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Vertical structure and biological activity in the bottom nepheloid layer of the Gulf of Maine

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Abstract—The bottom nepheloid layer (BNL) was investigated at a number of hydrographically different sites in the Gulf of Maine during August 1987. Observations were based on hydrographic measurements made from a surface ship and closely-spaced, near-bottom samples collected using a submersible. The BNL generally occurred as a turbid layer which extended 15–30 m above the bottom (m.a.b.), as indicated by *in situ* light transmission and increased concentrations of total suspended particulate matter (SPM). Phytoplankton pigments, electron transport activity (ETS), extracellular proteolytic enzyme activity (EPA), concentrations of particulate organic carbon and nitrogen (POC and PON), and protein were generally elevated in the BNL. They also displayed vertical distribution patterns in relation to near-bottom depth zones of increased abundances of zooplankton, bacteria and autotrophic and heterotrophic nanoplankton. We describe two zones of biological significance in the BNL. The first, at about 20 m.a.b. at most stations, was associated with greater zooplankton biomass (>80 μm) and copepod abundances than those depth strata either above or below, and appeared to be related to a higher quality of food particles near the top of the BNL. A second zone was seen 1–3 m.a.b. at most stations in association with the greatest levels of SPM. This deeper zone was generally of a poorer food quality, as reflected by ratios of protein-N to total-N and showed increases in cell-specific EPA. We discuss the areal variability of the BNL in the Gulf of Maine as well as the biological enhancement and vertical structure as likely influenced by both physical and biological processes.

INTRODUCTION

SINKING particulate organic material produced in surface waters is frequently concentrated at depth in particle maximum layers. Both mid-water particle maxima and bottom nepheloid layers are common and have been described for a number of continental shelf and deep-sea environments. Each depends on various physical and biological processes for formation and maintenance and often exhibits enhanced biological activity (KARL *et al.*, 1976; PAK *et al.*, 1980; KARL and KNAUER, 1984; GARFIELD *et al.*, 1983; TOWNSEND and CAMMEN, 1985). The bottom nepheloid layer (BNL), defined as a zone of increased SPM concentrations, is a more common feature throughout the world ocean and is known to vary in intensity both temporally and spatially (DRAKE, 1976; GARDNER and SULLIVAN, 1981; NEWBERGER and CALDWELL, 1981; SPINRAD and ZANEVELD, 1982; MCCAVE, 1983,

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1986; NYFFELER and GODET, 1986; SPINRAD, 1986). The BNL is thought to result primarily from resuspension of bottom sediments and thus its variability may be a function of bottom fluid motion and sediment type. However, the organic material in the BNL may at times represent resuspension of recently deposited detrital material from the fluff layer at the sediment–water interface after some period of degradation (LAMPITT, 1985). Consequently, the BNL shows evidence of relatively enhanced biological activity and may represent a source of nutrition for organisms dwelling on or near the bottom (SMITH, 1982; SMITH *et al.*, 1983; LAMPITT, 1985; WISHNER, 1980a,b; WISHNER and MEISE-MUNNS, 1984; GOWING and WISHNER, 1986; WISHNER and GOWING, 1987; DORTCH *et al.*, 1988; CHILDRESS *et al.*, 1989). The nature of organic material in the BNL has been described as being relatively labile with lower C:N ratios and high concentrations of organic carbon, protein and labile fatty acids than either the clearer water immediately above or the sediment below (ROWE and GARDNER, 1979; KAWANA and TANIMOTO, 1984; NORIKI and TSUNOGAI, 1986; MAITA and TANADA, 1978; SMITH *et al.*, 1983). Reflecting the relatively rich particulate food quality and quantity, the BNL supports a higher living biomass (KARL *et al.*, 1976; WISHNER, 1980a,b; ANGEL and BAKER, 1982; GOWING and WISHNER, 1986) and higher rates of zooplankton grazing (WISHNER and MEISE-MUNNS, 1984) and respiration (SMITH, 1982).

It has been shown recently that, apart from the more intense biological activity, there are indications of vertical structure in the BNL which results in various zooplankton taxa exhibiting maxima at some depth stratum above the bottom (CHILDRESS *et al.*, 1989, and refs therein). Detailed studies of vertical structure in the BNL have been few, however, and many of the previous investigations have generally been carried out at depths several tens of meters above the bottom and in the deep ocean where the bottom nepheloid layer is not as intense as that seen on continental shelves. We report here the results of investigations of the BNL in the Gulf of Maine based on a wide range of chemical and biological measurements on samples collected using a submersible to obtain vertical profiles beginning at only a few centimeters above the bottom. Results from our earlier work suggested biological enhancement in the BNL of the Gulf of Maine (DORTCH *et al.*, 1988). Our purpose here was to determine the existence and zonation of enhanced biological processes in the BNL over a range of continental shelf environments.

MATERIALS AND METHODS

The results reported here are based on measurements obtained using the submersible *Johnson Sea Link* and its mother ship the R/V *Seward Johnson* on a cruise in the Gulf of Maine 21–30 August 1987. The dive stations (Fig. 1) represent a spectrum of physical regimes which range from the well-stratified waters overlying the central basins of the Gulf to more shallow depths representing relatively low (Station BB) to high (Station CB) tidal current speeds. Measurements at each station included those performed from the mother ship using a hydrowire as well as those collected using the submersible. The same measurements were not performed at all stations and or the same depths, primarily because of various limitations imposed by daylight and sea state on the time we were able to spend at depth using the submersible. The more complete stations, for which we were able to make measurements at a significant number of depths, were Stations JB230 and JB242, each in Jordan Basin in the eastern Gulf, CB, which was on Clay Bank off the Maine coast, and BB in Bigelow Bight in the western Gulf.

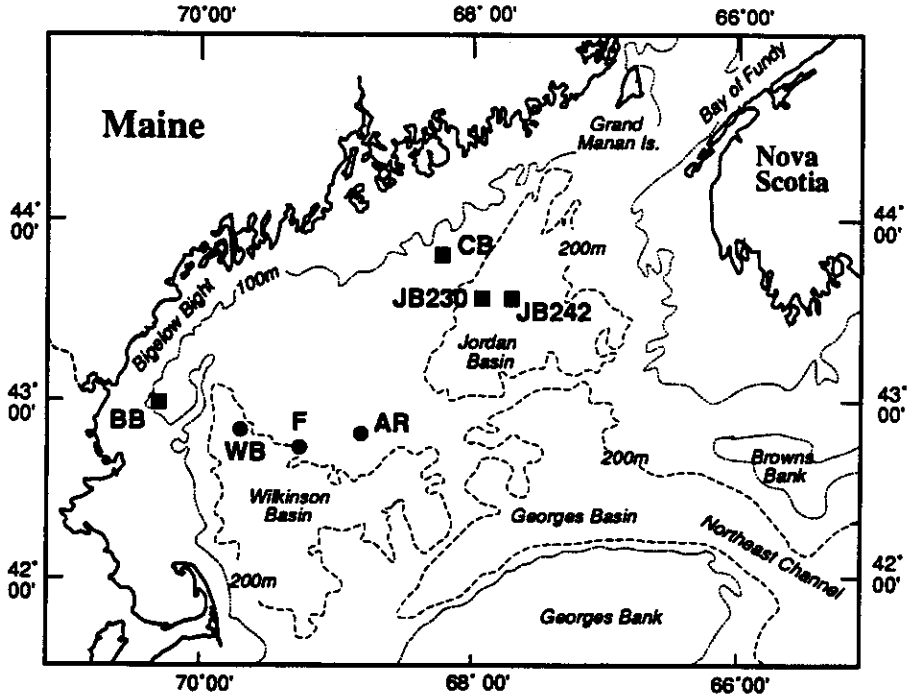

Fig. 1. Map of the Gulf of Maine showing station locations and major features referred to in the text. The stations designated by a box are those where more detailed measurements were made on discrete water samples in the BNL; those designated by a filled circle indicate those where only a few water samples were taken.

