the structure of ecological communities, they have been an important tool in community ecology (Margalef 1972).

In the current paper I have used biomass-size diversity and evenness indices as means of comparison between biomass size-distributions, and as a way to summarize information contained in biomass size-distribution data. It is important to remark that although the biomass-size diversity approach has its methodological roots in the study of species diversity, it is based on a different conceptual framework. An advantage of the biomass-size diversity approach in comparison to the species diversity one is its closer link to the energetics of the ecosystem. Since body size is related to respiration, turnover rate and many other bioenergetic characteristics of organisms (for a review see Peters 1983a), the study of biomass-size diversity should provide some insight into the structure of the system.

The idea of using a diversity index to characterize particle size-spectra was pioneered by Parsons (1969). His index, based on the Shannon-Wiener Index, did not achieve popularity in the particle size-distribution research. Subsequently, Margalef (1980) based on the ideas of Harte and Morowitz (1975; cited in Margalef 1980) suggested the analysis of the structure of ecosystems by studying the diversity of biomass by compartments characterized by defined turnover rates. The advantage of using such an approach is that it allows a thermodynamic interpretation (Margalef 1980). Ulanowicz (1981), like Parsons (1969), proposed an index to be used with particle size data generated with electronic counters. Ulanowicz's index was designed to deal with the analysis of particle size-distribution variability through time using Fourier time spectra. To the best of my knowledge Ulanowicz's index has never been used with empirical data.

Taking a different approach, Lurie and Wasenberg (1983) and Lurie et al. (1983) have defined an index (μ) for the biomass diversity per individual (in practice it is by size class) which is, to a certain extent, analogous to my modification of the Shannon-Wiener Index. However, Lurie and colleagues modified the Shannon-Wiener index to be used

with continuous functions. Ruiz and Rodriguez (1992) have indicated that there is a relationship between μ and the slope of the NBS-spectrum. They suggest that a flatter NBS-spectrum would indicate a higher evenness and biomass diversity than in the case of a steeper NBS-spectrum (Ruiz and Rodriguez 1992). I think that there might be a relationship between the slope of the biomass spectrum and a measure of biomass diversity provided that the slope of the NBS-spectrum represents the data extremely well. For instance, a slope with a numerical value close to zero but with high degree of scatter may have a lower diversity than a steeper slope but with a better fit (i. e. higher correlation coefficient).

In the current research, I have shown, using the biomass-size diversity and evenness indices listed in Table 2.3, that the planktonic biomass size-distribution in Georges Bank differs among mixed, frontal and stratified waters. However, at this time I cannot attempt to give a mechanistic explanation for this observed pattern. My interpretation is limited by the sampling design both in time and space. In addition, a comparative approach in the search of patterns is impossible since there are no other studies done on biomass size-diversity, without the interference of non-living matter, in the pelagic system.

In spite of these limitations, there are some features and hypotheses emerging from my results. Very high biomass-size diversity and evenness were found both in central Georges Bank and in the two stations from the oligotrophic ocean (Table 2.7). Therefore, it seems very unlikely that high biomass-size diversity or evenness values in a planktonic community are related to the rate of primary production of the system. Two alternative hypotheses are that high levels of biomass-size diversity are related to the stability of primary production rates or to the relative constancy of the system. It is known that central Georges Bank presents higher and less fluctuating rates of primary

production than frontal and stratified waters throughout the year (O'Reilly et al. 1987). A more constant system would allow organisms with different turnover rates (i. e. size) to be reasonably represented in the system. As I mentioned before these hypotheses are highly speculative however, these hypotheses are able to be falsified (*sensu* Popper 1959) with proper experimental design or by comparing biomass-size diversity indices in different kinds of ecosystems.

Some limitations and advantages of NBS-spectra for the study of biomass size-distributions.

There are several ways to represent and analyze biomass size-distribution data. For example, pelagic biomass size-distributions have been analyzed using diversity indexes (Parsons 1969), Sheldon's spectra (Sheldon et al. 1972), normalized biomass-spectra (e. g. Platt et al. 1984, Rodriguez and Mullin 1986b) and fractals (Haedrich 1986). There are several other methods that have the potential to be used in analyzing biomass size-distribution such as Junge distributions (Junge 1963), factor analysis (Klovan 1966, Syvitski 1991), and detailed analysis of the statistical moments of a size frequency distribution (e. g. Friedman 1962, Friedman and Johnson 1982). The problem of comparing and analyzing size-distributions is not a simple one and the method to be used depends on the objectives of the research. In other words, one of the more important elements in analyzing size-distribution data is that the researcher should decide precisely what information is required from the data (McCave 1979).

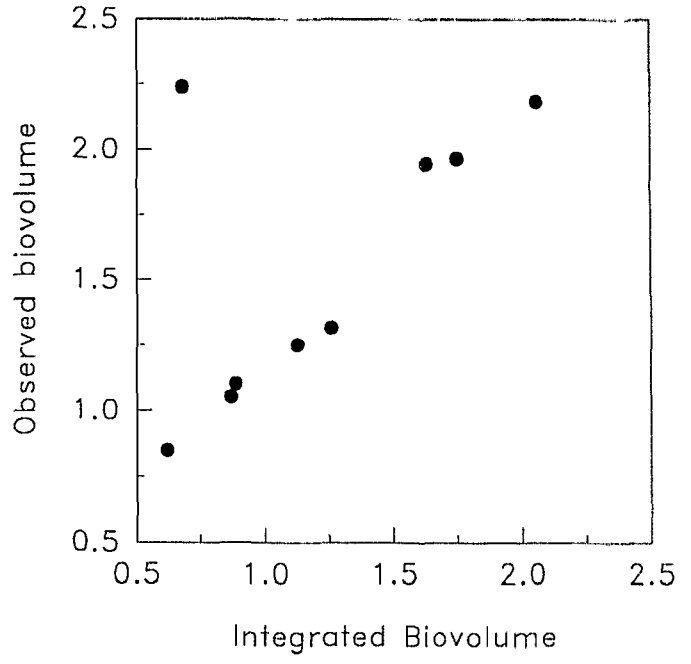
One of the approaches chosen throughout this thesis is the normalized biomass spectrum (Platt and Denman 1977, 1978). The approach is holistic and the whole size-structure of a planktonic community is summarized by only two parameters which are the slope and the intercept of the ordinate of the NBS-spectrum. This representation has been

criticized by an apparent lack of sensitivity to the detailed size structure (e. g. Ahrens and Peters 1991a). However the same authors recognized that

"the low variability of the parameters of these ... models reflects both an underlying similarity in the average trends of the various size-spectra and the insensitivity of the statistical models to departures from these averages among individual size classes".

I agree with Ahrens and Peters (1991a) that the NBS-spectrum is not very sensitive to particular changes in some size classes. For example Figure 2.12 shows the relationship between the observed total planktonic biomass in each of the stations and those ones estimated from the integration under the NBS-spectrum. The total biomass predicted by the NBS-spectra is underestimated by a factor of 4.7 % to 27.2 % when biomass is expressed as biovolume and 16.6% to 39.7 % when biomass is expressed as carbon (these estimations exclude Stn. GB9). Ahrens and Peters (1991a) also found in their study of limnoplankton that the NBS-spectra underestimated the total observed biomass. Analyzing my own data it became clear that the non-linearities found in the bacterioplankton size-range are the main responsible for the detected underestimation. Non linearities in the bacteria size range are crucial due to their enormous contribution to the total biomass of the community. In addition, the major peak of biomass due to the high concentration of *Calanus* sp. observed in station GB9 is clearly not represented properly by the parameters of the NBS-spectrum (see Figure 2.12). Indeed, the total biomass of station GB9 was underestimated by the NBS-spectrum model by 69.8 % and 64.8 % when biomass is expressed as biovolume and carbon respectively. Obviously, the NBS-spectrum is a linear representation and consequently any departures from linearity will affect the accuracy of the predictions of the NBS-spectrum.

Figure 2.12.- Relationship between observed and estimated total planktonic biomass from NBS-spectra in each station. Biovolume = $\mu m^3\ m^{-3} \times 10^{12}$, Biomass = $\mu gC\ m^{-3} \times 10^3$.


2.5
2.0
1.5
1.0
0.5
Observed biovolume
0.5
1.0
1.5
2.0
2.5
Integrated Biovolume

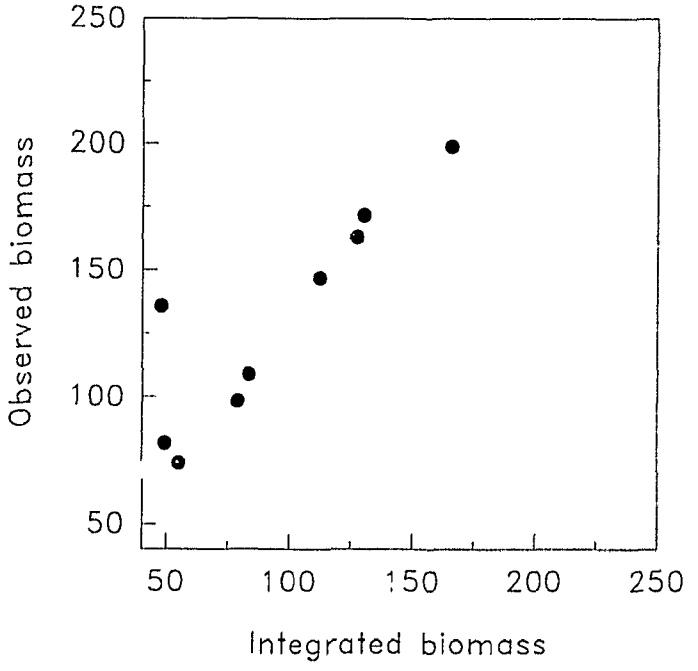

250
200
150
100
50
Observed biomass
50
100
150
200
250
Integrated biomass

Figure 2.12

Notwithstanding the apparent insensitivity of the NBS-spectrum this representation has several positive characteristics. For instance,

a) It is a model with sound biological bases. It was developed from general allometric principles (Platt and Denman 1977, 1978, see chapter 1). Other representations or parameters extracted from size distribution data have no ecological meaning (e. g. fractal dimensions, Haedrich 1986);

b) As a holistic method, the NBS-spectrum allows the elucidation of general trends in ecosystems and not to be overwhelmed by the details. As Ursin (1982) stated:

"When a marine biologist discovers that something has changed or oscillates he is inclined to write a paper on it. When he finds that everything is as usual there is no investigation to write. He is looking for changes. There is an extensive literature on variability, but not much on the fundamental stability of marine ecosystems";

c) The NBS-spectrum the use of statistics with a relatively low number of observations. Other techniques such as factor analysis would require a much more extensive data set.

In my opinion the most appropriate way to analyze biomass size-distribution data is using several complementary methods. For example, in the current study NBS-spectra were used to find the general patterns of the biomass size-distribution in Georges Bank. Using this representation, I found out that in Georges Bank, biomass, as biovolume, increases as a power function of body size and that the increase of biomass among successive size classes is even greater in the zooplankton size-range. In addition, the NBS-spectrum allowed the comparison of biomass size-distribution patterns between Georges Bank and the oligotrophic ocean. However, the NBS-spectrum approach did not provide clear information on biomass size-distribution patterns within Georges Bank and its surrounding waters. In other words the NBS-spectrum approach was relatively

insensitive to the horizontal changes within the bank and vicinity. The biomass-size diversity and evenness indexes, however, clearly detected a horizontal pattern in the distribution of biomass by size in Georges Bank.

In brief, it must be emphasized that NBS-spectrum is only one approach to the analysis of biomass size-distribution and although it does not extract full information from the data it is still a very useful tool. More research on the statistical methodology to be used to extract information from biomass size-spectra is necessary.

CHAPTER 3

BIOMASS, RESPIRATION, AND SIZE IN THE PELAGIC ECOSYSTEM: AN EMPIRICAL STUDY USING SIZE-SPECTRA.

ABSTRACT

A study of the size-distributions of metabolic activity and biomass in the pelagic ecosystem was carried out at several stations on Georges Bank, North-East Channel, Gulf of Maine, and on the Scotian Shelf. Metabolic activity was estimated using the electron transport system activity technique. Biomass was estimated by microscopy, image analysis and gravimetry. The results show that in the pelagic zone metabolic activity decreases as a power function of body size at the community level of organization. The slopes of the normalized biomass size-spectra (NBS-spectra) indicate that biomass remains constant or slightly decreases with increasing body-size (when plotted on a log-log scale) at all stations in this study. This finding is in agreement with the hypotheses of Sheldon et al. (1972) and Platt and Denman (1977, 1978) regarding the distribution of biomass by size in the oceanic ecosystem. The slopes of the NBS-spectrum and the normalized metabolism size-spectrum (NMS-spectrum) are -1.07 (carbon units) and -1.22 , respectively, when all stations studied are combined. At all stations the NMS-spectrum has a more negative slope than the NBS-spectrum. This indicates that the smallest organisms play even a more important role than the larger ones from a metabolic activity than from a biomass point of view. The results of this study, and an analysis of other published data suggest that the linearity of the NMS-spectrum and the numerical value of its slope (-1.2) may be characteristics of the pelagic ecosystem.

INTRODUCTION

A major goal in contemporary oceanographic research is to predict the response of oceanic ecosystems to continuing anthropogenic stresses and to natural global changes. However, the analysis of the marine ecosystem is particularly difficult because of the nature of its complexity (O'Neill et al. 1986). One way to deal with ecosystem complexity is to analyze the behavior of some macroscopic properties of the whole system (Platt et al. 1981). The remaining question, however, is which ecosystem properties are important in predicting ecosystem behavior. Since an ecosystem is governed by the cycling of matter and the flow of energy, we must select macroscopic properties that are closely related to these driving forces.