Hydrography

Vertical profiles of temperature, salinity, light transmission and *in situ* chlorophyll fluorescence were made by conducting standard casts using a Neil Brown Smart CTD and a Sea Tech 25-cm path length transmissometer and *in situ* fluorometer. The casts were conducted to within about 3 m above the bottom as monitored by the echo from a Benthos pinger attached to the CTD package. Density (sigma-*t*) and salinity were computed from the CTD data. The beam attenuation coefficient was computed from the light transmission as: $c = -\ln(V_1/5 \times V_2/V_3)/0.25$, where V_1 is the *in situ* voltage reading, the factor 5 is the full range transmission voltage, V_2 is the factory air calibration and V_3 is the pre-cruise air calibration. The *in situ* chlorophyll fluorescence is presented as relative chlorophyll fluorescence, which roughly corresponds to the concentration of chlorophyll *a*.

Sample collection

Separate Niskin bottle casts were made to collect water for the various water column analyses. Upper water column samples were collected using the hydrowire and Niskin bottles. We collected near-bottom water samples from the bottom nepheloid layer using the *Johnson Sea Link* submersible. Four 10-l Go-Flo bottles were mounted horizontally on the front of the submersible such that each could be closed using the submersible's

mechanical arm. During these dives the submersible hovered just above the bottom with water bottles oriented into the current assuring complete flushing of the bottles as well as making certain that we were not resuspending bottom sediment and thus contaminating the samples. Successive samples were collected during ascent.

Water samples were analysed for: chlorophyll *a* and phaeopigments, POC, PON, protein, ETS activity, EPA, numbers of bacteria and autotrophic and heterotrophic nanoplankton.

Sediment samples were also taken from the submersible with a stainless steel box corer operated by the robotic arm. The top centimeter was subsampled on board ship and frozen until analysis.

Phytoplankton pigments, POC, PON and SPM

Replicate phytoplankton chlorophyll concentrations were determined from acetone extracts of 0.45 μm Millipore filters as given in PARSONS *et al.* (1984). Total particulate carbon and nitrogen was determined with a Carlo-Erba 1106 CHN analyser on samples collected by filtering 1 l of water through a precombusted Whatman GF/F filter which were stored frozen until analysis. Before analysis filters were subjected to a vapor phase HCl acidification to remove carbonate material. SPM concentrations were measured as dry weight of seston in 1 l of sample water collected on a GF/F filter. We did not take replicate SPM or CHN samples; analytical precision of the CHN analyser determinations was ± 1.2% for carbon and ± 2.9% for nitrogen.

Nanoplankton and bacteria

Autotrophic and heterotrophic nanoplankton were enumerated on board the ship using epifluorescence microscopy and the fluorochrome stain Primulin (CARON, 1983). A single subsample of 10–50 ml of 1% glutaraldehyde-preserved sample was filtered onto a 3.0 μm Nuclepore filter prestained with Irgaline Black and backed with a 0.45 μm Millipore filter. This was rinsed with 0.1 M Tris buffer, stained with Primulin for about 15 min and mounted on a microscope slide for microscopic examination. A total of 20 fields or 100 cells, in the 3–8 μm size range, were counted and cells classified as either autotrophic (containing chlorophyll) or heterotrophic.

Abundances of attached and free-living heterotrophic bacteria were determined following the cruise on formalin-preserved water samples using DAPI stain and epifluorescence (PORTER and FEIG, 1980). The water samples were subjected to sonification for 1 min before preparing the slides, thus freeing the attached cells.

ETS, protein and EPA

We estimated relative water column respiration rates by measuring respiratory electron transport (ETS) activity, which is an enzyme assay that can be converted to respiration rates (PACKARD, 1986). Samples for measuring ETS activities were collected by filtering 1 l through GF/F filters, frozen in liquid nitrogen and analysed at the laboratory following the cruise using the procedures detailed in PACKARD (1986). The incubations were carried out at 20°C and corrected to *in situ* temperatures as in PACKARD (1986).

The protein content of the particulate organic matter was measured by a slight modification of the method of MAYER *et al.* (1986) which measures only those larger polypeptides (equivalent to "protein") that are amenable to enzymatic digestion, using commercially available proteases. Seston was filtered from large volumes of sample water (12–15 l) onto precombusted GF/F filters and stored at −15°C. Two, rather than one, extractions with NaOH were found to be necessary to remove all protein from the filters. Sediment samples were analysed by the normal method described in MAYER *et al.* (1986).

Extracellular proteolytic activity (EPA) was measured by a modified version of HOPPE's (1983) method, by incubating subsamples of collected, unfiltered seawater spiked to 10 μM with alanine-methylcoumarinyl amide immediately after collection. Incubations were carried out in fluorescence cuvets, which were read at the appropriate time intervals in a Perkin–Elmer 650-10S spectrofluorometer. Standards were made from methylcoumarinyl amide added to seawater samples, which remained stable with time. Controls of seawater without any additions were analysed to correct for background fluorescence. Analytical precision was ± 12.5%.

Zooplankton

Zooplankton samples were collected using the submersible's *in situ* pumping system. A 5 cm diameter intake hose fitted with a flow meter and with the outer end attached to the robotic arm was used to pump water at a rate of *ca* 300 l min^{-1} through one of six 80 μm mesh Nitex nets mounted in moveable plexiglass collection chambers positioned on the front of the submersible. As each chamber moved onto place the previous chamber and net closed. The first sample was collected while the submersible hovered above the bottom and the robotic arm placed the intake hose a few centimeters above the bottom. Approximately 0.25 m^3 were filtered for each of six samples as the submersible ascended; samples were collected at 0.1, 1, 5, 10, 20 and 40 m above the bottom at five of the stations (Stas JB230, JB242, BB, CB and WB; Fig. 1). Upon surfacing the net contents were washed into sample containers and preserved with 4% borate-buffered formalin for later identification of major taxonomic groups.

RESULTS

Hydrography

Summary plots of the vertical structure of the water column are presented in Fig. 2 for each of the seven stations. The deeper stations show quite clearly the presence of the three Gulf of Maine water masses: Surface Water, the warm, seasonally stratified surface layer; Intermediate Water, a cold remnant of the previous winter's cooling and convective sinking of surface waters; and Bottom Water, a relatively warm and salty layer of slope water origin which enters the Gulf of Maine through the Northeast Channel (HOPKINS and GARFIELD, 1979).

The presence of Maine Bottom Water, as well as the extent of tidal mixing, which is greatest in the eastern Gulf, appear to exert considerable influence on the vertical structure and distributions of mid-water and bottom nepheloid layers. The two Jordan Basin stations, JB242 in the eastern basin and JB230 in the western basin show the influence of slope water on the water column quite clearly. There is much more slope water at JB242, as revealed by the shallower depth of 34 ppt salinity, which can be used to

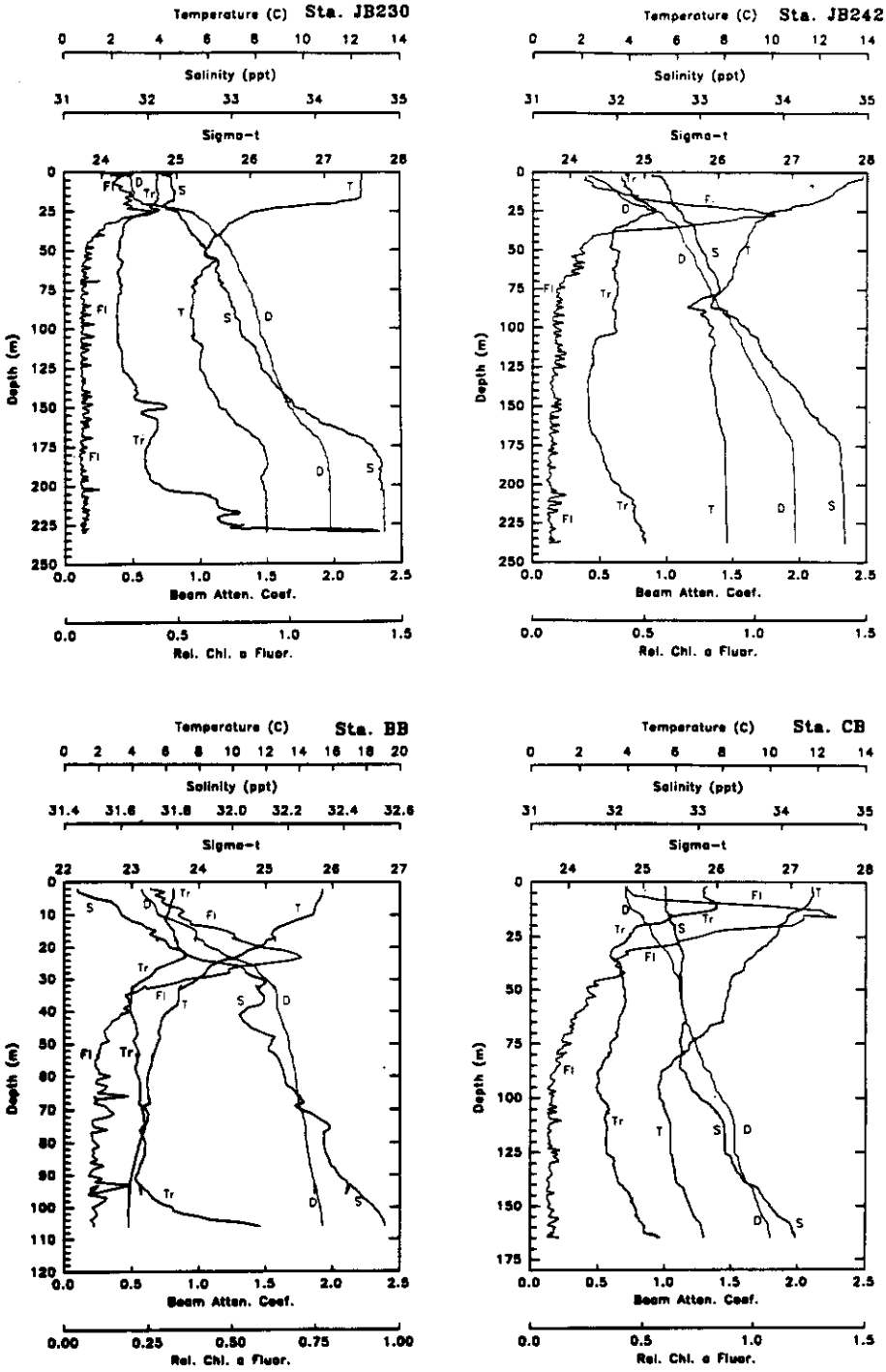

Fig. 2. Vertical profiles of temperature (T, °C), salinity (S, ppt), density given as sigma-t (D, kg m^{-3}), relative *in situ* chlorophyll fluorescence (Fl), and light transmission, given as beam attenuation coefficient (Tr, m^{-3}), for each of the seven stations in Fig. 1.

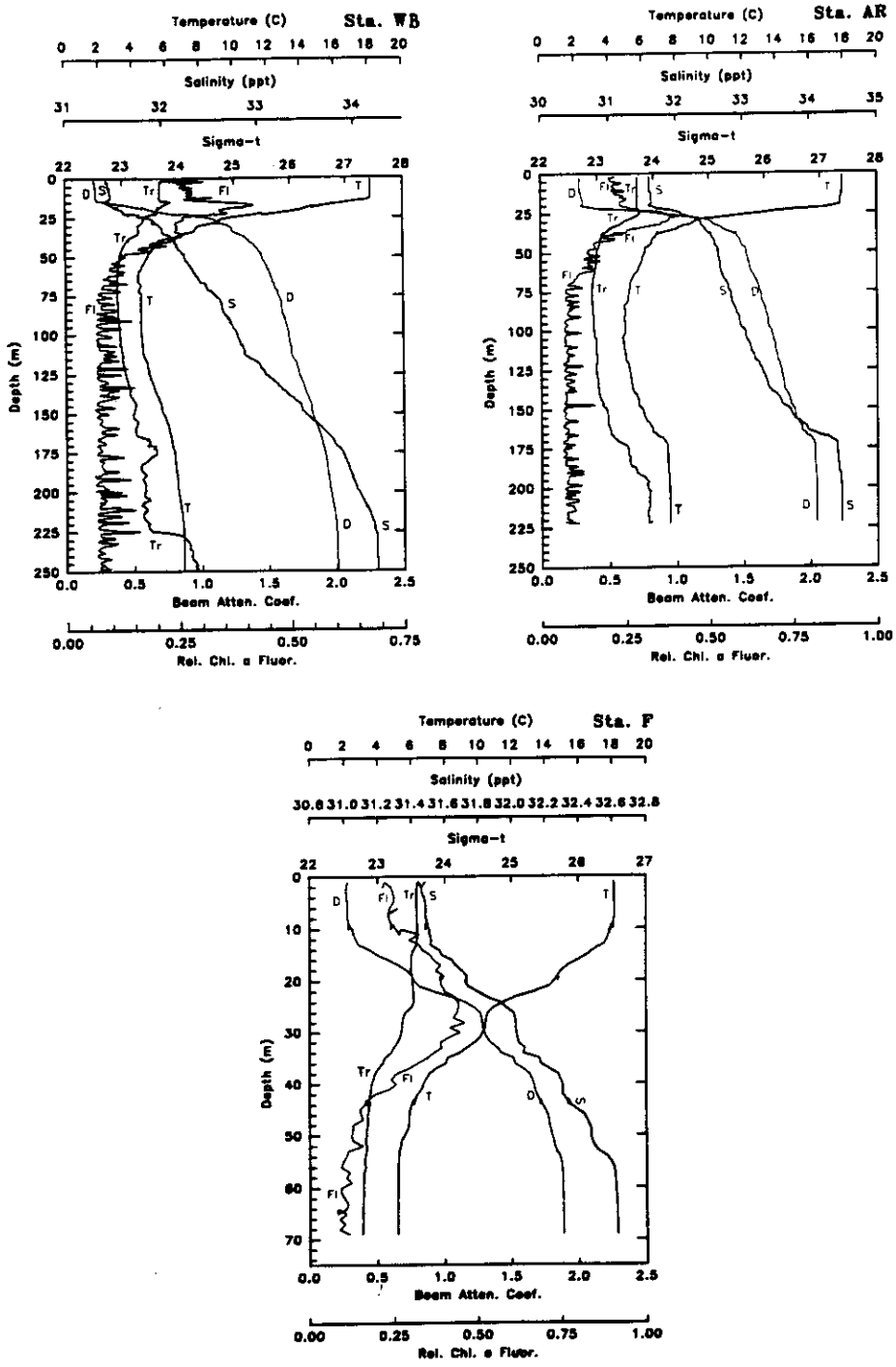

Fig. 2. *Continued*

arbitrarily define Bottom Water. Also, the cold Intermediate Water layer is confined to a narrower depth zone at JB242. The contrast between these two adjacent stations is the result of slope water hugging the southwestern Nova Scotian Shelf in response to the coriolis effect as it enters and spreads throughout the Gulf (HOPKINS and GARFIELD, 1979). Both stations show a pronounced BNL, indicated by an increase in the beam attenuation coefficient below 25 to 30 m.a.b.; the sharp increase in beam attenuation coefficient just off the bottom at JB230 may have resulted from the CTD package touching the bottom and stirring up sediment. Station JB230 shows some evidence of a mid-water particle maximum just above the interface between the Intermediate Water and Bottom Water layers as has been described earlier (TOWNSEND and CAMMEN, 1985).

Station AR, further to the west from Jordan Basin, but still in relatively deep water (225 m), also exhibits a pronounced Bottom Water layer, but it is confined to greater depths (175 m) than either JB230 (160 m) or JB242 (130 m). The mid-water particle maximum, if it exists at Station AR, is blurred with the BNL, as the beam attenuation coefficient begins to increase first between 150 and 175 m and then again at about 190 m depth, or about 25 m above the bottom. Still further to the west at Station WB in Wilkinson Basin, the Bottom Water layer is confined to depths greater than about 190 m. The BNL begins at about 225 m, or 25 m above the bottom, and there is evidence of a mid-water particle maximum at about 175 m.

The effects of local tidal mixing and advection of tidally-mixed coastal waters out over the northeastern Gulf of Maine (TOWNSEND *et al.*, 1987; BROOKS and TOWNSEND, 1989) reduce the contrast between water layers at Station CB. Two shoulders in the beam attenuation coefficient profile at 105 and 130 m may represent mid-water particle maxima in association with changes in temperature and salinity between Bottom Water and Intermediate Water. The BNL begins at about 135 m depth, or 25 m above the bottom.