Respiration is a key process in the use of biological energy in the ocean, and it is therefore an obvious choice for a macroscopic ecosystem property. Overall, most energy is dissipated through the trophic web as respiratory loss. Since the intensity of heat production or respiration can be equated, with some approximation, to the specific rate of entropy production in the system (Zotina and Zotin 1982), the energy expended in respiration should be equal to the minimum energy necessary to maintain the biological structure in the ecosystem. On the other hand, biomass can be viewed as the ordered structure of a community (Odum 1971), and, consequently, the relationship between biomass and respiration is crucial in determining the flux of energy in the pelagic ecosystem.

Until recently, the compartmentalization of ecosystems was usually accomplished by grouping organisms according to taxa or trophic levels. These two formulations seem to be, however, insufficient to describe the structure and dynamics of a given ecosystem

(Rigler 1975, Cousins 1980, Platt 1985). A more recent approach to analyze the structure of the pelagic ecosystem is to specify the distribution of biomass as a function of organism size. This approach has been used both in theoretical (e.g. Kerr 1974, Platt and Denman 1977, 1978, Silvert and Platt 1978, 1980, Borgmann 1982, 1983, 1987, Dickie et al. 1987a) and empirical (e.g. Sheldon et al. 1972, 1973, Sprules et al. 1983, Platt et al. 1984, Rodriguez and Mullin 1986 a, b, Sprules and Munawar 1986, Warwick and Joint 1987, Jimenez et al. 1987, 1989, Witek and Krajewska-Soltys 1989, Ahrens and Peters 1991a) analyses of ecosystems. It has also formed the basis for the construction of models to estimate fish production in multispecies fisheries (e.g. Sheldon 1977, Borgmann 1982, Boudreau and Dickie 1989).

However, despite the growing descriptive information about biomass size-structure in the pelagic system, the study of the relationship between biomass size-distribution and the rate of ecological processes at the community level of organization has largely been ignored. Some exceptions related to respiration rates have been the theoretical analysis of Kamenir and Khaylov (1987) and the recent empirical study of Ahrens and Peters (1991b) on limnoplankton.

The simultaneous study of the size-distribution of biomass and metabolic activity can increase understanding of the fluxes of energy and matter in the pelagic ecosystem. In addition, it can provide insight into the understanding of the underlying causes of the observed regularities in the size-structure of pelagic systems. Consequently, the present study was designed to achieve the following objectives:

1.- To determine the relationship between respiration and body size (metabolic size-spectra) at the community level of organization in several pelagic ecosystems, and;

2.- To analyze the relationship between biomass size-spectra and metabolic size-spectra in planktonic communities.

MATERIAL AND METHODS

The sampling was conducted in the North West Atlantic during September 1990 on board the CSS Dawson (Department of Fisheries and Oceans, Canada). The location of the stations is described in Table 3.1 and shown in Figure 3.1.

Bacterio-, Nano- and Microplankton sampling

Prior to every sampling, all material was carefully washed with 10% HCL and distilled water. At each station, water was taken every 10 m with 10 liter Niskin bottles from surface to 100 m depth or few meters above the bottom when shallower. The water taken from each of the sampling depths was mixed in a 100 l tank to provide an integrated sample of the water column. The integrated sample was size-fractionated immediately by gentle reverse filtration through Nytex plankton netting. Then, 2 to 4 l of every size-fraction were filtered onto glass fiber filters (Whatman GF/F) with a pressure of less than 100 mm Hg for future ETS analysis. During the whole process, special care was taken to maintain the temperature within $\pm$ 2 ^{o}C of the *in situ* temperature of the integrated sample. The filters were then stored at once in liquid nitrogen. In addition, 500 ml subsamples of every size fraction were fixed with 2% buffered formaldehyde for future biomass estimations of nano- and microplankton For bacterial biomass estimation, 20 ml subsamples from the integrated samples were fixed with pre-filtered (0.2 µm Nucleopore filters) formaldehyde to a final concentration of 2%.

Zooplankton sampling

Vertical tows were carried out with Bongo nets (mesh size 64 µm) provided with a frame specially designed (Bedford Institute of Oceanography) to hold the net in vertical

TABLE 3.1.- Location of the stations.

Station number	Location		Geographical name
	Lat (N)	Long (W)	
1	42° 22.74'	66° 38.43'	North East Channel
2	41° 42.38'	66° 42.83'	Georges Bank
3	41° 56.59'	66° 14.98'	Georges Bank
4	42° 22.59'	66° 15.61'	North East Channel
5	43° 27.75'	66° 57.74'	Jordan Basin
6	42° 48.61'	65° 19.96'	Scotian Shelf

Figure 3.1.- Location of sampling stations.

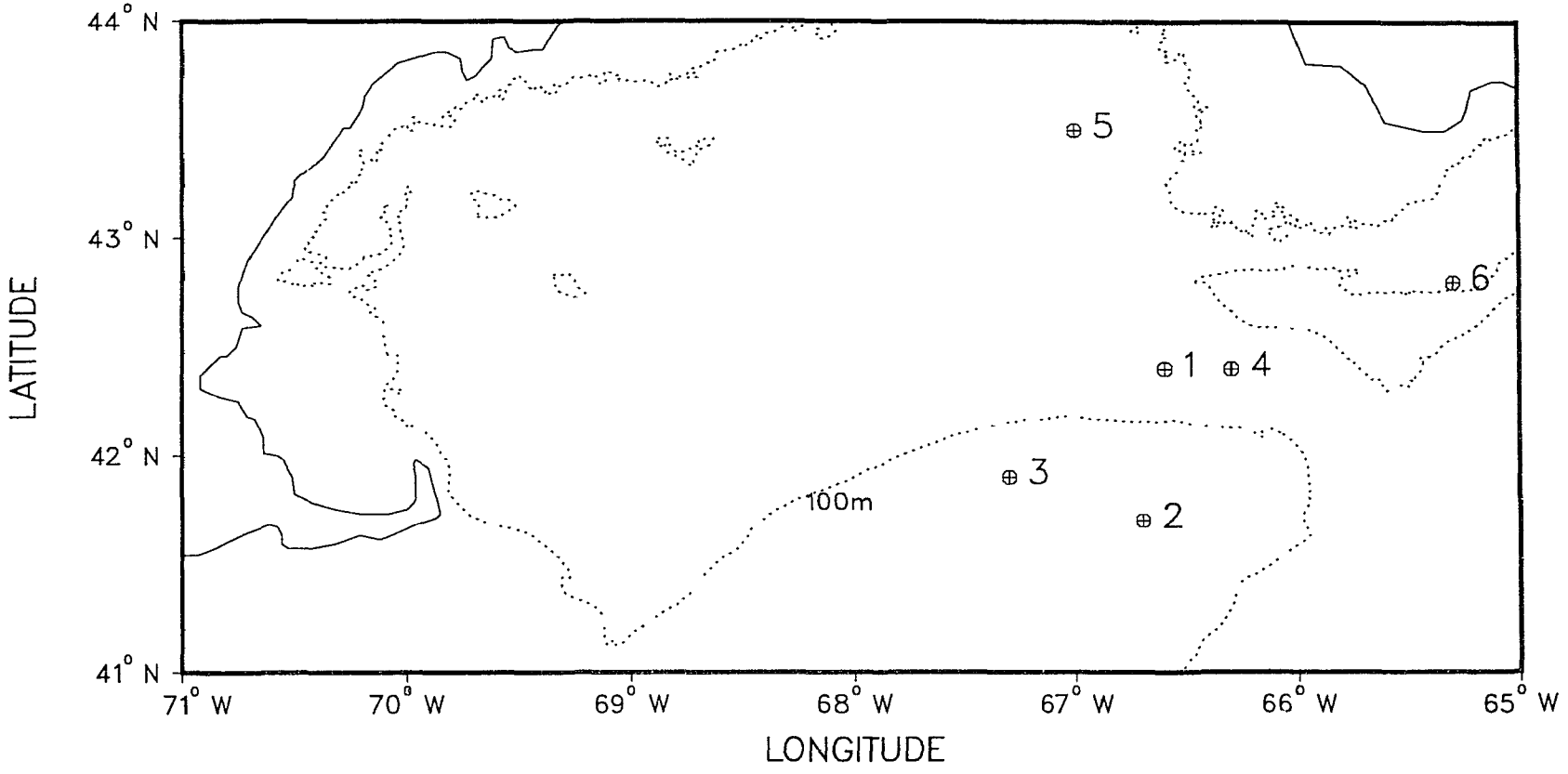

44° N
43° N
42° N
41° N
LATITUDE
71° W
70° W
69° W
68° W
67° W
66° W
65° W
LONGITUDE
5
6
1
4
3
2
100m

Figure 3.1

position during the tows. A TSK flowmeter (Tsurumi-Seiki Co., Ltd., Japan) was attached to each side of the Bongo.

Since the objective of the sampling was to have a representative sample of the zooplankton actively interacting with the nano- and microplankton of the upper 100 m of the water column, the maximum depth chosen for the vertical tow was usually about 200 m - or a few meters above the bottom when shallower - to account for the vertical migration of zooplankters. Immediately after the tow, the catch from one of the bongo sides was processed for ETS analysis as follows: the zooplankton was size fractionated using sieves of 4000, 2000, 1000, 500, 250, 125, and 64 μm mesh size. The organisms were then filtered onto glass fiber filters (Whatman GF/F) with a pressure of less than 100 mm Hg. Whenever necessary, a Folson splitter was used to divide the biomass of the size-class, and consequently, diminishing the amount of biomass per filter. However, all the splitter aliquots were processed. The filters were then stored immediately in liquid nitrogen until their analysis in the laboratory.

The catch from the other net of the Bongo was used to estimate zooplankton biomass. The zooplankton was passed through the same set of sieves than for the ETS analysis and then filtered onto pre-weighted, pre-combusted (450 °C) glass fiber filters (Reeve Angel 934 AH). The filters were then dried in an oven at 60 °C for 36 hr and kept in desiccators.

Bacterial biomass

The cells were stained with DAPI (4',6-Diamidino-2-phenylindole dihydrochloride hydrate) according to Porter and Feig (1980) and filtered onto 0.2 μm pore size black filters (Nucleopore Corp., Pleasonton, Calif.) by using vacuum pressure of less than 100 mm Hg. Three replicates were obtained from each sample. In each of the

replicates, 10 microscopes fields were counted with the help of an ocular grid. The bacteria were counted using a Leitz Orthoplan epifluorescence microscope under 1000X magnification.

Photographs (Kodak Ektachrome, P800/1600, slides) were taken of fields randomly selected. The slides were projected to a final magnification of 1500X and then analyzed by image analysis. Between 250 and 400 cells were measured in each sample. Biovolumes were calculated by the following formula:

$$V = (\pi / 4) W^2 (L - W/3) \quad (1)$$

where L is the length of major axis, and W is the length of minor axis.

Nano- and Microplankton Biomass

From each sample 100 ml were sedimented using the Uthermol technique (Lund et al. 1958). Subsequently, the organisms were observed under 125X, 200X, 500X and 1250X magnifications. Rose Bengal was added to the samples in the settling chambers to enhance image contrast and to facilitate separation between living and non-living matter. The sizing and counting of organisms were carried out using an Image Analyzer as described by Campana (1987) with the following modifications: (a) Video camera with a Newvicon tube; and, (b) Oculus 300 (Coreco Inc.) framegrabber video digitizer board. An ocular micrometer and a Newporton Graticule (May 1965) were also used for direct sizing and counting. Approximately 200 organisms were sized at each magnification. The volume of the organisms larger than 20 μm (linear dimension) was estimated according to the recommendations of Miyai et al (1988) as well as those of the Baltic Marine Environment Protection Commission (1983). The volume of organisms smaller than 20

μm (linear dimension) was estimated assuming basic geometrical shapes. Biovolumes were converted to Carbon using the equations of Strathmann (1967).

The nano- and microplankton biomass data are presented in two forms. When the goal is the comparison of biomass- to metabolism size-spectra, the total biomass of each of the fractionated samples is used. Thus, for example, the total biomass in the size fraction 20-50 μm is obtained by subtracting the total biomass in the less than 20 μm size-fraction from that of the less than 50 μm fraction. On the other hand, when the objective was to report the shape of biomass size-distribution, or to compare biomass size-spectra from different stations, the microplankton size-spectra generated from the less than 130 μm sample was merged with the bacterioplankton and zooplankton size-spectra.

Zooplankton biomass

The size-fractions were weighed, on the land, with an electronic balance (Mettler AE163, 0.01mg). The carbon content of the zooplankton size-fractions was determined using a Perkin Elmer 2400 CHN Elemental Analyzer.

To convert zooplankton biomass to biovolume the following equation from Wiebe (1988) was used:

$$\log F = -1.842 + 0.865 \log D \qquad (2)$$

where F is Displacement volume (cc m^{-3}), and D is dry weight (mg m^{-3})

To change the scale from length to weight as carbon, the following regression was used (Rodriguez and Mullin 1986b):

$$\log T = 2.23 \log G - 5.58 \quad (r^2 = 0.98) \qquad (3)$$

where T is organism size (µg C) and G is the geometric mean (µm) of the mesh size retaining the organism and the next largest mesh size.

Measurement of the respiratory electron transport activity

Most of the oxygen consumption in eukaryotes and prokaryotes is due to oxidative phosphorylation (Tzagoloff 1982). The process of oxidative phosphorylation is driven by the respiratory electron transport system (ETS), which is located in the inner membrane of eukaryotic mitochondria and in the cell membrane of prokaryotes (Packard 1985 a, b). Since the ETS regulates respiratory oxygen consumption, a measurement of the ETS activity provides an estimation of the metabolic activity of organisms.

The activity of the respiratory electron transport system (ETS) of the bacterio-, nano- and micro-plankton was determined according to the method described by Packard and Williams (1981). The zooplankton ETS activity was determined using the method of Owens and King (1975).

Briefly, the ETS-technique consisted of:

1) Generation of a cell-free homogeneate of the organisms. The homogeneates were obtained by grinding the plankton with phosphate buffer in a teflon-glass tissue grinder at 0-4 ^{o}C. Subsequently, the homogeneate was centrifuged for 7 minutes in a thermoregulated centrifuge at 3000 rpm.

2) Incubation (20 minutes) of the clarified supernatant fluid from the centrifuged homogeneate with: (a) succinate and NADH to saturate the mithocondrial ETS; (b) NADPH to saturate microsomal and some bacterial ETS; and, (c) an artificial electron acceptor [2- (*p*-iodophenyl) - 3 - (*p*-nitro-phenyl) - 5 -phenyl tetrazolium chloride (INT)] to register the electron transmission rate. The incubation was stopped with the addition of a phosphoric acid-formalin quench solution. A second centrifugation (7 minutes, 3000 rpm.) was then carried out to diminish the turbidity of the solution. The solution was then kept in the dark and at 0-4 ^{o}C until the spectrometric determination (less than 1 hour).

The incubation temperature of the assay was 14 ^{o}C, which corresponded approximately to the surface temperature of the stations studied at the time of sampling (CTD data). The ETS activity was corrected to *in situ* temperature (i. e. the average temperature of the water column sampled) using the Arrhenius equation (Packard et al. 1971). The activation energy was obtained according to the following equation as given by Packard et al. (1975):

$$E_a = 0.118\,T + 13.7$$

where E_a is the Arrhenius activation energy and T is temperature in degrees Celsius.

3) Spectrophotometric determination of the rate of INT reduction to formazan. The absorbance was measured at 490 nm and at 750 nm on a spectrophotometer (PYE Unicam PV 8600 UV/VIS, Philips). The 490 nm reading is proportional to INT-formazan production; the 760nm reading serves as a turbidity blank.

4) To calculate the ETS activity, the following equation was used:

$$\text{ETS activity} = \frac{60 \times H \times N \times (A - S)}{1.42 \times J \times P \times G}$$

where:

H is the crude homogeneate volume (ml); N is the volume of the quenched reaction mixture (ml); A is the difference between the 490 nm and the 760 nm reading with each measurement zeroed against the pigment blank; S is the A of the reagent blank; J is the volume of clarified homogeneate used in the enzyme assay (ml); P is the volume of filtered seawater (l); and G is the incubation time (minutes). The two constants , 60 and 1.42, convert the measurement to units of hours and oxygen volume (µl), respectively.

The plankton samples for ETS analysis were stored in liquid nitrogen for approximately three weeks. It is known that liquid nitrogen preserves the ETS activity appropriately (Relexans and Etcheber 1985).

Some microplankton samples were lost due to problems with the quality of the tetrazolium salt (INT). High reagent blanks, exceeding by far the recommended 0.05 (A_{490} ; Packard and Williams 1981), were found when the INT acquired from Aldrich (USA) was used. However, the INT provided by Aldrich (Germany) was up to the standards necessary to carry out the ETS essay.

Since Whatman GF/F filters retain particles down to 0.7 µm (Whatman Laboratory Products Inc. technical information), the ETS activity measurements are considered to be representative of organisms larger than 0.7 µm.

In this study, the enzyme activity is reported as the reduction rate of the electron acceptor in stoichiometrically equivalent units of oxygen. The results were not converted to *in situ* oxygen consumption due to the controversy regarding the conversion factors to be used (e.g Bamsted 1979, 1980, Kenner and Ahmed 1975, King and Packard 1975; for a review see Packard 1985a).

Data presentation and statistical considerations

Normalized size-spectra were constructed to analyze the size-distribution of the variables of interest (i. e. biomass and metabolic activity). The spectra were normalized as described by Platt and Denman (1977, 1978). The normalization is necessary because the variable has to be expressed relative to some size range. A biomass size-spectrum has no meaning unless the width of the size classes is carefully defined (Borgmann 1987).

In brief, the procedure consists in taking the variable of interest $y(s)$ in the size class characterized by the weight or volume (s) and dividing it by the width of the size class Δs. Thus the normalized version of the variable y is equal to :

$$Y(s) = y(s) / \Delta s \qquad (4)$$

Regression analysis was carried out using least squares (Model I) linear regression. In comparing the slopes and intercepts of the regression lines an F test and the Newman-Keuls multiple range test were used as described by Zar (1984). Barlett's test was used to check the assumption of homogeneity of variance.

Hydrographic variables

Temperature, salinity and density (σ_t) of the water column were obtained with a CTD deployed at each station.

RESULTS

The total metabolic activity of the micro- and zooplankton from the stations studied is shown in Table 3.2. These results are within the range of values previously reported for the same geographical area (Jones and Setchell 1979). However, the metabolic activity of microplankton reported by Packard and Williams (1981) for some stations in the region is considerably higher than my estimates, suggesting that fluctuations in total metabolic activity of the planktonic community may be considerable.

The normalized biomass size-spectra (NBS-spectra) in biovolume units (NB_VS-spectra) from the stations studied are shown in Figure 3.2. The parameters of the NBS-spectra can be seen in Table 3.3. The data have been presented in carbon as well as in biovolume units because the slope of the NBS-spectrum varies depending on how biomass is expressed (see Chapter 1). Indeed, the slopes of the NBS-spectra were found to be more negative when constructed in carbon units than in volume units. The slopes of the NBS-spectra indicate that biomass remains constant or slightly decreases with increasing body-size (when plotted on a log-log scale) at all stations in this study. This finding is in agreement with the hypotheses of Sheldon et al. (1972) and Platt and Denman (1977, 1978) regarding the distribution of biomass by size in the oceanic ecosystem.

The coefficient of determination (r^2) for the NBS-spectra is highly significant in all the stations studied (Table 3.3). Slight deviations from a linear NBS-spectrum occur at sizes where different methods for estimating biomass interface (Figure 3.2). This is particularly evident at the methodological interface between epifluorescence microscopy and inverted microscopy. On the other hand the bacterioplankton size-distribution seems to deviate from linearity, having a bell-shaped distribution. This characteristic shape has been noticed in other studies on bacterial size-distribution (e.g. Robertson and Button

TABLE 3.2. Total microplankton and zooplankton ETS activity at the stations studied. The term microplankton as used here includes all organisms between 0.7 μm and 130 μm (linear dimension) captured by a 10 l Niskin bottle. Zooplankton as used here define all those organisms captured by vertical tows (mesh size 64 μm) with a body size between 64 and 8000 μm (linear dimension).

	Microplankton		Zooplankton	
Station	Depth (m)	ETS ($\mu l\ O_2\ h^{-1}\ m^{-3}$)	Depth (m)	ETS ($\mu l\ O_2\ h^{-1}\ m^{-3}$)
1	-----	-------	0-270	56.51
2	0-45	2670.00	0-45	495.20
3	0-60	1319.70	0-65	187.33
4	0-100	541.12	0-200	44.66
5	0-100	697.20	0-170	59.34
6	0-100	310.00*	0-100	131.14

* Respiration of organisms from 0.7 μm to 20 μm (linear dimension) only.

Figure 3.2.- Biomass size-spectra from the locations studied. Normalized Biomass ($\mu m^3\ m^{-3} / \Delta\ \mu m^{-3}$) and body size ($\mu m^{-3}$).

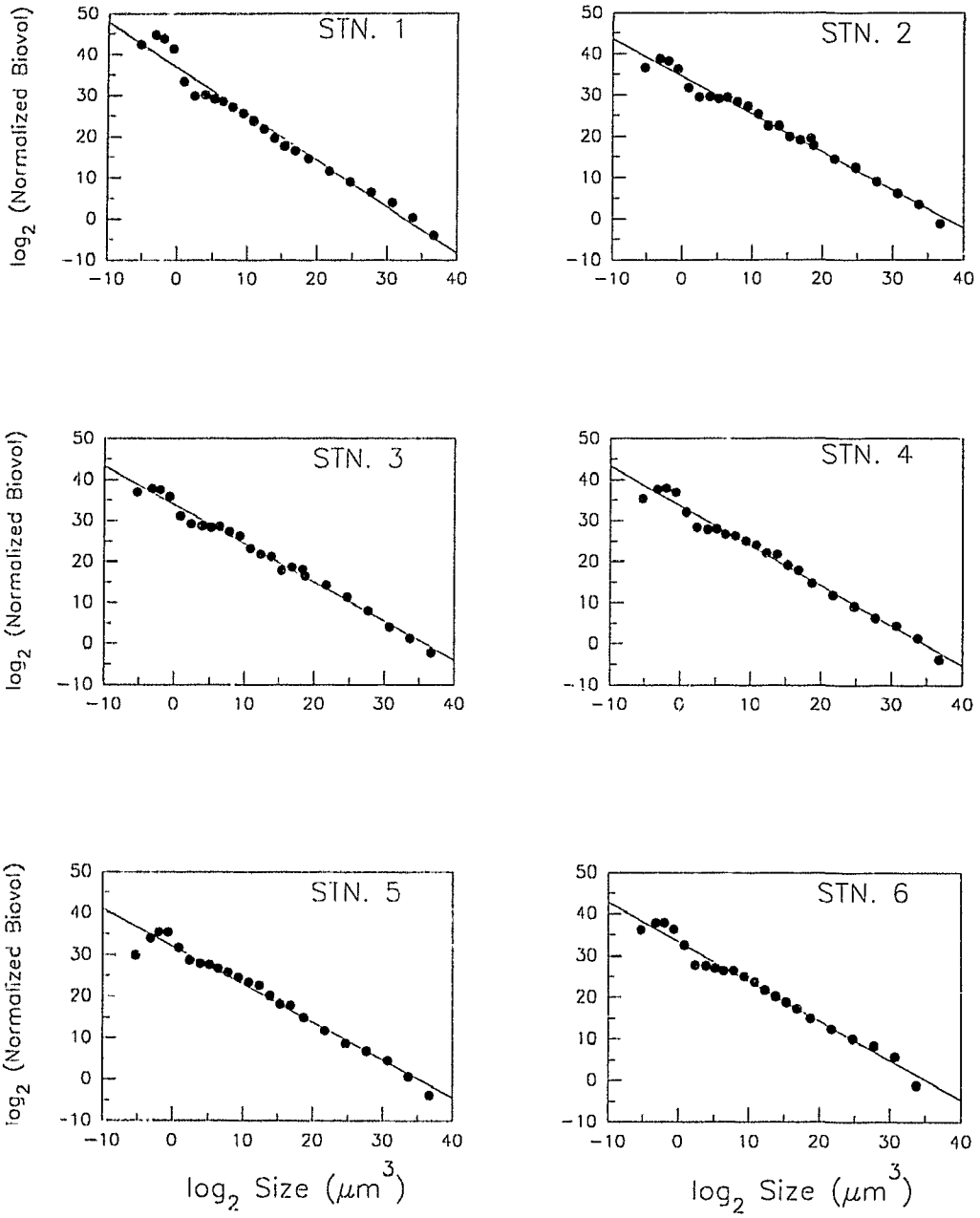

STN. 1
STN. 2
STN. 3
STN. 4
STN. 5
STN. 6
log2 (Normalized Biovol)
log2 Size (μm3)
50
40
30
20
10
0
-10
-10
0
10
20
30
40

Figure 3.2

TABLE 3.3. Regression parameters of the normalized biomass size-spectra from each station. Model: $\log_2$ (Normalized biomass) = $\log_2$ intercept + b $\log_2$ Size. Biovolume units: Normalized biomass ($\mu m^3\ m^{-3} / \Delta\mu m^3$), Nominal Size ($\mu m3$). Carbon units: Normalized biomass ($\mu g\ C\ m^{-3} / \Delta\mu g\ C$), Nominal size ($\mu g\ C$).

Station	Geographical Name	Slope	$\log_2$ Intercept	r^2	N	Std. Err. Slope	Std. Err. Y Est.
Biomass in biovolume units							
1	Northeast Channel	-1.13	36.65	0.97	23	0.040	2.292
2	Georges Bank	-0.92	34.49	0.98	24	0.024	1.382
3	Georges Bank	-0.95	33.87	0.998	24	0.022	1.280
4	Northeast Channel	-0.97	33.59	0.98	23	0.027	1.542
5	Jordan Basin	-0.91	32.03	0.97	23	0.034	1.924
6	Scotian Shelf	-0.95	33.32	0.98	22	0.030	1.564
All stations combined		-0.97	34.00	0.97	139	0.014	2.010
Biomass in carbon units							
1	Northeast Channel	-1.26	9.37	0.97	23	0.047	2.371
2	Georges Bank	-1.01	12.58	0.98	24	0.027	1.370
3	Georges Bank	-1.04	11.21	0.99	24	0.024	1.221
4	Northeast Channel	-1.08	10.14	0.98	23	0.032	1.603
5	Jordan Basin	-1.00	10.31	0.97	23	0.040	1.986
6	Scotian Shelf	-1.05	10.62	0.97	22	0.037	1.702
All stations combined		-1.07	10.72	0.97	139	0.017	2.071

1989, Ulloa et al. 1992). However, it is unknown to what extent the size-distribution of bacterioplankton, particularly the decay noted at the smallest sizes, is affected by the resolution of the methods used (see Chapter 1).

The slopes of the NB_VS-spectra (see Table 3.3) range from -1.13 in the North East Channel to -0.91 in Jordan Basin. The two stations located in the North East Channel (stations 1 and 4), the most oligotrophic of the stations studied, presented the more negative slopes. This is in accordance with observed relations between trophic state of ecosystems and the slope of the NBS-spectra (Sprules and Munawar 1986). The slope of the NBS-spectrum from station 1 was significantly different ($P < 0.01$) from the rest of the stations located off the Northeast Channel. The slope of the NBS-spectrum from the other station located in the Northeast Channel (Station 4) was not significantly different ($P < 0.01$) from the other stations studied. On the other hand, no conspicuous differences were detected ($P < 0.01$) among the slopes of the NBS-spectra from the stations located on Georges Bank and those located in the Gulf of Maine or Scotian shelf areas.