The shallowest station we sampled, Station F over Fippenies Ledge, showed no BNL or mid-water particle maximum, and the vertical water column structure is dominated by the seasonal thermocline/pycnocline which extends from about 12 to 35 m from the surface. The upper water column structure is similar at Station BB in Bigelow Bight, except that the BNL is very prominent, with the beam attenuation coefficient increasing abruptly at about 15 m above the bottom. This BNL at Station BB is in contrast to those seen at each of the other deep stations, which begin at about 25–30 m above the bottom. The thinner turbid layer of the BNL at Station BB may represent a reduction in the degree of resuspension from tidal currents, which are less energetic in the western Gulf of Maine.

Chlorophyll, SPM, POC and PON

Only stations JB230, JB242, CB and BB (Fig. 1) were profiled in detail and much of the following pertains to those stations with regard to vertical distributions of water sample variables (Table 1).

Chlorophyll and phaeopigments were highest in the upper water column in conjunction with the *in situ* fluorescence maxima (Figs 3–6). Phaeopigments were elevated in the BNL at each station; chlorophyll, however, was strongly elevated only at Station CB and were slightly elevated at JB242. The upper water column chlorophyll values at Stations CB and JB230 were the highest among the seven stations, reaching about 6 $\mu g\ l^{-1}$ total pigments. Station CB was in the productive waters of the Maine coastal current, while Station JB230 was in a filament of that coastal water that had been advected offshore (BROOKS and

Table 1. Summary of measurements on discrete water samples for the seven stations in Fig. 1

Station	Depth (m above bottom)	Suspended particulate material ($mg\ l^{-1}$)	Particulate organic carbon ($\mu g\ C\ l^{-1}$)	Particulate organic nitrogen ($\mu g\ N\ l^{-1}$)	C/N Ratio	Exoproteolytic enzyme activity ($nM\ MCA\ h^{-1}$)	Protein ($\mu g\ l^{-1}$)	Chl. *a* ($\mu g\ l^{-1}$)	Phaeo ($\mu g\ l^{-1}$)	Bacteria (cells × $10^4\ ml^{-1}$)	Autotrophic nanoplankton ($cells\ ml^{-1}$)	Heterotrophic nanoplankton ($cells\ ml^{-1}$)	ETS activity ($\mu l\ O_2\ l^{-1}\ h^{-1}$)
Jordan	0.2	2.3	55.2	6.9	8		0.9	0.04	0.11	29.95	39	91	0.3
Basin	0.3	1	78.3	9.8	8	1.5	4.9	0.02	0.09	22.80	52	154	0.2
(JB230)	0.4	2.2	71.2	8.8	8.1		5.9	0.04	0.1	27.86	39	180	0.2
	0.5	2.9	56.6	6.7	8.4		2.7	0.03	0.13	25.78	14	193	0.4
	1	1.9	130.9	17.6	7.5		5.1	0.03	0.1	30.10	39	232	0.5
	2	1.6	51.7	5.6	9.3	2.2	3.6	0.02	0.07	34.12	0	218	0.2
	21	0.7	55.4	5.5	10.1	2.3	3.8	0.01	0.04	33.68	0	207	0.5
	41	0.7	36.5	4.5	8.1	0.7	10.4	0.26	0.05	23.39	14	251	0.3
	65	2.3	38.8	4.1	9.6		8.2	0.03	0.08	28.01	0	207	0.8
	130	1	22.9	2.5	9.1		1	0.01	0.11	31.89	14	180	0.7
	207	1	272	36.5	7.5		85.3	0.99	0.4	103.11	708	1183	13.1
	208						0.24	0.15					
	218							0.6	0.25				
Clay Bank	0.2	1.9	86.4			6	13.3	0.15	0.39	34.72	116	270	0.3
(CB)	0.6	3.3	134.3	16.1	8.4	5.3	24.2	0.3	0.41	32.33	102	400	0.7
	2	1.7	85	11	7.7	8	23.6	0.56	0.27	30.25	141	463	0.6
	3	2.1	37.7	4.4	8.6	1.7	12.1	0.12	0.25	25.63	77	207	0.3
	5	2.1	102	8.7	11.8	1.9	7.5	0.02	0.05	39.64	97	97	0.3
	50	1.4	53	6.3	8.5	1.4	8.7	0.05	0.09		174	521	0.4
	153	5.4	117.6	10	11.7	23.9	250.3	5.23	0.84	320.07			3.8
Jordan	0.2	2	91.9	10.1	9.1	5.4	6.1	0.06	0.07	28.46	39	251	0.4
Basin	0.5	2.4	60.9	7.2	8.5	16.7	5.8	0.04	0.06	24.44	58	116	0.3
(JB242)	1.2	4	89.1	10.2	8.8	3.3	11.7	0.05	0.13	23.99	39	97	0.5
	5	1.1	72.8	6.4	11.4	2	6.5	0.02	0.06	27.57	232	58	0.5
	26	1.2	47.7	5.9	8.2	2	28.7	0.03	0.06	253.33	39	367	0.9
	42	0.7	55.5	7.4	7.5	4.8	22.2	0.01	0.06	25.78	97	309	0.4
	162	1.2	34	4.7	7.3	9.6	19			108.17	483	241	0.1
	207	0.9	100.4	15.5	6.5	7.8	35.5	1.88	0	33.53	39	97	2.8
	217	8.8	585.3	88.2	6.6	22.3	349.9	5.23	2.41	154.22	328	540	34
E. Ammen	0.4	2.6	82.7	9.2	9	2.1	4.2	0	0.13	34.42	0	116	0.4
Rock (AR)	0.7	3.1	86	10.8	8	0.8	13.9	0.01	0.13	13.56	39	174	0.4
Fippenies	0.15	0.8	43.2	5.5	7.9	7.5	6.9	0.07	0.28	32.19	232	463	0.6
Ledge	0.6	0.7	39.5	5	8	13.2	12.9	0.07	0.17	36.51	290	405	0.6
(F)	15	0.9	58.4	9.2	6.4	5.7	12.4	0.08	0.14	38.15	174	367	1.7
Bigelow	0.4	3.1	113.5	16.6	6.8	25.5	14.5	0.03	0.17	39.64	39	521	0.7
Bight	0.7	6.3	104.4	16.6	6.3	15.5	25.6	0.02	0.12	0.00	154	637	3.1
(BB)	1	3.5	131.6			10.6	13.5	0.04	0.3	33.82	77	483	0.1
	3	3.1	112.2			10.4	14.8	0.04	0.32	39.34	174	212	0.1
	5	3	337.4			12.4	25	0.04	0.3	30.10	39	270	0.2
	23	0.4	45	6.7	6.7	4.8	22	0.02	0.14	140.36	97	1158	0.6
	68	0.4	80.4	15.2	5.3	3.8	27.5	0.86	0	38.00	251	405	1.5
	93	0.7	241	41.4	5.8	8	95.5	0.47	0.5	32.19	19	97	8.4
Wilkinson	0.2	2.6	72.6	9.9	7.4	11.6	14.7	0.01	0.08	24.74	0	232	0.8
Basin	0.5	1.2	60.8	9	6.8	3.7	19	0.01	0.07	27.57	58	251	0.7
(WB)	1	2.1	81.7	10.8	7.6	7.6	16.1	0.02	0.11	27.86	135	290	0.8