The intercept of the normalized-biomass axis of the NBS-spectra is considered to be an index of organism abundance in the community (Sprules and Munawar 1986). Obviously, the use of intercepts to compare abundances among spectra is only valid provided that the slopes of the NBS-spectra are not too different from each other. When comparing the intercepts from the different zones studied (Table 3.3), no clear pattern emerges. Caution must be exercised, though, in generalizing the results regarding slopes and intercepts since my sampling program is very limited both in the temporal as well as in the spatial scales.

The contribution of the different size-fractions to the overall metabolism of the community is shown in Figure 3.3. If the objective of a study is to analyze the

Figure 3.3.- Metabolic activity ($\mu l\ O_2\ h^{-1}\ m^{-3}$) of each size fraction from all the stations studied.

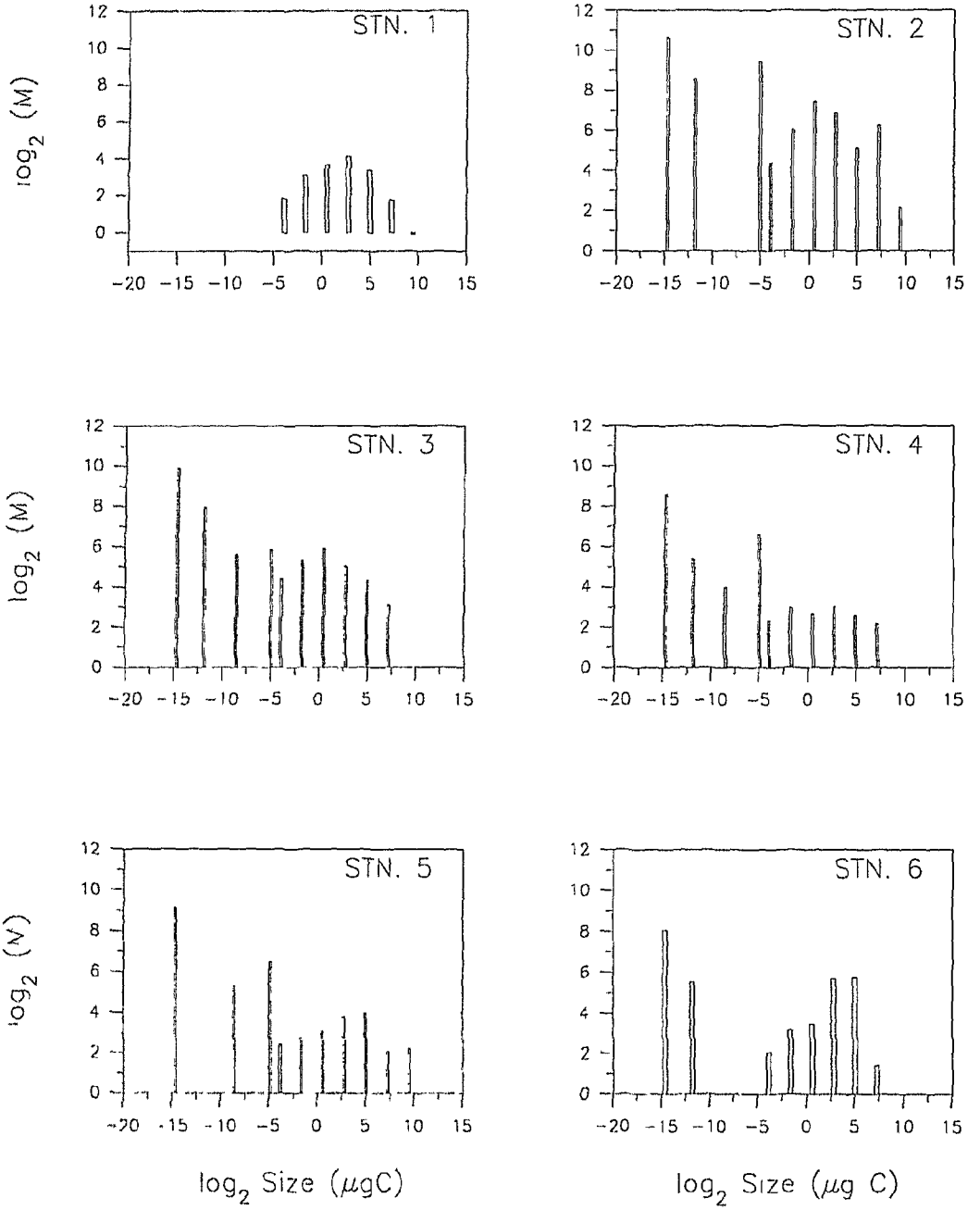

STN. 1
STN. 2
STN. 3
STN. 4
STN. 5
STN. 6
log2 (N)
log2 Size (μgC)
log2 Size (μg C)

Figure 3.3

distribution of metabolic activity through the whole size-spectrum, the interpretation of results from size-fractionation studies can be difficult unless the data is normalized by the width of the size-fractions used. For example, in station 6 (Scotian Shelf) the size-fractions 523.6 - 4188.8 μm^3 and 5.23 x 10^8 - 4.18 x 10^9 μm^3 have ETS activities of 45.53 $\mu l O_2 h^{-1} m^{-3}$ and 53.45 $\mu l O_2 h^{-1} m^{-3}$ respectively. Evidently, the size fraction 5.23 x 10^8 - 4.18 x 10^9 μm^3 has a slight higher respiration than the size-fraction 523.6 - 4188.8 μm^3. However, the window through which metabolic activity is evaluated (i. e. the width of the size-fraction) corresponds to 3.66 x 10^9 μm^3 for the size fraction 5.23 x 10^8 - 4.18 x 10^9 μm^3 and only 3665.2 μm^3 for the size-fraction 523.6 - 4188.8 μm^3. After normalizing the spectrum by the width of the size-fractions it becomes clear that metabolic activity decreases with size.

The normalized metabolism size-spectrum (NMS-spectrum) from each of the stations can be described by a straight line (see Figure 3.4, Table 3.4). The coefficients of determination (r^2) of the regression lines are highly significant (Table 3.4). The parameters of the NMS-spectrum from the Georges Bank stations present the most negatives slopes and the highest intercepts on the normalized-metabolism axis of all stations studied. This indicates that there is a much higher metabolic activity, particularly in the smallest size classes, on Georges Bank than at the rest of the stations. My results suggest that metabolic activity decreases steadily with body size in the pelagic system with a slope of approx. -1.22 for a NMS-spectrum and of -0.22 for an unnormalized metabolism size-spectrum.

To compare NMS-spectra with NBS-spectra I constructed biomass-spectra based on the observed total biomass of each size-fraction (SFS). In this way, the efficiency of the size-fractionation procedure is taken into account. The parameters of the NBS-spectra(SFS) slightly differ from those of the NBS-spectra. This is likely to be the effect

Figure 3.4.- Normalized metabolism size-spectra from the location studied. Normalized ETS ($\mu l\ O_2\ h^{-1}\ m^{-3}\ \mu g\ C^{-1}$); Body size μg C.

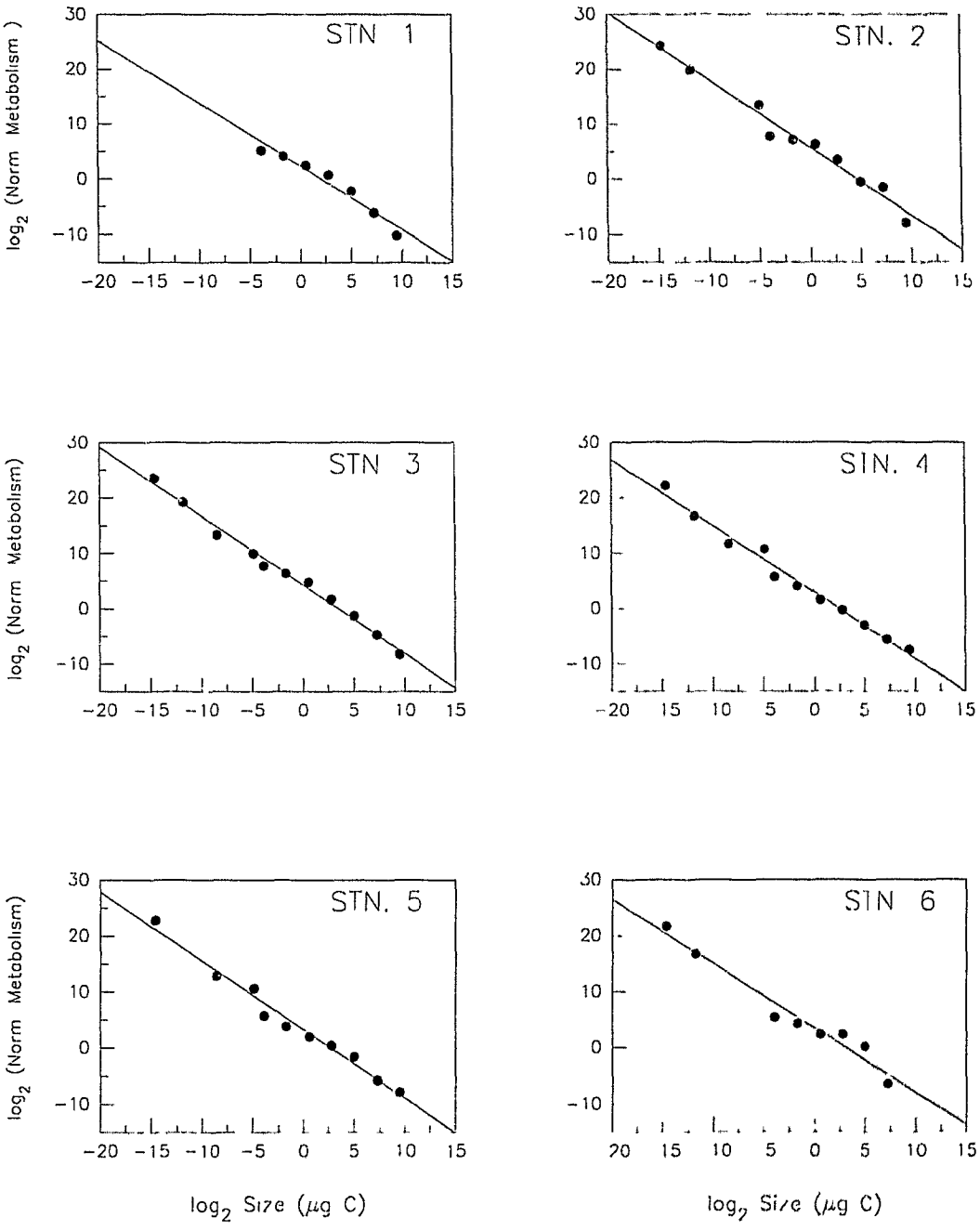

STN 1
STN. 2
STN 3
STN. 4
STN. 5
STN 6
log2 (Norm Metabolism)
log2 Size (μg C)
30
20
10
0
-10
-20 -15 -10 -5 0 5 10 15

Figure 3.4

TABLE 3.4.- Regression parameters of the normalized metabolism size-spectra from each station studied. Model: $\log_2$ (Normalized metabolism) = $\log_2$ Intercept + b $\log_2$ (Nominal Size). Carbon units: Normalized metabolism ($\mu l\ O_2\ h^{-1}\ m^{-3}\ \mu g\ C^{-1}$), Size (μg C). Volume Units: Normalized metabolism ($\mu l\ O_2\ h^{-1}\ m^{-3}\ \mu m^{-3}$), Size (μm^3).

Station number	Geographical Name	slope	$\log_2$ Intercept	r^2	N	Std. Err Slope	Std. Err. Y Est.
Carbon units							
1	Northeast Channel*	-1.14	2.35	0.95	7	0.119	1.406
2	Georges Bank	-1.23	5.76	0.98	10	0.068	1.612
3	Georges Bank	-1.24	4.30	0.99	11	0.040	0.974
4	Northeast Channel	-1.20	2.91	0.98	11	0.052	1.274
5	Jordan Basin	-1.22	3.26	0.98	10	0.062	3.259
6	Scotian Shelf	-1.15	3.45	0.96	8	0.094	3.453
	All stations combined	-1.22	3.76	0.96	57	0.032	1.718
Volume units							
1	Northeast Channel*	-1.11	4.44	0.97	7	0.089	1.405
2	Georges Bank	-1.21	10.56	0.98	10	0.062	1.741
3	Georges Bank	-1.22	9.44	0.99	11	0.035	1.007
4	Northeast Channel	-1.18	6.96	0.98	11	0.050	1.457
5	Jordan Basin	-1.20	7.79	0.98	10	0.060	1.588
6	Scotian Shelf	-1.14	6.43	0.97	8	0.085	2.048
	All stations combined	-1.20	8.21	0.97	57	0.028	1.821

* Zooplankton data only.

of both the size-fractionation procedure and the averaging of biomass from different size-classes. Table 3.5 shows the regression parameters for the NBS-spectra (SFS) as well as those for the NMS-spectra. It is important to note that at all stations, the NMS-spectra have a more negative slope than the NBS-spectra, indicating that the smallest organisms play even a more important role than the larger ones from a metabolic activity, than from a biomass standpoint. It also suggests that for the same metabolic activity, more community biomass is supported in the bigger size classes than in the smaller ones.

The ratio of total community respiration to total community biomass is considered to be an index of the amount of energy spent by a community to maintain its structure (Odum 1971). At the organismic level of organization, this concept is analogous to specific respiration. The same idea can be applied to different size-classes as compartments of an ecosystem. The change of the metabolic activity *(M)* to biomass *(B)* ratio *(M/B)* with size indicates how the energy cost of maintaining living biomass varies through the size-spectrum. I have shown that both normalized-respiration and normalized-biomass are related to size in a linear manner when plotted on a log-log scale. Since the numerical value of the slopes of the NBS-spectra and those of the NMS-spectra are very close to each other (see Table 3.5), it is expected that the relationship between the *(M/B)* ratio and nominal-size would have a very low slope (i.e. close to 0). Table 3.6 shows the regression parameters for the relationship between the *(M/B)* ratio and nominal-size (see also Figure 3.5). It is interesting to note that the coefficient of determination of this relationship is significant ($r^2 = 0.60$) when the data are expressed in volume units but it is not when they are expressed in carbon units ($r^2 = 0.36$). This seems to indicate that metabolically-active tissue is more related to biovolume than to carbon content. Indeed, it has been suggested that production and respiration are better correlated with the metabolically-active surface area of organisms, which is likely to be more correlated to organism volume than to carbon content (Kamenir and Khaylov 1987). The

TABLE 3.5.- Regression parameters of the normalized-metabolism and normalized-biomass spectra from each station. Model : $\log_2 Y = \log_2 a + b \log_2 X$. Carbon units: Normalized biomass (μg C m^{-3} / Δμg C), Normalized metabolism (μl O_2 h^{-1} m^{-3} μg C^{-1}), Size (μg C). Volume Units: Normalized biomass (μm^3 m^{-3} / Δμm^3), Normalized metabolism (μl O_2 h^{-1} m^{-3} μm^{-3}), Size (μm^3).

	Biomass size-spectra (SFS)				Metabolic size-spectra			
Station	slope	$\log_2 a$	r^2	N	slope	$\log_2 a$	r^2	N
Carbon units								
1	-0.97	9.12	0.97	7	-1.14	2.35	0.95	7
2	-1.08	12.76	0.98	10	-1.23	5.76	0.98	10
3	-1.07	11.19	0.97	11	-1.24	4.30	0.99	11
4	-1.16	10.24	0.97	11	-1.20	2.91	0.98	11
5	-1.14	10.30	0.98	10	-1.22	3.26	0.98	10
6	-1.12	10.89	0.95	8	-1.15	3.45	0.96	8
All stations combined	-1.12	10.87	0.96	57	-1.22	3.76	0.96	57
Volume units								
1	-0.99	33.56	0.99	7	-1.11	4.44	0.97	7
2	-1.00	36.57	0.97	10	-1.21	10.56	0.98	10
3	-1.01	35.49	0.99	11	-1.22	9.44	0.99	11
4	-1.04	35.24	0.99	11	-1.18	6.96	0.98	11
5	-1.04	35.16	0.99	10	-1.20	7.79	0.98	10
6	-1.02	35.25	0.98	8	-1.14	6.43	0.97	8
All stations combined	-1.03	35.54	0.97	57	-1.20	8.21	0.97	57

TABLE 3.6. Regression parameters from the relationship between $\log_2$ *(M/B)* and $\log_2$ Nominal size. Model : $\log_2$ *(M/B)* = $\log_2$ Intercept + b $\log_2$ Size. Volume Units : *M/B* ratio (µl O_2 h^{-1} μm^{-3}), Nominal Size (μm^3). Carbon Units: *M/B* ratio (µl O_2 h^{-1} mg C^{-1}), Nominal Size (µg C).

Stn	Geographical Name	Slope	$\log_2$ Intercept	r^2	N	Std. Error Slope	Std Error of Y Est.
Biovolume units							
1	N.EastCH*	-0.11	-29.12	0.43	7	0.058	0.913
2	G. Bank	-0.21	-26.01	0.62	10	0.059	1.643
3	G.Bank	-0.21	-26.05	0.77	11	0.039	1.132
4	NEastCH	-0.14	-28.27	0.63	11	0.036	1.040
5	Jordan B.	-0.16	-27.38	0.53	10	0.053	1.413
6	Sct. Shelf	-0.12	-28.82	0.56	8	0.043	1.024
All stations this study		-0.17	-27.32	0.60	57	0.019	1.207
Carbon units							
1	N.EastCH*	-0.17	-6.77	0.64	7	0.058	0.678
2	G. Bank	-0.15	-7.00	0.61	10	0.042	0.997
3	G.Bank	-0.17	-6.89	0.60	11	0.046	1.135
4	NEastCH	-0.04	-7.33	0.13	11	0.036	0.885
5	Jordan B.	-0.08	-7.04	0.32	10	0.044	0.980
6	Sct. Shelf	-0.03	-7.44	0.16	8	0.025	0.514
All stations this study		-0.10	-7.11	0.36	57	0.018	0.977

* Zooplankton data only.

Figure 3.5.- Relationship between the metabolic activity to biomass ratio ($\mu l\ O_2\ h^{-1}\ \mu g\ C^{-1}$) and body-size. Body size (μg C).

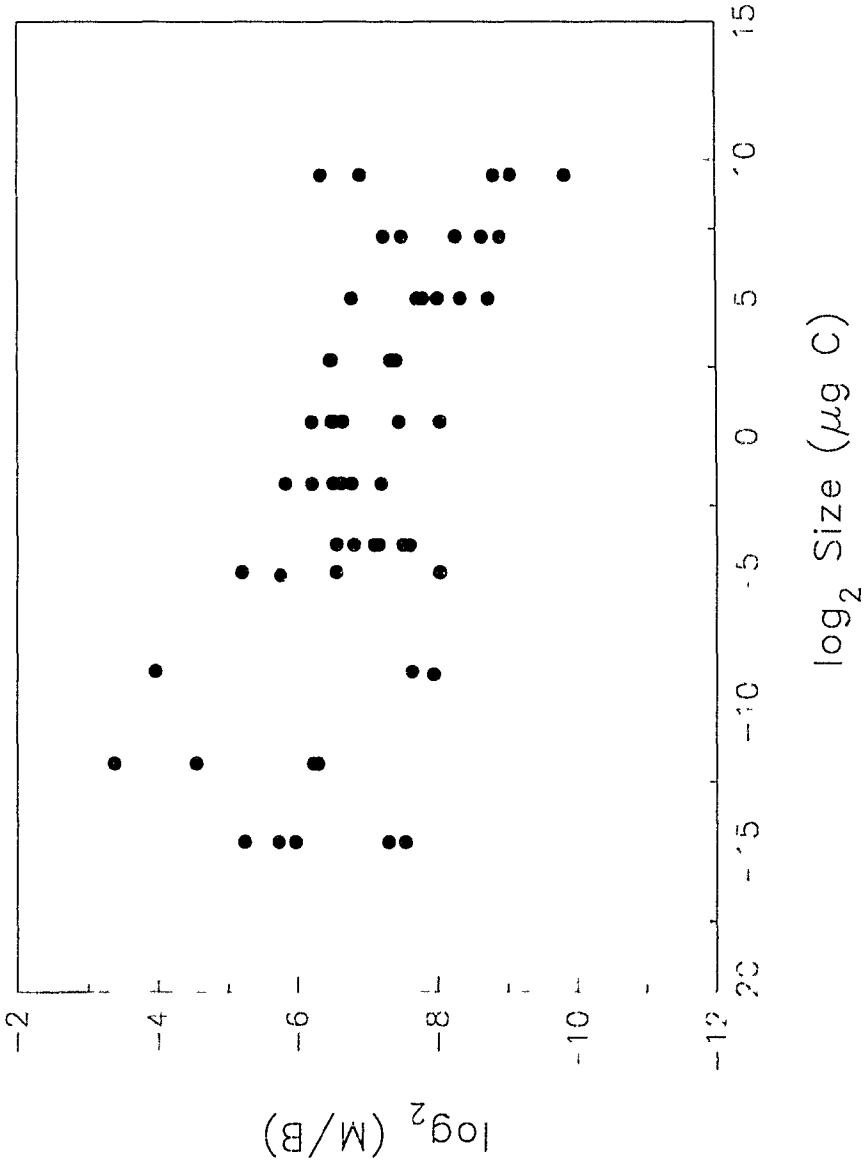


Figure 5.5

numerical value of the slope of the relationship between *(M/B)* and size is -0.17 in biovolume units and -0.10 in carbon units. These slopes are lower than that from the interspecific scaling of weight-specific respiration (i. e. -0.25; Hemmingsen 1960).

DISCUSSION

I.- Methodological considerations and the *(M/B)* ratio versus nominal size

Every technique used to measure respiration in size-fractionation studies on planktonic communities (e.g. Winkler method, microelectrodes, ETS technique) has important shortcomings. The researcher is, then, left to choose the method which is likely to be less artifactual for a particular objective. For example, at the beginning of this research, in 1988, I attempted to accomplish the objectives using a very sensitive microprocessor controlled version (Williams and Jenkinson 1982) of the Winkler titration method. I conducted size-fractionation studies in the Sargasso Sea and in Bedford Basin (unpublished results), but methodological artifacts distorted my results. High bacterial growth, and changes in community size-structure during incubations were detected. Furthermore, in most cases, the sum of the respiration of the size-fractions was higher than that of the sample without size-fractionation. It became evident that the disruption of the system by size-fractionating prior to incubation was a major impediment to the success of this research. Consequently, I decided to use the ETS technique, which is a method with no *in vitro* effect. However, the ETS technique is not, by any means, free of criticism (e.g. Bamsted 1980). This technique has been used in the study of metabolic activity of marine plankton since late 1960's (e.g. Packard 1969). It has been especially useful in circumstances where the Winkler method is not sensitive enough as, for example, in deep waters (e.g. Packard et al. 1971, King et al. 1978, Packard et al 1988). The conversion procedure from ETS activity to *in situ* oxygen consumption is the most controversial aspect of the technique. Experiments carried out to define the relation between ETS activity (*M*) and *in situ* oxygen consumption (*R*) have shown a clear correlation between these two variables (e.g. King and Packard 1975, Owens and King 1975, Packard and Williams 1981, Packard et al. 1983). However, high variability of the *R/M* ratio in relation to the type of organisms (for a review see Packard 1985a) and with

certain environmental factors have also been reported (Bamsted 1979, 1980, Kenner and Ahmed 1975, King and Packard 1975). Nevertheless, there is general agreement that the ETS technique does measure the maximum velocity (V_{max}) of electron transfer (Kenner and Ahmed 1975, Packard 1985b), and consequently, a maximum potential respiratory activity. Considering the controversy regarding the *R/M* ratio, and that my goal in using the ETS technique was to obtain only a relative index of metabolic activity in different size-classes, I decided to present the data as ETS activity without attempting to convert the ETS measurements to *in situ* oxygen consumption.

An example of the kind of conversion factor that could have been used in this study is given by Packard and Williams (1981). They reported the following relationship between ETS activity and oxygen consumption for nano- and microplankton assemblages from some stations located in the same geographical area of the current study:

$$M = 2.92\ R + 99, \qquad (r = 0.89, n = 21) \qquad (7)$$

where *R* and *M* are in $\mu g\ O_2\ l^{-1}\ d^{-1}$. However, the spatial and temporal variation as well as the size dependence, if any, of this relationship are unknown.

The slope of the relationship between the *(M/B)* ratio and nominal-size found in the current study (see Table 3.6) is more positive than those found in the interspecific scaling of weight-specific respiration (slope = -0.25, Hemmingsen 1960), the *R/B* versus size relationship from field populations of invertebrates (slope = -0.35; Banse 1979), and the *R/B* versus size relationship from the field study of Ahrens and Peters (1991b) in limnoplankton communities (slope = -0.30).

One possible explanation for the low numerical value of the slope of the *(M/B)* ratio versus nominal-size, and the weak correlation of this relationship, lies in the fact that the ETS activity technique measures a maximum potential respiration and not an *in situ* oxygen consumption. It is known that the *R/M* ratio varies considerably among different groups of organisms. Packard (1985a) gives the following mean values for the *R/M* ratio: bacteria 1.1, protozoans 0.25, phytoplankton 0.172 and crustacean zooplankton 0.49. However, despite the variability in the experimental *R/M* ratio, Packard (1985a), citing the data from Finlay et al. (1983), affirmed *"that respiration and ETS data from metazoan zooplankton, a protozoan , and bacteria all fall on the same line argues that at least within heterotrophic organisms the ETS activity-respiration relationship is the same"*. On the other hand, it is known that ETS activity responds slowly to environmental changes (Bamsted 1980, Smith and Chong 1982, Cammen et al. 1990) and therefore, the relationship between *(M/B)* and nominal-size can be affected by the difference in the time-scale of response between, first, an environmental stimulus and a noticeable ETS activity change, and second, between the same environmental stimulus and a change in the biomass of the size-fraction.

The low numerical value of the slope of the relationship between (M/B) and size as well as the low coefficient of determination (r^2) may be also due to the fact that in each size-class there is an assemblage of very different kind of organisms (i.e. different kingdoms, and phyla) presenting different size-dependent scaling relationships. For example, the interspecific scaling of specific respiration in phytoplankton is a controversial matter (e.g. Lewis 1989). In fact, Ahrens and Peters (1991b) using the Winkler technique, found a correlation (r^2) of only 0.59 between *(R/B)* and body-size in limnoplankton communities.

Finally, it has been suggested that the relationship between *(R/B)* and size tends to decrease with an increase in the range of body-sizes incorporated in the regression (Banse and Mosher 1980, Dickie et al. 1987a, Ahrens and Peters 1991b). This could explain the difference between the slope reported by Ahrens and Peters (1991b) and ours since the current study covers a much wider size range than theirs.