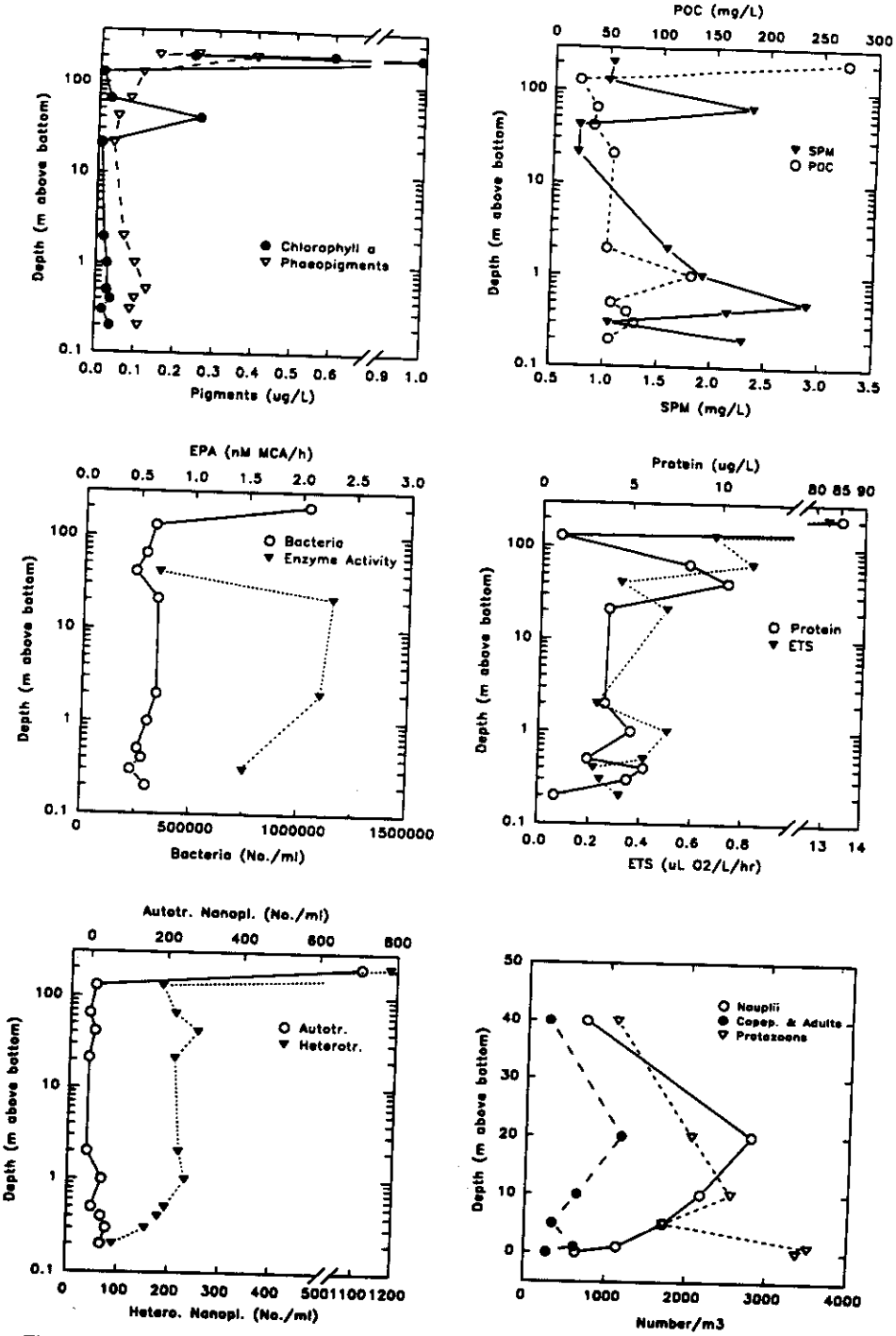

Fig. 3. Station JB230. Vertical profiles of extracted chlorophyll *a* and phaeopigments, particulate organic carbon (POC) and suspended particulate matter (SPM), extracellular proteolytic enzyme activity (EPA) and numbers of heterotrophic bacteria, protein and electron transport system activity (ETS), autotrophic and heterotrophic nanoplankton and major groups of zooplankton. Depths are given on the vertical axis as meters above the bottom and, except for the zooplankton, are plotted on a log scale.

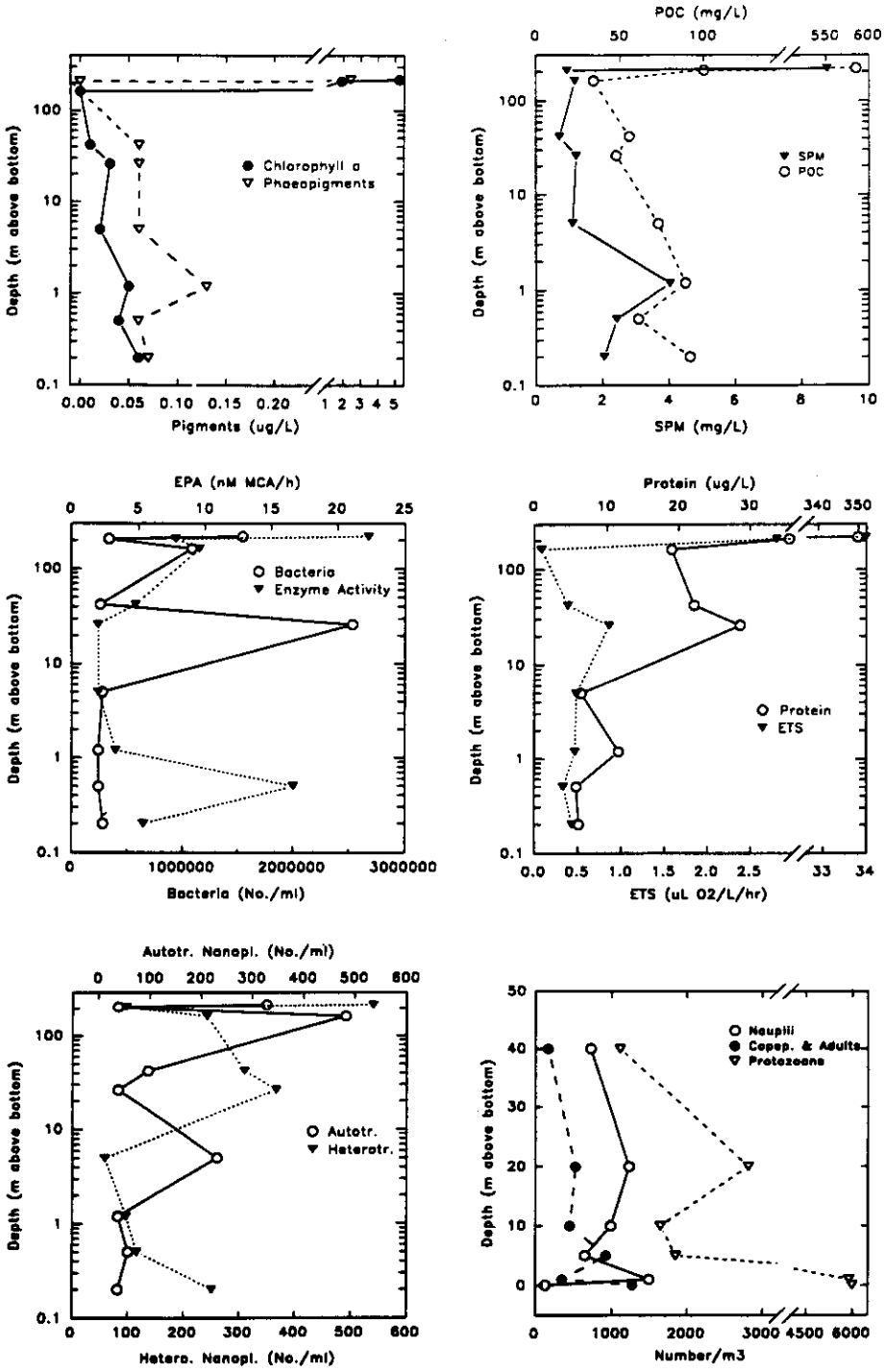

Fig. 4. Same as Fig. 3, except for Station JB242.