I have presented some possible explanations for the differences found between my results regarding the *(M/B)* to nominal-size relationship and those from other published studies. However, the question of the extent by which these methodological limitations may affect my results remains open. Consequently, it is also possible that the flatter slopes found in the current study are a real characteristic of the marine systems studied. To the best of my knowledge this is the only study analyzing the *(M/B)* to size relationship done with natural community assemblages in the marine pelagic ecosystem. The slopes found in the current study (i.e. -0.17 in biovolumen units, -0.10 in carbon units) indicate that the energy expenditure to maintain a defined biological structure at the community level of organization slightly decreases with increasing nominal-size.

II.- General trend in the size-structure of metabolism in planktonic communities.

The study of size-fractionated respiration in planktonic communities started in the middle of the 1960's (Pomeroy and Johannes 1966). The main objective of these studies was to determine the contribution of the microbial component to the total respiration of the community. The finding that a large fraction of the total respiration was accounted for by microorganisms (e.g. Pomeroy and Johannes 1968) was an important contribution to the recent conceptual reformulation of the trophic web in the ocean (Pomeroy 1974). However, the study of planktonic respiration by size is still in early stages and the amount of information available has been considered to be too limited to make

generalizations for planktonic systems as a whole (Williams 1984). Certainly, size-fractionation studies suffer from a lack of information quantity. Nevertheless, a conceptual framework able to unify data already available and to direct and organize future collection of data is also needed.

In this paper I suggest an alternative approach for size-fractionation studies of planktonic respiration. In brief, I propose to adopt the same data representation and conventions used in the study of planktonic biomass size-distribution as described by Platt and Denmann (1977, 1978). The width and quantity of size-classes to be selected depend on the sensitivity of the method used and the amount of biomass present in the system. For the parameters of the NMS-spectra to be representative of the system under study, a wide body-size range should be covered. Among other advantages, the NMS-spectrum generates a continuous function with parameters potentially representative of the whole system. The analysis of the variation of slopes, intercepts and residuals of the NMS-spectra provides a means to confront time-space variability.

Using the NMS-spectrum approach I have shown that metabolic activity is not distributed randomly in relation to body size at the community level of organization. Normalized-respiration decreases steadily with size, when plotted on a log-log scale, with a slope of the regression line close to -1.2. The negative slope of the NMS-spectra confirms the importance of small organisms in the flux of energy of the pelagic system. It is interesting to note that the parameters of the NMS-spectra clearly differentiate between systems with different trophic state. Thus Georges Bank stations have very different NMS-spectra in comparison with the rest of the stations. The NBS-spectra however did not differentiate between the highly productive Georges bank and the stations located in Jordan Basin and the Scotian Shelf. It seems that NBS-spectrum is a very conservative property of pelagic ecosystems (Platt 1985, see also Chapters 1 and 2) and, therefore,

comparative studies which do not consider simultaneously the size-distribution of rate processes (e.g. production, respiration) are not able to give clear insights regarding the dynamics of the energy flux of the different systems under study.

The main question emerging from my findings is to what extent it is possible to generalize the steady decrease (slope approx. -1.2) of the normalized-metabolic activity with size (plotted on a log-log scale) to other pelagic ecosystems or different time-space scales. Although, ultimately, the only way to answer this question is by carrying out more empirical studies covering wider spatial and temporal scales, there are several lines of evidence suggesting that the observed decline of respiration as a power function of body-size is indeed a general feature of the pelagic ecosystem. Two arguments from the current study support this hypothesis: first, my data, even though limited in time and space, cover ecosystems with very different trophic state; second, the wide size range used in this study is sufficient to ensure a representative coverage of metabolic activity through body-size. Another line of support for the generality of this pattern comes as a logical consequence of the size-dependence of respiration as shown by numerous interspecific studies (for a review, see Peters 1983a, Schmidt-Nielsen 1984, Calder 1984). Recently, Ahrens and Peters (1991b) have shown that the allometric relation between respiration and body-size calculated in the laboratory can be extrapolated to field limnoplankton.

Finally, I have attempted to test the regular decline of normalized-respiration by size (slope close to -1.2) using published size-fractionated respiratory data from other marine pelagic communities. It is important to note that the published data have two major limitations: first, the methodological problems mentioned in section (I) of this discussion, and , second, the fact that the majority of the published empirical studies cover only few size-classes and they are usually restricted to the nano- microplankton size range. Figure 3.6 shows the normalized respiration size-spectrum (NRS-spectrum)

Figure 3.6.- The relationship between respiration and body-size in marine systems from published data. The respiration of each size-class is expressed as a percentage of the total respiration of the non-fractionated sample, and subsequently, normalized by the width of the size class. Nominal size corresponds to the arithmetic mean of the size class given in linear dimensions. Data from the following marine systems: Canadian Arctic (Winkler method, average of the stations given in Harrison 1986, Table 2, p. 150); Grand Banks (Newfoundland, Winkler method, Harrison 1986, Table 3, P. 150); Grand Banks (Newfoundland, Winkler method, Smith et al. 1986, according to Harrison 1986, Table 3, p. 150); Saanich Inlet (Winkler method: Williams 1984, Table 8, p.378); Gulf of Maine and Georges Bank (Winkler method, Williams 1984, Table 8, p.378); Loch Ewe (N.W. Scotland, Winkler; Williams 1984, Table 8, p.378); Gulf of Maine (Stn 67,73; ETS; Packard 1980, Table 7, p. 53); Gulf of Maine (Winkler, Stn. 67, Williams 1980, Table 7, p. 53). The open ended size-class >20 μm from Williams (1980) and Packard (1980) was considered to be 20-150 μm.

The regression line is described by the equation:

$$\log_2 R_{\%} = 4.89 - 1.28 \log_2 \text{Size } (\mu m)$$

where $R_{\%}$ is the percentage of the total respiration being respired by a particular size-class (r^2=0.89, Std Err of Y est. 1.054, N= 33, Std. Err of the slope 0.082).

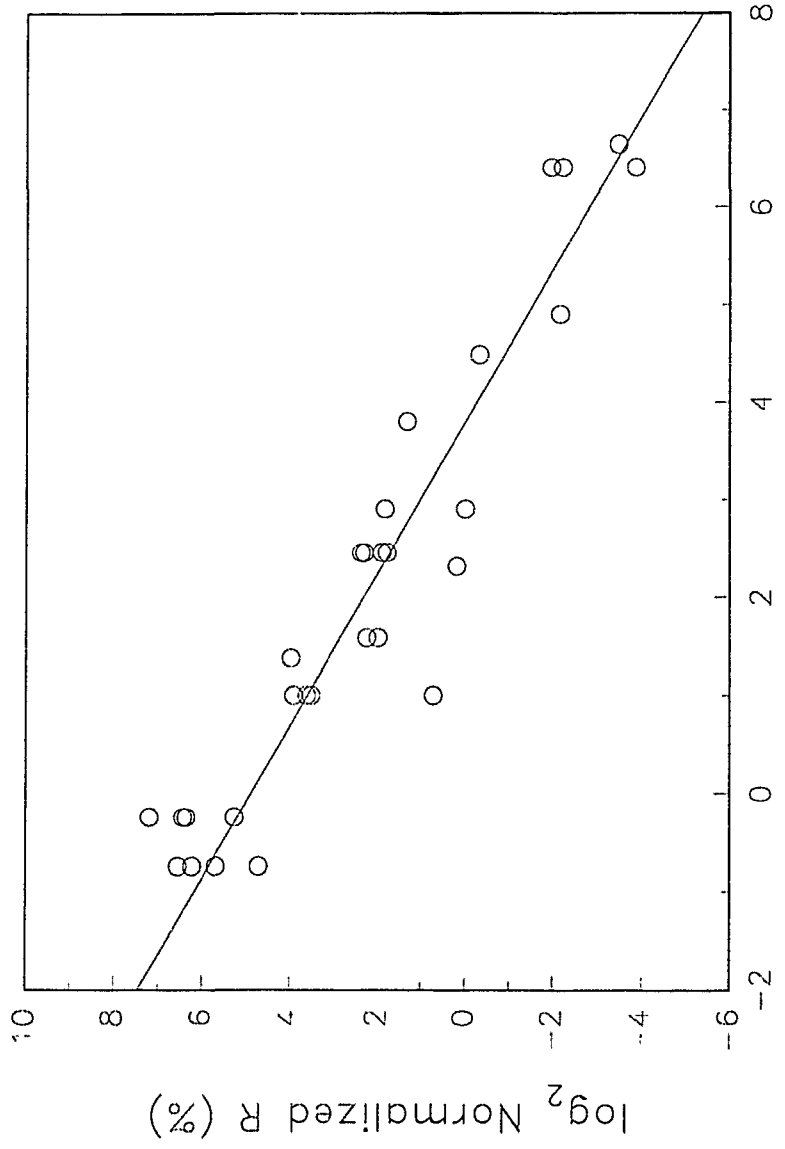


Figure 3.6

for the pelagic system constructed with independent data, most of which were obtained by direct measurement of oxygen consumption (Winkler method). This NRS-spectrum is clearly in agreement with the findings of the current paper. It can be seen that there is a decline of normalized-respiration with size and the slope of the NRS-spectrum is -1.28 ($r^2 = 0.89$) which is remarkably close to my results.

CONCLUDING REMARKS

This thesis has examined patterns in the distribution of biomass and metabolic activity by size in the pelagic ecosystem.

The results of the studies on biomass size-distribution reported in this thesis support the hypothesis that the planktonic size-structure of offshore systems is a conservative property. This feature of the oceanic system should have a wider recognition in marine ecology, a discipline so often criticized for a lack of generalizations.

The observed regularity of the biomass size-distribution is represented by the linearity of the NBS-spectra in all systems studied. It is shown that the slope of the normalized biomass size-spectrum (NBS-spectrum) varies depending on whether biomass is expressed as biovolume or carbon content. This finding is significant regarding the question of the numerical value of the theoretical slope for a steady state system. According to the results of this thesis, and in agreement with Sheldon's linear biomass hypothesis (Sheldon et al. 1972), biomass expressed as biovolume is roughly the same at all size classes in oceanic systems. However, biomass expressed as carbon content slightly decreases with size as predicted by the model of Platt and Denman (1977, 1978). It is also shown that Platt and Denman's model yields predicted theoretical slopes of the NBS-spectrum ranging from -0.82 to -1.23 for varying parameters, and thus allows the -1.0 slope predicted by the linear biomass hypothesis (Sheldon et al. 1972).

Georges Bank, a highly productive marine system, also presented clear biomass size-distribution regularities. Two main differences were evident in the Georges Bank distribution of biomass by size in comparison to oceanic systems. The slopes of the NBS-

spectra were more positive, particularly at the zooplankton size-range, and the scatter around the slope of the NBS-spectrum in the zooplankton size-distribution was much higher than that observed in oceanic areas. The change in the slope of the NBS-spectrum at the zooplankton size-range indicates that caution is advisable in predicting fish stocks based on the stocks of smaller organisms.

In Georges Bank the use of biomass-size diversity and evenness indexes to complement the information provided by the NBS spectrum is explored. These indexes provide an additional tool to analyze the biomass size-distribution data. Biomass-size diversity and evenness are highest in mixed waters, decreasing in frontal waters and presenting the lowest values in stratified waters. Further comparative studies and theoretical analysis of biomass size-diversity are recommended.

This thesis provides the first generalization regarding size-fractionated respiration. The linearity of the normalized metabolism size-spectrum (NMS-spectrum) and the numerical value of its slope (approx. -1.2) are suggested to be fundamental characteristics of the pelagic ecosystem. Both the linearity and the slope of the NMS-spectrum, should prove useful in modelling the fluxes of energy and matter in the pelagic ecosystem.

Although the regularities in the distribution of biomass and metabolic activity by size identified in this thesis are useful for holistic studies of ecosystems, they may be of limited use in studies that require detailed information on a narrow portion of the biomass spectrum. For example, the residuals around the slope of the NBS-spectrum may be crucial for certain applications such as fisheries management.

Body size has been recognized as a critical variable and an organizing property in studies at the organismic, population and community levels of organization. Significant effort has been directed towards integration of knowledge on size-based interactions between the organismic and population level of organization (e.g. Pauly and Morgan 1987, Ebenman and Persson 1988), as well as between the organismic and community (see General Introduction) levels of organization. Nevertheless further research is essential in order to combine and synthesize knowledge on population dynamics with the size-structure patterns observed at the community level of organization. Interesting developments towards an integration of these two subjects have been made by Griffiths (1986) and Pagel et al. (1991).

Holistic and reductionistic approaches are too often viewed as completely opposite approaches to ecosystem ecology. A synthesis of both approaches is probably our best prospect for an ecology with predictive power.

APPENDIX 1

IMAGE ANALYSIS

The following is a brief description of the image analysis techniques used. The sizing of organisms was carried out using an image analyzer, similar to that described by Campana (1987). The components of the image analyzer are: (a) IBM AT-compatible; (b) Video Monitor (Black and White); (c) Newvicon Video Camera (Hitachi CCTV, black and white); (d) Oculus 300 (Coreco Inc.) framegrabber video digitizer board. The software is a library of 74 image analysis functions Gray Library (Coreco Inc.). Applications programs are written in C language, through which the required Gray library functions are called up.

I.- Bacterioplankton:

The program BACT is a program in C language to determine bacteria size from projected slides. The program is a modification of the program "features" created by Campana (1987).

BACT works in the following manner:

1) The program first requests header information about the slide to be analyzed: location, optional comment, station number, depth, slide number, and picture number.

2) The image from the projected slide is captured with the video camera. After the image is grabbed (reverse video) by the image analyzer, a threshold level is set visually and the image is frozen.

3) A window is drawn automatically on the graphic plane. The dimensions of the window can be modified by the user.

4) The program automatically calculates the total number of objects in the window.

5) BACT requests the calibration factors which have been previously obtained using a stage micrometer (photography projected at the final magnification).

6) The maximum and minimum object area to be considered in the processing is selected.