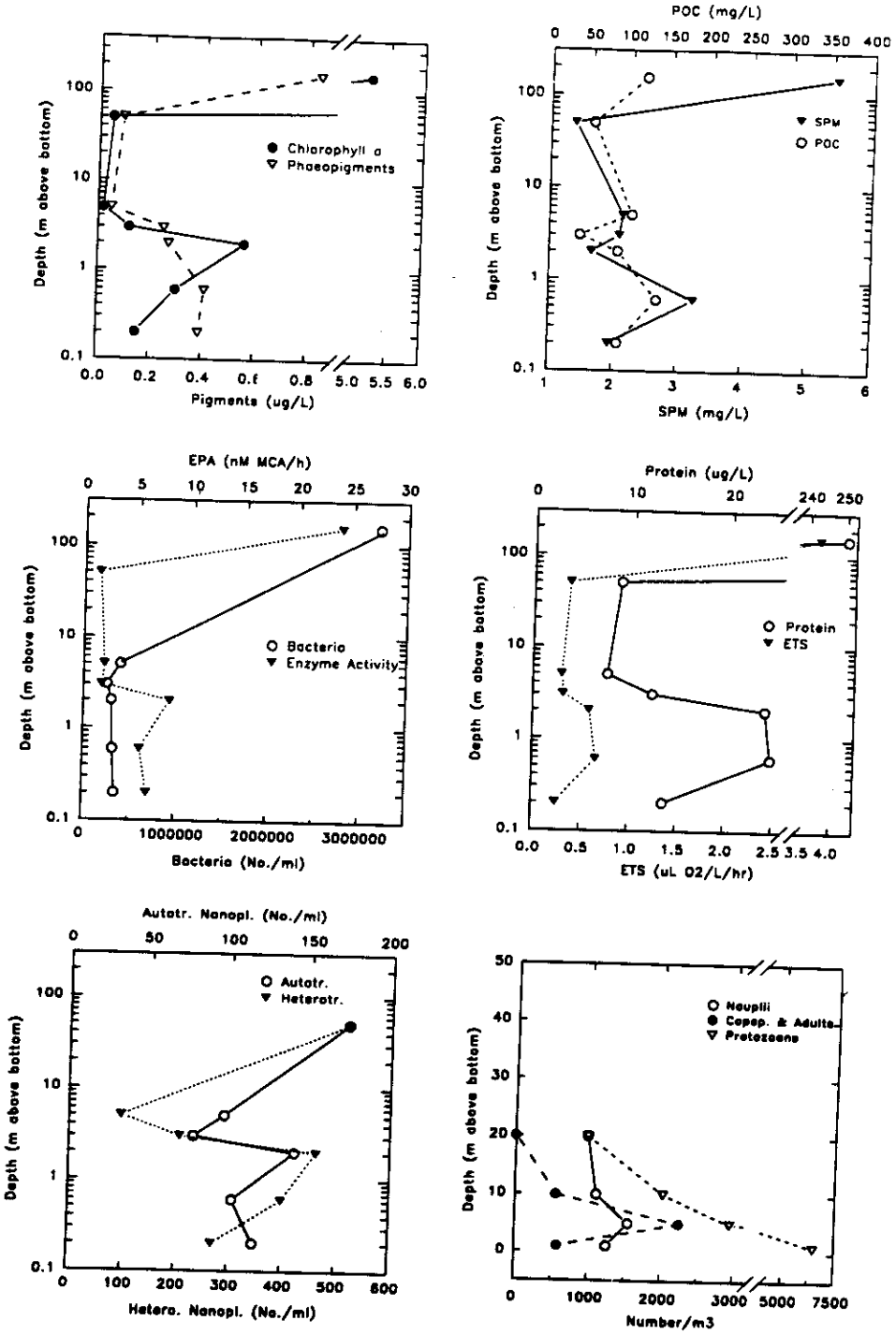

Fig. 5. Same as Fig. 3, except for Station CB.

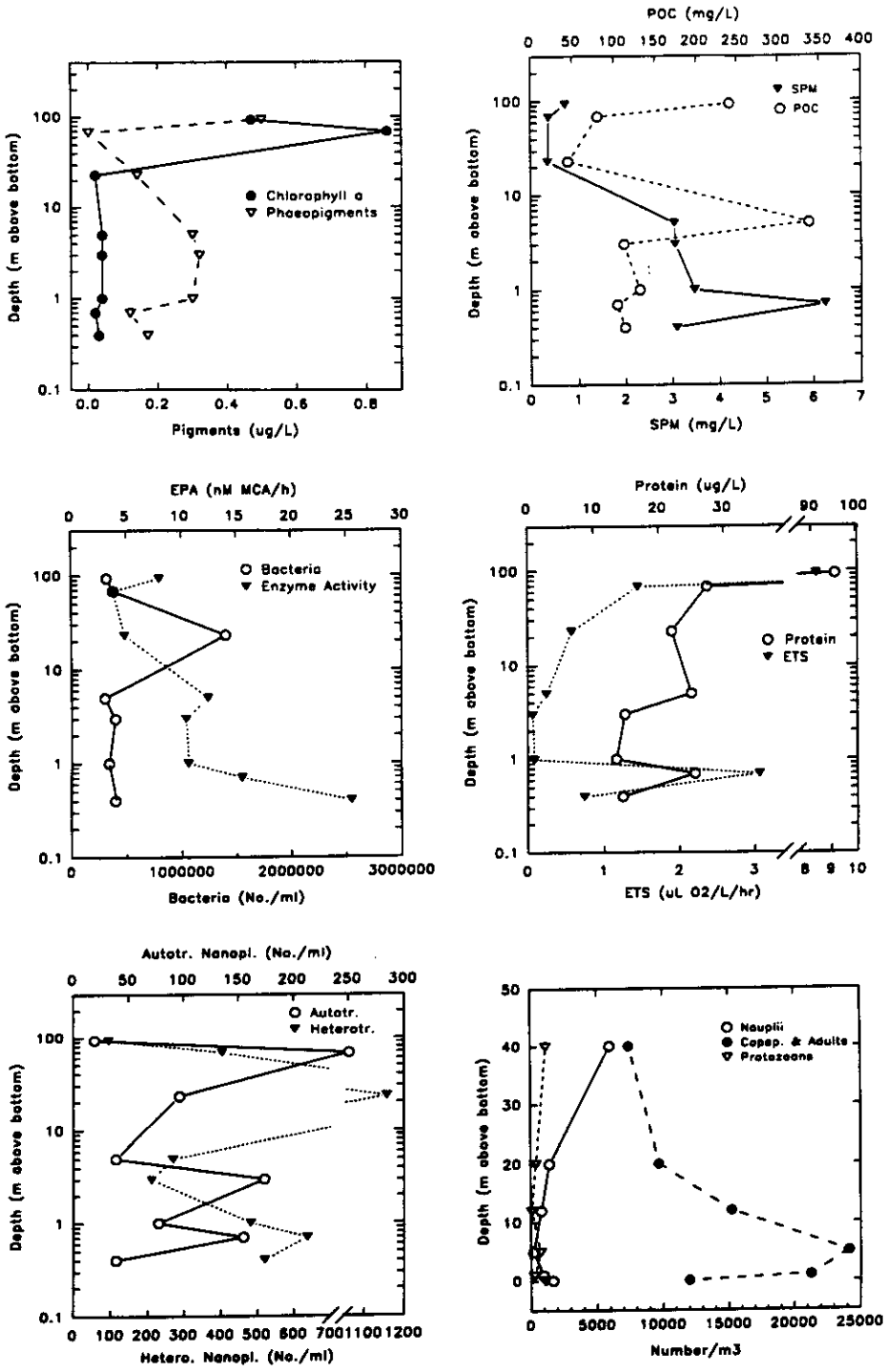

Fig. 6. Same as Fig. 4, except for Station BB.

TOWNSEND, 1989). There was generally no clear *in situ* fluorescence signal apart from noise in the BNL.

The suspended particulate material increased in the BNL overall, but showed maxima at each station between about 0.5–1 m above the bottom (Figs 3–6). The same was true for the vertical distributions of particulate organic carbon and particulate organic nitrogen, which tracked one another fairly consistently. C:N ratios varied between 11.8 and 5.3, with the lowest ratios in the upper water column. There was some evidence of greater C:N at 5–21 m.a.b. (Table 1). Interestingly, there did not appear to be a relationship between SPM and beam attenuation coefficient, which suggests that factors such as variable particle size distribution or particle type may be important in the differences in intensity of the BNL as determined by the transmissometer.

ETS, protein and EPA

There were deep water maxima in the vertical distributions of protein and ETS in association with the BNL at each of the four detailed stations (CB, BB, JB242, JB230). Stations BB and CB each had maxima in protein and ETS between 0.5 and 2 m above the bottom, with lower values between these depths and the surface (Figs 5 and 6). Both ETS and protein showed maxima at 26 m above the bottom at JB242, with no clear pattern discernible at Station JB230 (Figs 3 and 4). Protein concentrations at most stations decreased close to the sediment.

Extracellular proteolytic enzyme activity (EPA) also showed maxima in the surface waters of most stations while mid-depth values were generally low. BNL waters usually showed marked enhancements, often comparable and in one case (Station BB) exceeding those of surface waters. Elevated levels in the BNL were generally found within 5 m.a.b. Enhancements of EPA at Station CB followed those of protein and phytopigments, indicating a response to settled algal material from the photic zone. The sediments showed protein and total organic matter concentrations typical of those described in MAYER *et al.* (1988).

Nanoplankton and bacteria

The vertical distributions of both bacteria and heterotrophic nanoplankton did not show a clear trend among the four detailed stations (Figs 3–6). Both groups showed a maximum at 26 m above the bottom at station JB242, with the densities of bacteria at that depth exceeding those densities at the surface. This vertical pattern did not hold for JB230, where bacteria and heterotrophic nanoplankton were maximal at the surface and mirrored one another below the surface. Both groups showed maxima at 23 m above the bottom at Station BB, with each exceeding surface values. The heterotrophic nanoplankton showed a second maximum at 0.7 m.a.b. The densities of bacteria at Station CB showed no deep water trends, while the heterotrophic nanoplankton showed a maximum at 2 m.a.b.

The densities of autotrophic nanoplankton also showed deep maxima but not necessarily in association with trends in bacteria. The greatest densities of nanoplankton were generally in the surface waters with the exception of Station BB where the maximum was at 23 m.a.b. (Fig. 6). There were secondary maxima just off the bottom at three of the four stations in Figs 3–6.

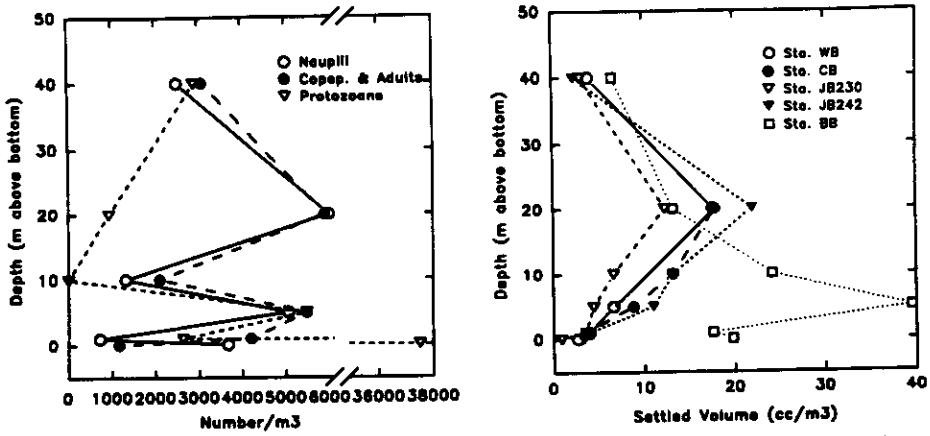

Fig. 7. Vertical distributions of the major groups of zooplankton at Station WB (left panel), and zooplankton settled volume biomass for the five stations indicated (right panel).

Zooplankton

The vertical distributions of the major groups of zooplankton are given for the four detailed stations, as well as in Wilkinson Basin at Station WB, in Figs 3–7. The copepods were for the most part those normally encountered in the Gulf of Maine (TOWNSEND *et al.*, 1984). The more important taxa, in order of abundance, were *Microsetella norvegica*, *Oithona similis*, *Pseudocalanus* sp., Microcalanus pygmaeus and *Paracalanus parvus*. Late copepodid stages of *Calanus finmarchicus*, though not numerically as abundant as the previous taxa, dominated the biomass at Station BB, and were an important biomass component at the other stations. The protozoans represented in Figs 3–7 (which included only those greater than 80 μm) were mostly tintinnids of the genera *Tintinnopsis* and *Parafavella*.

With the exception of Stations CB and BB, there was generally a peak in the abundances of naupliar and post-naupliar stages of copepods at about 20 m.a.b., with a second abundance peak just off the bottom (between 1 and 5 m.a.b.). There was only one abundance peak at Stations CB and BB, however, which was between 1 and 5 m.a.b. The general trend in the abundances of the >80 μm protozoans was to increase with proximity to the bottom; the exception was Station BB where there were only trace abundances. The settled-volume biomass had a maximum at 20 m.a.b. and was controlled primarily by *Calanus finmarchicus*.

DISCUSSION

As has already been reported (SPINRAD, 1986) the bottom nepheloid layer is a pervasive and dramatic feature of Gulf of Maine waters. Generally, it occurs as a turbid layer that extends upward 15–30 m from the bottom and varies in intensity among the stations we sampled. This variation, as determined from the transmissometer profiles of beam attenuation coefficient as well as total measured SPM, does not correspond well to areal differences in tidal current speeds predicted throughout the Gulf (GREENBERG, 1983), which are generally greatest in the eastern-most areas. As others have reported (MOODY *et*

al., 1987) there does not appear to be a clear relationship between total SPM loads and *in situ* light transmission. The greatest SPM loads were found at Station BB in Bigelow Bight which is in the western Gulf where tidal current speeds are not as great as those stations further east. The lowest SPM loads were at Station JB230 which had the highest beam attenuation coefficients among the benthic nepheloid layers sampled (although this station also had the greatest degree of fine structure in transmission). At each of the four detailed stations SPM reached its maximum value in the BNL at 0.4–1 m elevation above the bottom, rather than nearest the bottom as might be expected. Each of the other parameters also displayed peaks at various elevations above the bottom, rather than nearer the bottom, and it thus would appear that processes other than simple resuspension of sediment are important in the overall makeup and vertical structure of the BNL.

The peak abundances of copepods in the BNL were surprisingly high and were of the same magnitude as those previously recorded for surface waters of the Gulf of Maine. For example, TOWNSEND *et al.* (1984) found abundances of post-naupliar copepods in the range of 5000–40,000 m^3 within the upper 40 m of the water column at offshore stations in the Gulf in June and September, with densities dropping off to about 1000–2000 m^{-3} at depths greater than 50 m. We found peak abundances of post-naupliar copepods in the BNL that ranged from a low of 1170 m^{-3} at 20 m.a.b. at Station JB230 to 24,150 m^{-3} at 5 m.a.b. at Station BB. The settled volume biomass estimates reported here for the BNL (Fig. 7) are approximately twice those reported by TOWNSEND *et al.* (1984) for surface waters, and may reflect a greater contribution by *C. finmarchicus*, which was probably captured more efficiently in the darkness of the BNL.

There appear to be two zones of biological significance in the BNL: the first at about 20 m above the bottom, and the second much closer to the bottom, within 3 m at all stations, and within 1 m at some. The first zone, about 20 m above the bottom, was associated with a maximum in zooplankton abundance and biomass. The peaks in zooplankton biomass and copepod densities at about 20 m.a.b. were seen in three of the five stations sampled (Figs 3–7). The two exceptions were Stations CB and BB which had maxima at 5 m.a.b. Station CB was one of the most productive stations, having had high phytoplankton biomass in the upper water column, as revealed by pigment concentrations. [Station JB230 also had high surface chlorophyll concentrations, but this was due to our having sampled in a filament of coastal water that had been advected out over Jordan Basin (BROOKS and TOWNSEND, 1989).] At Station JB242 (Fig. 3), there was a double peak in copepods and protozoans, one at about 20 m.a.b. and another within 1 m of the bottom. The peak at 20 m.a.b. was coincident with peaks in protein, ETS, bacteria and heterotrophic nanoplankton, which suggests that conditions near or at the top of the BNL are more favorable for zooplankton feeding. The peak within 1 m.a.b. at Station JB242 was coincident with a peak in particulate organic carbon as well as a secondary peak in heterotrophic nanoplankton densities. The relationships between zooplankton abundances and other variables at the other stations were less clearly defined. For example the copepod peak at 20 m.a.b. at Station JB230 corresponded with maxima in ETS activity and extracellular proteolytic enzyme activity. Though particulate organic carbon was, in general, greater in depths closer to the bottom than 20 m, total SPM also generally increased below 20 m.a.b. at each station. Thus, it is possible that the copepod maxima at about 20 m.a.b. may be due to a relatively "cleaner" food source near the top of the BNL than that found closer to the bottom.