7) The subroutine FEATURE computes selected characteristic features of each bacteria in the image. However, before the parameters of an object are measured, the program requests a category of classification. The category of classification can be any integer. If the category of classification is zero the computer ignores the object. If the category of classification is any integer except zero, the category is recorded and the following features of the object are computed: area (including holes), number of holes, total area of holes, outer perimeter, x coordinate of centroid, y coordinate of centroid, angle of major axis, length of major axis, length of minor axis, width of smallest straight box enclosing object, height of smallest straight box enclosing object.

8) The program output is printed as an ASCII file.

9) Data is transferred to LOTUS 1-2-3 for further analysis.

10) Bacterial volume is estimated using the following formula:

$$V = (\pi / 4) W^2 (L - W/3)$$

where L is the length of major axis, and W is the length of minor axis.

PROGRAM BACT.C

```
#include "math.h"
#include "stdio.h"
#include "oc200.h"
#include "fcntl.h"
/*
* Program to determine features of objects
*
*/
int _stack=64500;
int matrix[480][32];
main (argc,argv)          /*prompt for targeted file*/
int argc;
char *argv[];
{
register int kk, k, cc;
char loc[81], comment[81];
int stat, depth, slide, pict, nsubt, categ, nobjs, count;
int lastpg, nowpg, pg, numanc, numdes, anc1, anc2, des1, des2;
int xx, yy, curs;
int y3, x3, *line, *start, *length;
int imax, maxnb, nobj;
int file;
int *object, *fgrp, *next, *panc, *pdes, *anc, *des;
```

```
int mode, thresh, lut;
int i, xlen, ylen, x1, x2, y1, y2, xword, xadj;
int xmin,xmax,ymin,ymax,y;
int mask, er, respon, error;
int *jline, *jstart, *jlen, lastj;
int nfeat[12];
float feat[12], calib, mnarea, mxarea, toarea;
char *name;
char *malloc();
char ch, ch2, ans, ans2;
unsigned int nbyte;
long int date;
FILE *fp, *fq;
if (argc !=2) {
        printf("you forgot to enter the targeted data file name\n");
        printf("on the command line\n");
        exit(0);
}
printf("DOS file = %s\n",argv[1]);

if ((fp=fopen (argv[1],"wa")) == NULL) {
        printf("Cannot open file\n");
        exit (0); }

/*----------Memory Allocation---------------------*/
maxnb=10500;
nbyte=maxnb*2;

next=(int *)malloc(nbyte);
if (next == NULL) {er=1; goto end;}
object=(int *)malloc(nbyte);
if (object == NULL) {er=2; goto end;}
panc=(int *)malloc(nbyte);
if (panc == NULL) {er=3; goto end;}
pdes=(int *)malloc(nbyte);
if (pdes == NULL) {er=4; goto end;}
```

```
line=(int *)malloc(nbyte);
if (line == NULL) {er=5; goto end;}
start=(int *)malloc(nbyte);
if (start == NULL) {er=6; goto end;}
length=(int *)malloc(nbyte);
if (length == NULL) {er=7; goto end;}
fgrp=(int *)malloc(nbyte);
if (fgrp == NULL) {er=8; goto end;}
jline=(int *)malloc(nbyte);
if (jline == NULL) {er=9; goto end;}
jstart=(int *)malloc(nbyte);
if (jstart == NULL) {er=10; goto end;}
jlen=(int *)malloc(nbyte);
if (jlen == NULL) {er=11; goto end;}

nbyte=maxnb*3*2;
anc=(int *)malloc(nbyte);
if (anc == NULL) {er=9; goto end;}
des=(int *)malloc(nbyte);
if (des == NULL) {er=10; goto end;}

restart:

/********** header information **********************/

count = 0;
fq=fopen ("temp.dat","wa");
rewind (fq);

printf ("Enter location <= 80 characters)\n");
gets (loc);
printf ("Enter optional comment (<= 80 characters)\n");
gets (comment);
printf ("Enter station number\n");
scanf ("%d",&stat);
printf ("Enter depth\n");
```

```
scanf ("%d",&depth);
printf ("Enter slide number\n");
scanf ("%d",&slide);
printf ("Enter picture number\n");
scanf ("%d",&pict);

fprintf(fp, "%s\n", loc);
fprintf(fp, "%d %d %d %d\n", stat,depth,slide,pict);
fprintf(fp, "%s\n", comment);

/*-----------------------------------------------*/

screen(0);
mode=0;
thresh=50;
grclo(100);
grdeflut();
ch=ch2='x';
do
        {
        printf ("Image: 0-Normal 1-Reverse 2-HC 3-Reverse HC\n");
        scanf ("%d", &lut);
      if (lut == 0 || lut == 2) mode=0;
      else mode=1;
        printf ("Use > and < to increase/decrease threshold\n");
      printf("Type T when threshold selected\n");
      do {
        grgrab (lut,0,0,0);
        ch=getch();
        switch (ch)
            {
            case ',':
            case '<':
                thresh=thresh-1;
                grthrs (lut,thresh,mode);
                break;
```

```
            case '.':
            case '>':
                thresh=thresh+1;
                grthrs (lut,thresh,mode);
                break;
            case 't':
            case 'T':
                break;
            default:
                printf("Unrecognized keystroke\n");
                break;

            }                   /* end of switch */
                locate (14,60);
                printf("threshold : %d  \n", thresh);
        } while (ch != 't' && ch != 'T');  /* end of do-while */
        printf ("Enter 'a' to adjust, any other key to continue\n");
        ch=getch();
    } while (ch == 'a' || ch == 'A');     /* end of do-while */

/*--------Window development in prep for Grencod----------------------*/

screen(0);
x1=y1=50;
x2=y2=450;
grbox(x1,y1,x2,y2);
printf ("Is window OK? Y/N\n");
ch=getch();
if (ch == 'n' || ch == 'N') {          /* prepare own window */
grebox(x1,y1,x2,y2);
ch=ch2='x';
xx=yy=x1=x2=y1=y2=250;
curs=20;
grtarg(xx,yy);
printf ("Use cursor arrows to move monitor cursor\n");
printf("Type U to mark upper left corner of desired window\n");
```

```
printf("Type L to mark lower right corner of desired window\n");
printf ("Type 'F' to finish\n");
do
 {
 ch=getch();
 switch (ch)
   {
   case '\0':                  /* call for cursor */
   ch2=getch();
      switch (ch2)
        {
        case  72:                  /* cursor up */
             gretarg(xx,yy);
             yy=yy-curs;
             grtarg(xx,yy);
             break;
        case  80:                 /* cursor down */
             gretarg(xx,yy);
             yy=yy+curs;
             grtarg(xx,yy);
             break;
        case  75:                  /* cursor left */
             gretarg(xx,yy);
             xx=xx-curs;
             grtarg(xx,yy);
             break;
        case  77:                 /* cursor right */
             gretarg(xx,yy);
             xx=xx+curs;
             grtarg(xx,yy);
             break;
        default:
             printf("Use arrows only\n");
             break;
        }                           /* end of cursor switch */
   locate (1, 60);
```

```
    printf("Cursor x: %d \n", xx);
    locate(2,60);
    printf("Cursor y: %d \n", yy);
    break;
  case 'u':
  case 'U':
      grebox(x1,y1,x2,y2);
      x1=xx;
      y1=yy;
      grbox (x1, y1, x2, y2);
      break;
  case 'l':
  case 'L':
      grebox(x1,y1,x2,y2);
      x2=xx;
      y2=yy;
      grbox(x1,y1,x2,y2);
      break;
  case 'f':
  case 'F':
      grebox(x1,y1,x2,y2);
      gretarg(xx,yy);
      break;
  default:
      printf("Unrecognized keystroke\n");
      break;
  }                                   /* end of switch */
 } while (ch != 'f' && ch != 'F');    /* end of do-while */
                }                          /* end of if */
else grebox(x1,y1,x2,y2);

xadj=xword=xlen=ylen=0;
xlen=x2-x1+1;              /* from the box coordinates */
ylen=y2-y1+1;              /* we calculate dimensions  */
if (ylen &1) ylen-=1 ;      /* test if number is even   */
                            /* adjust if not            */
```

```
xword=(int)xlen/16;            /* for encoding in the matrix*/
xadj=xlen-xword*16;             /* xadj is the number of empty*/
if (xadj!=0) xword+=1;          /* bytes in the leftmost  */
                                /* word to be filled with 1  */
if (xword>32) xword=32;
x3=xword-1;
xadj=xword*16-xlen;
y3=ylen-1;
grwindo (matrix,x1,y1,xword,ylen);/* load the matrix */

if (xadj!=0)                   /* mask the unused bit with  */
  {                             /* 1 in the window          */
  mask=0xffff ;
  mask= mask >> (16-xadj) ;
  for (y=0; y<=y3; y++)
     matrix[i][xword]=matrix[i][xword] | mask;
  for (y=y3+1; y<=2*y3+1; y++)
     matrix[i][xword]=matrix[i][xword] | mask ;
  }

screen(0);
locate(1,1);
printf ("Encode and link in progress...\n");
er=grencod(matrix,y3,x3,line,start,length,&imax,maxnb);
if (er) goto end;
er=link(line,start,length,object,fgrp,next,imax,panc,pdes,anc,des,&nobj);
if (er) goto end;
printf ("Completed...\n");
printf ("Number of objects=%d\n",nobj);
nobjs = nobj;

printf ("Do you want to measure the objects? (Y or N)\n");
ans = getch();
if (ans == 'n' || ans == 'N')
  {
  printf ("Do you want to subtract some objects? (Y or N)\n");
```

```
  ans2 = getch();
  if (ans2 == 'y' || ans2 == 'Y')
    {
    printf ("How many do you want to subtract?\n");
    scanf ("%d", &nsubt);
    nobjs = nobj - nsubt;
    printf ("Number of objects after subtraction: %d\n",nobjs);
    }
  }

fprintf(fp, "%d %d\n",nobj, nobjs);
if (ans == 'n' || ans == 'N') goto again;

printf("Enter calibration coefficient (no. of horiz. pixels per unit measure)\n\n");
printf("Values for Wild epifluorescence microscope are:\n");
printf("6.4X objective - 19.2/mm\n");
printf("16X  objective - 47/mm\n");
printf("40X  objective - 120/mm\n\n");
printf("Values for Zeiss inverted microscope are:\n\n");
printf("6.3X objective - 0.323/um\n");
printf("10X objective - 0.521/um\n");
printf("16X  objective - 0.815/um\n");
printf("40X  objective - 2.12/um\n");
printf("100X objective - 4.9/um\n");
printf("Value for projected slides is approx 7.54 /um\n");
scanf("%f", &calib);

printf("Enter maximum acceptable total area\n");
scanf("%f", &mxarea);

Printf("Enter minimum acceptable total area\n");
scanf("%f", &mnarea);

screen(0);
```

```
                                /* select object of interest */
for (k=1;k<=nobj;++k)
   {
    nfeat[0]=11;
    for (kk=1;kk<12;kk++) nfeat[kk]=kk;
    er=features (fgrp[k],line,start,length,next,panc,pdes,anc,des,
              nfeat,feat,0.8);
    if (er) continue ;

    toarea = feat[1]/(calib*calib);
    if (toarea <= mxarea && toarea >= mnarea)
     {
      printf("Object %d: \n", k);
      grcurs(x1,y1,line,start,length,fgrp[k],next,&xmin,&xmax,&ymin,&ymax);
      printf ("Enter category of classification \n");
      scanf ("%d",&categ);
      if (categ != 0)                  /* if categ = 0 then don't measure */
        {
         printf ("feature # 1:area including holes: %f\n",
               feat[1]/(calib*calib));
         printf ("feature # 2:number of holes: %f\n",feat[2]);
         printf ("feature # 3:total area of holes: %f\n",feat[3]/(calib*calib));
         printf ("feature # 4:outer perimeter: %f \n",feat[4]/calib);
         printf ("feature # 5:x coord of centroid: %f\n",feat[5]/calib);
         printf ("feature # 6:y coord of centroid: %f\n",feat[6]/calib);
         printf ("feature # 7:angle of major axis w.r. to horiz.: %f \n",
               feat[7]);
         printf ("feature # 8:length of major axis: %f\n",feat[8]/calib);
         printf ("feature # 9:length of minor axis: %f\n",feat[9]/calib);
         printf ("feature #10:width of smallest box enclosing: %f\n",feat[10]/calib);
         printf ("feature #11:height of smallest box enclosing: %f\n",feat[11]/calib);

         count = count + 1;

         fprintf(fq, "%d %f %f %f %f %f %f %f %f %f %f %f %f \n",
               categ,
```

```
                feat[1]/(calib*calib),
                feat[2],
                feat[3]/(calib*calib),
                feat[4]/calib,
                feat[5]/calib,
                feat[6]/calib,
                feat[7],
                feat[8]/calib,
                feat[9]/calib,
                feat[10]/calib,
                feat[11]/calib);
          }

        printf ("Enter 'C' to continue to next object\n");
        printf ("Enter 'Q' to end display \n");
        ch=getch();
        if (ch == 'q' || ch == 'Q') goto again;

        }                              /* end of if(toarea... */


    }                                  /* end of for */

again:
    fclose (fq);
    fq = fopen ("temp.dat","ra");
    rewind (fq);
    fprintf(fp, "%d \n",count);

    for (kk=1;kk<=count;++kk)

      { fscanf(fq, "%d %f %f %f %f %f %f %f %f %f %f %f \n",
            &categ,
            &feat[1],
            &feat[2],
            &feat[3],
```

```
            &feat[4],
            &feat[5],
            &feat[6],
            &feat[7],
            &feat[8],
            &feat[9],
            &feat[10],
            &feat[11]);

        fprintf(fp, "%d %f %f %f %f %f %f %f %f %f %f %f \n",
            categ,
            feat[1],
            feat[2],
            feat[3],
            feat[4],
            feat[5],
            feat[6],
            feat[7],
            feat[8],
            feat[9],
            feat[10],
            feat[11]);
      }

    fclose (fq);

    for (k=1;k<3;k++) printf("                    \n");
    printf ("Enter 'C' to analyze another sample\n");
    printf ("   or 'F' to finish\n");
    ch=getch();
    if (ch == 'c' || ch == 'C') goto restart;

/*****************************************************************
*/
end:
fclose (fp);
```

```
if(er)
  {
  printf("error=%d\n",er);
  while(!kbhit());
  printf("Strike key to continue\n");
  respon=getch();
  }


    /***********************************************/

/*---------------------- deallocation of dynamic memory ----------------------*/

if (free((char *)next) != 0)
  sound (200,100);
if (free((char *)object) != 0)
  sound (200,100);
if (free((char *)panc) != 0)
  sound (200,100);
if (free((char *)pdes) != 0)
  sound (200,100);
if (free((char *)line) != 0)
  sound (200,100);
if (free((char *)start) != 0)
  sound (200,100);
if (free((char *)length) != 0)
  sound (200,100);
if (free((char *)fgrp) != 0)
  sound (200,100);
if (free((char *)anc) != 0)
  sound (200,100);
if (free((char *)des) != 0)
  sound (200,100);
if (free((char *)jline) != 0)
  sound (200,100);
if (free((char *)jstart) != 0)
```

```
  sound (200,100);
if (free((char *)jlen) != 0)
  sound (200,100);
/*-------------------------------------------------------------------------*/

}
```

II Microplankton

The program NVISION is a program in C language to determine the size of planktonic organisms from an inverted microscope. Since the automatic image analysis of a plankton sample is extremely difficult due to the spatial distribution and different levels of transparency of the organisms, a simple program (NVISION) that emulates a digitizing table was used.