Apart from a likely cleaner food source at the top of the BNL, there also is evidence for higher quality food particles there as well, as shown by the vertical distributions of the ratio

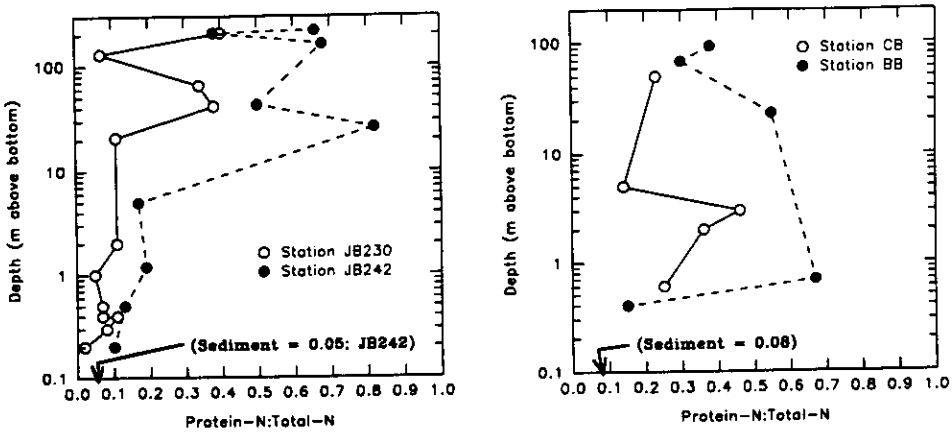

Fig. 8. Vertical profiles of the ratios of protein-nitrogen to total-nitrogen for Stations JB230 and JB242 (left panel) and Stations CB and BB (right panel). Also given are the same ratios for the surface sediment at Stations JB242, BB and CB; Stations CB and BB both had ratios of 0.08.

of protein-nitrogen to total-nitrogen (Fig. 8). Fresh, labile organic matter (e.g. biomass) shows values close to 1, while refractory materials often show values <0.1 (MAYER *et al.*, 1986; 1988). There was a peak at 41 m.a.b. at Station JB230 and at 26 m.a.b. at Station JB242; each of these values exceed those measured at the surface. Station BB also shows a peak in protein-N: total-N ratio at 23 m.a.b., which is greater than surface values. Judging from these results, it would appear that feeding conditions for copepods in the BNL are best some distance above the bottom, rather than in the BNL itself, and that this position above the bottom may represent a compromise between a greater concentration of food in the BNL and a higher quality of that food at the upper part of the BNL.

The ratio of extracellular protease activity to bacterial numbers (cell-specific EPA) generally showed minimum values at the top of the BNL (Fig. 9). This ratio has not been well-explored, but is perhaps indicative of the amount of enzyme needed by bacteria in order to hydrolyse protein substrate and hence procure nitrogenous compounds. This trend is perhaps indicative of the ease of hydrolysis of substrate with high protein-N: total-N ratios found at these depths. Alternatively, these minima may result from an opportunity for bacteria to obtain nitrogenous compounds as low molecular weight excreta (e.g. ammonia, amino acids) from the abundant zooplankton found at similar depths, which do not require proteolytic enzymes.

The peaks in protein-N: total-N at Stations JB230 and JB242 were coincident with peaks in the abundances of heterotrophic nanoplankton at the same depths. Bacteria, on the other hand, were at a minimum at those depths, which might reflect a food chain operating from detritus to bacteria to heterotrophic nanoplankton to zooplankton, giving the zooplankton peak at that depth and suggesting a biological control on the vertical structure. Others have reported peaks in zooplankton abundances at some height above the bottom. For example, CHILDRESS *et al.* (1989) sampled zooplankton at depths of 1, 5, 10, 20, 50 and 100 m above the bottom in deep basins off the California continental shelf and observed maxima in various zooplankton groups some distance off the bottom. SMITH *et al.* (1987) reported greater abundance and biomass of macrozooplankton at 20 m.a.b. in

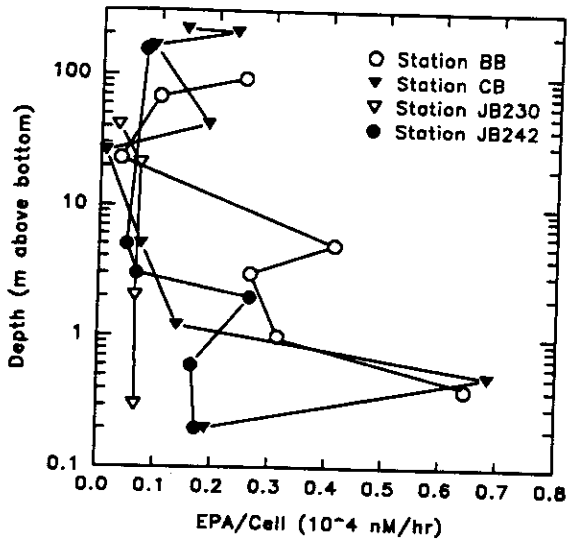

Fig. 9. Vertical profiles of the cell-specific extracellular proteolytic enzyme activity (EPA) for the stations indicated. EPA per cell is given as that per 10^4 bacteria as in Table 1.

the Santa Catalina Basin, which corresponded to increased concentrations of particles, POC, total dissolved free amino acids and ATP at that depth.

Vertical structure in the BNL may also be controlled by physical processes. For example, the abundances of autotrophic as well as heterotrophic nanoplankton show a peak in the BNL at 2 m.a.b. at Station CB, which in turn may be associated with a peak in zooplankton at about that depth (5 m.a.b.; Fig. 5). The presence of photoautotrophs at such a depth is likely due to their having recently settled out of the surface waters with marine snow, since many of the cells we counted were associated with macroaggregates, as has been reported by others (ALLDREDGE, 1979; SILVER and ALLDREDGE, 1981). These aggregates somehow become concentrated at a particular height above the bottom (MUSCHENHEIM, 1987). Such a physical mechanism that could concentrate setting material at the top of the BNL has been invoked previously by TOWNSEND and CAMMEN (1985) to explain a peak in bacteria and protozoans at the mid-water particle maximum in the Gulf of Maine. Their vertical profiles of relative current speeds through the mid-water maximum suggested that a current shear between water masses served to concentrate particles.

The second zone of biological importance, which was within 2 or 3 m of the bottom, was generally associated with the greatest suspended particulate loads, presumably as a result of resuspension of bottom sediments. This resuspension resulted in a decrease in labile food, expressed by protein concentrations, at all stations but CB, rather than an increase as would be expected from a resuspended addition to material normally present in the water column. Apparently a high resuspension (and presumably similarly high redeposition) rate clears the water column of labile proteinaceous materials at these stations, perhaps due to particle scavenging, or to differential hydrodynamic sorting of particles near the bottom (MUSCHENHEIM, 1987). Alternatively, benthic filter feeders may be responsible for this clearance (FRECHETTE *et al.*, 1989), though we observed no significant

filter feeder populations from the submersible at most of the stations. Frequent decreases in other variables such as ETS and bacterial numbers accompanied the drop in protein concentrations near the bottom.

This resuspension also caused a shift in the quality of the protein substrate available for particle feeders, as expressed by the fraction of total nitrogen in the form of enzymatically available protein (Fig. 8). Accompanying this decrease in food quality was an increase in the cell-specific EPA (Fig. 9). The high ratios found at all stations in the lower BNL contrast sharply with the low ratios found in the upper parts of the BNL. The high values found in the lower BNL may result from the need to use relatively large amounts of enzyme in a dilute medium with poor quality substrate. Alternatively, these ratios may be indicative of a starvation state in bacteria of this zone (ALBERTSON *et al.*, 1990).

In general, we found that the greatest biological activity in the BNL occurred at the shallower stations (Stations BB and CB), and may simply reflect a closer proximity to the source of organic material in surface waters. The BNL was most intense at Station CB which may be due to being beneath higher productivity waters or because it is the least stratified station. We found that biological enhancements are occasionally detectible, but are hardly marked, under stratified, more oligotrophic areas near the center or the basin gyres. Our results thus indicate that biological activity in the BNL is tied to the spatial variations in delivery of organic matter from the euphotic zone. It seems only reasonable that temporal variations in biological activity will occur and also reflect temporal variations in this organic matter delivery term.

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