1) The program first requests header information about the plate chamber (Uthermol Technique) to be analyzed: location, optional comment, sample number, volume sedimented, magnification, Y coordinate of the transect to be started, X coordinate of the transect to be started.

2) The image from the inverted microscope is captured with the video camera and grabbed (normal video) by the image analyzer.

3) NVISION requests the calibration factors, which have been previously obtained using a stage micrometer.

4) A category of classification (an integer) is requested for the organism to be measured.

5) The user locates the cursor in 4 locations (2 pairs) of the organism to be measured.

6) The distance between each pairs of locations is calculated by NVISION and recorded together with the category of classification.

7) At users request the program return to any of the steps 1-6 described above.

8) The final Y and X coordinates of the transect are requested.

9) The program output is printed as an ASCII file.

10) Data is transfer to LOTUS 1-2-3 for further analysis.

11) The volume of the organism is estimated using standard geometric shapes.

NVISION.C

```
#include "math.h"
#include "oc200.h"
#include "stdio.h"
int _stack=64500;
main (argc, argv)        /*prompt for targeted file*/
int argc;
char *argv[];
{
```

```
int i, lut, z;
int  xlength, ylength;
int curs;
register int x, y, k;
char ans;
char loc[81], comment[81];
int samp, vsed, mag, categ, hor, vert;
int x1, y1, x2, y2, xx, yy, xlen, ylen;
char ch, ch2, resp, res, comm[10];
double lrdist, aldist;
double magpn;
double lx, ly, rx, ry, hx, hy, bx, by;
double calib, xxx, yyy, otocal;
float tran1, tran2, tran3, tran4, tranx, trany;

FILE *fp;
if (argc !=2)  {
        printf("you forgot to enter the targeted data file name\n");
        printf("on the command line\n");
        exit (0);
}

screen(0);
printf("/*************************************************************\n");
printf("/*                    NVISION                                */\n");
printf("/*      Program to display and store linear measurements     */\n");
printf("/*                Version  - 13/1/90                         */\n");
printf("/*************************************************************\n");

printf("DOS file = %s\n", argv[1]);

if ((fp=fopen  (argv[1], "wa")) == NULL)    {
        printf ("Cannot open file\n");
        exit (0);         }
/********** header information ************************/
screen(0);
```

```
printf ("Enter location <= 80 characters)\n");
gets (loc);
printf ("Enter optional comment (<= 80 characters)\n");
gets (comment);
printf ("Enter sample number\n");
scanf ("%d", &samp);
printf ("Enter vol sedimented\n");
scanf ("%d", &vsed);
printf ("Enter magnification\n");
scanf ("%d", &mag);
printf("Enter Y axis of the transect to be started\n");
scanf ("%f", &tran1);
printf("Enter X axis of the transect to be started\n");
scanf ("%f", &tran2);


fprintf(fp, "%s\n", loc);
fprintf(fp, "%d %d %d\n", samp, vsed, mag);
fprintf(fp, "%s\n", comment);

/* ------------------------------------------------------------ */

x=y=250;
xxx=yyy=i=lut=0;
lx=ly=rx=ry=hx=hy=bx=by=z=magpn=0;
otocal=calib=0.640;              /* pixel to um conversion at 10X */
ch=ch2='x';
curs=1;
grdeflut();
grclo(100);
printf("Strike key to grab image\n");
grgrab(0,0,0,0);                 /* grab in normal mode only */
resp=getch();
if (resp=='\0') resp=getch();
grtarg(x,y);
```

```
screen(0);
printf("if you want to change magnification default at 10x pressM\n");
ans = getch();
if (ans == 'M' || ans == 'm') {
        screen(0);
      locate(1,1);
      printf("Enter calibration coefficient (no. of horiz. pixels per unit measure)\n\n");
      printf("Values for Zeiss Inverted are:\n");
      printf("6.3X objective - 0.383/um\n");
      printf("10X  objective - 0.640/um\n");
      printf("16X  objective - 0.980/um\n");
      printf("40X  objective - 2.580/um\n");
      printf("100X objective - 6.240/um\n");
      scanf("%lf", &calib);
            }

screen(0);
menu();
locate(3,60);
printf("----------------\n");
locate(9,60);
printf("----------------\n");
locate (1,1);
/******************* organism classification***************/
 locate (1,1);
  printf ("Enter category (number) of classification\n");
  scanf ("%d", &categ);

  fprintf(fp, " %d ", categ);
  printf ("Start measurements\n");

/* ----------------------------------------------------------*/
do
 {
 ch=getch();
 switch (ch)
```

```
{
case '\0':                    /* call for cursor */
   ch2=getch();
   switch (ch2)
       {
       case  72:              /* cursor up */
           gretarg(x,y);
           y=y-curs;
           grtarg(x,y);
           break;
       case  80:              /* cursor down */
           gretarg(x,y);
           y=y+curs;
           grtarg(x,y);
           break;
       case  75:              /* cursor left */
           gretarg(x,y);
           x=x-curs;
           grtarg(x,y);
           break;
       case  77:              /* cursor right */
           gretarg(x,y);
           x=x+curs;
           grtarg(x,y);
           break;
       default:
           locate(1,1);
           printf("Keystroke not recognized\n");
           break;
       }                      /* end of cursor switch*/
     cursupdate:
  locate (1, 60);
  printf ("Cursor x: %d \n", x);
  locate (2,60);
  printf ("Cursor y: %d \n", y);
  break;
```

```
case 56:            /* <shift>cursor up */
            gretarg(x,y);
            y=y-10;
            grtarg(x,y);
            goto cursupdate;
case 50:            /* <shift>cursor down */
            gretarg(x,y);
            y=y+10;
            grtarg(x,y);
            goto cursupdate;
case 52:            /* <shift>cursor left */
            gretarg(x,y);
            x=x-10;
            grtarg(x,y);
            goto cursupdate;
case 54:            /* <shift>cursor right */
            gretarg(x,y);
            x=x+10;
            grtarg(x,y);
            goto cursupdate;
case 'f':
case 'F':
      screen(0);
   break;
case 'e':
case 'E':
     grebit8 (0, 0, 512, 512); /*erase the whole graphic plane.*/
     break;
case 'g':
case 'G':
     x=y=250;
     xxx=yyy=i=lut=0;
     lx=ly=rx=ry=hx=hy=bx=by=z=magpn=0;
     ch=ch2='x';
     curs=1;
     grdeflut();
```

```
            grclo(iv0);
            printf("Strike key to grab image\n");
            grgrab(0,0,0,0);              /* grab in normal mode only */
            resp=getch();
            if (resp=='\0') resp=getch();
            grtarg(x,y);

            screen(0);
            menu();
            locate(3,60);
            printf("----------------\n");
            locate(9,60);
            printf("----------------\n");
            locate (1,1);
              printf ("Enter category (number) of classification\n");
              scanf ("%d", &categ);

              fprintf(fp, " %d ", categ);
              printf ("Start measurements\n");
              break;
    case 'c':
    case 'C':
          screen(0);
printf ("Enter location <= 80 characters)\n");
gets (loc);
printf ("Enter optional comment (<= 80 characters)\n");
gets (comment);
printf ("Enter sample number\n");
scanf ("%d", &samp);
printf ("Enter vol sedimented\n");
scanf ("%d", &vsed);
printf ("Enter magnification\n");
scanf ("%d", &mag);
printf("Enter Y axis of the transect to be started\n");
scanf ("%f", &tran1);
printf("Enter X axis of the transect to be started\n");
```

```
scanf ("%f", &tran2);


fprintf(fp, "%s\n", loc);
fprintf(fp, "%d %d %d\n", samp, vsed, mag);
fprintf(fp, "%s\n", comment);

        screen(0);
        menu();
        locate(3,60);
        printf("----------------\n");
        locate(9,60);
        printf("----------------\n");
        locate (1,1);
         locate (1,1);
          printf ("Enter category (number) of classification\n");
          scanf ("%d", &categ);
          fprintf(fp, " %d ", categ);
          printf ("Start measurements\n");
                break;
   case 'n':
   case 'N':
        screen(0);
        menu();
        locate(3,60);
        printf("----------------\n");
        locate(9,60);
        printf("----------------\n");
        locate (1,1);
         locate (1,1);
          printf ("Enter category (number) of classification\n");
          scanf ("%d", &categ);
          fprintf(fp, " %d ", categ);
          printf ("Start measurements\n");
          break;
```

```
case 'm':
case 'M':
        screen(0);
      locate(1,1);
      printf("Enter calibration coefficient (no. of horiz. pixels per unit measure)\n\n");
      printf("Values for the Zeiss Inverted are:\n");
      printf("6.3X objective - 0.383/um\n");
      printf("10X  objective - 0.640/um\n");
      printf("16X  objective - 0.980/um\n");
      printf("40X  objective - 2.580/um\n");
      printf("100X objective - 6.240/um\n");
      scanf("%lf", &calib);
        screen(0);
        menu();
        locate(3,60);
        printf("----------------\n");
        locate(9,60);
        printf("----------------\n");
        locate (1,1);
    printf ("Enter category (number) of classification\n");
        scanf ("%d", &categ);
        fprintf(fp, " %d ", categ);
        printf ("Start measurements\n");
       break;
case 'l':
case 'L':
       lx=x;
       ly=y;
       x=x+1;              /* moves cursor so that target goes */
   y=y+1;              /* unerased                         */
       locate(4,60);
       printf("Left done\n");
       break;
case 'r':
case 'R':
       rx=x;
```

```
        ry=y;
        x=x+1;          /* moves cursor so that target goes */
        y=y+1;          /* unerased                         */
        locate(5,60);
        printf("Right done\n");
        break;
  case 'h':
  case 'H':
        hx=x;
        hy=y;
        x=x+1;
        y=y+1;
        locate(6,60);
        printf("uppest done\n");
        break;
  case 'b':
  case 'B':
        bx=x;
        by=y;
        x=x+1;
        y=y+1;
        locate(7,60);
        printf("lowest done\n");
        break;
  screen(0);


   default:
       locate(12,1);
       printf ("Unrecognized keystroke\n");
       break;
   }                            /* end of switch */

if (lx != 0 && rx != 0 && hx !=0 && bx !=0) {
  xxx=lx-rx;                    /* calculate distance */
  yyy=(ly-ry)*.8;
```

```
  xxx=xxx*xxx;
  yyy=yyy*yyy;
  lrdist=(sqrt(xxx+yyy))/calib;
  locate(7,1);
 printf("Linear horizontal distance is %f microns\n\n", lrdist);  /* display distance */

  xxx=hx-bx;                    /* calculate distance */
  yyy=(hy-by)*.8;
  xxx=xxx*xxx;
  yyy=yyy*yyy;
  aldist=(sqrt(xxx+yyy))/calib;
  locate(9,1);
 printf("Linear vertical distance is %f microns\n\n", aldist);  /* display distance */
 fprintf (fp, "%f %f\n", lrdist, aldist);
 lx=ly=rx=ry=hx=hy=bx=by=0;
} } while (ch != 'f' && ch != 'F');      /* end of do-while */
printf("Enter Y axis of the finished transect\n");
scanf ("%f", &tran3);
printf("Enter X axis of the finished transect\n"),
scanf ("%f", &tran4);
trany = tran1 - tran3;
tranx = tran2 - tran4;

fprintf(fp, "%f %f %f\n", tran1, tran3, trany);
fprintf(fp, "%f %f %f\n", tran2, tran4, tranx);

fclose(fp);

}
menu()
{
locate(14,1);
 printf ("         Menu Selection\n");
 printf ("\n");
 printf ("M: reset magnification calibration (Default=100X objective)\n");
 printf ("L: digitize left side of object\n");
```

```
  printf ("R: digitize right side of object\n");
  printf ("B: digitize lower side of object\n");
  printf ("H: digitize upper side of object\n");
  printf ("N: go to next object\n");
  printf ("C: to start again\n");
  printf ("G: to grab a new image (field)\n");
  printf ("E: to erase the graphic plane\n");
  printf ("F: Finished\n");
locate(1,1);
}
```

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