

Section 3

PRIMARY PRODUCTION, CARBON ENERGETICS,
AND NUTRIENT CYCLING

by

Donald Schell and Susan Saupe
Institute of Marine Science
University of Alaska, Fairbanks

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3.1 SUMMARY

This project seeks to describe the nutrient dynamics, primary productivity and trophic energetics of the nearshore waters of the NAS. Through consideration of the availability of nutrients and the consequent primary productivity, the carbon derived from in situ primary producers has been quantified and compared with that derived from allochthonous sources, in this case, the extensive eelgrass (Zostera marina) beds in Izembek Lagoon. We used natural abundances of radiocarbon isotopes as indicators of primary production by phytoplankton in upwelled waters and abundances of stable carbon isotopes as tracers of eelgrass carbon in the coastal food webs.

Our results confirm that the deep-mixing and advection of nutrient-rich waters onto the shelf in the vicinity of Unimak Pass subsequently produces very high rates of primary productivity over much of the study area during the spring and summer seasons. Vertical mixing in the region of the inner frontal system separating the coastal and middle shelf domains produces water columns rich in nutrients. Nitrate-N concentrations were often in excess of 5 mg-atoms/m³ in the euphotic zone with the exception of apparent nutrient depleted water sampled throughout the study area in July. Integrated water column productivities were high, with the fastest rate being 6.7 gC/m²-day. The annual productivity in the study area is about 220-240 gC/m²-yr although our temporal coverage is not sufficient for confident estimates.

In spite of the extensive Zostera beds in Izembek Lagoon, the role of eelgrass in the food web energetics of the nearshore zone appears to be minimal. The stable isotope data indicate that in situ phytoplankton production supplies nearly all carbon in the nearshore food web. Our estimates of primary productivity by phytoplankton also indicate that the in situ inputs of carbon to the inner shelf waters exceed that derived from **eelgrass** by about three-fold inside the 50-m contour near Izembek Lagoon. Although **eelgrass** has the potential to contribute a substantial amount of energy to the food web, the conversion of detrital **eelgrass** to animal biomass may proceed through a microbial-meiofaunal pathway, and the

conversion efficiency losses in the trophic steps alone might account for the lack of eelgrass carbon in higher levels.

3.2 INTRODUCTION AND CURRENT STATE OF KNOWLEDGE

The southeastern Bering Sea is one of the most biologically productive regions of the world oceans and has been the focus of several studies concerned with its abundant marine resources. These studies have been updated in Hood and Calder (1981) and the physical and biological processes have been most recently studied in the NSF-sponsored PROBES (1982) (**Processes and Resources of the Bering Sea Shelf**) and the current ISHTAR (Inner Shelf Transfer and Recycling) programs. This study seeks to build upon the database accumulated for the more offshore region and extend the information to include the waters inside of the 50-m contour to the beach. In some aspects, the nearshore zone is easier to describe: the stratified water types and structures described by Dodimead et al. (1963) and Kinder and Schumacher (1981) for the middle and outer shelf "domains" usually lie outside of the 50-m contour and the tidal and wind-mixing of the water nearshore leads to uniform vertical structure. Exceptions to this occur during early spring when runoff and/or coastal current inputs, such as the Kenai Current, can result in transitory stratification (Schumacher and Moen 1983). Phytoplankton respond to water column nutrient supply on a short time scale and depletion of nutrients can occur within a few days. Replenishment of nutrients recurs through periodic mixing in the frontal systems and active phytoplankton growth at rates typical of bloom conditions can be seen at any time during the summer months (Sambrotto 1983). Tidally driven mixing is the mechanism responsible for the vertical movement in the coastal domain in the Bering and the overall hydrographic environment is similar to situations found in the northeastern Atlantic (Pingree et al. 1978).

The plant biomass resulting from uptake of nutrients in the southeastern Bering Sea water column is transferred to higher trophic levels via two distinct pathways (Walsh and McRoy 1985). The efficiently grazed outer domain is closely coupled, supporting a large pelagic community. The middle and coastal domains are much less efficiently grazed and much of the early spring bloom sinks to the seafloor. This

contributes to the high secondary productivity of the benthos and demersal fishes in the middle and coastal domains.

On the NAS, especially in the vicinity of Izembek Lagoon and Port Moller, the extensive beds of **eelgrass** contribute large quantities of detrital carbon to the ecosystem. **Barsdate** et al. (1974) estimated that 1.66×10^8 kg/yr of **eelgrass** carbon was exported from Izembek Lagoon in the fall and the ubiquitous patches of **eelgrass** on the sea surface near Izembek Lagoon show that the process is active throughout the year. **McConnaughey** (1978) sought to determine the importance of **eelgrass** to benthic detrital consumers within the lagoon through the use of stable carbon isotope abundances in eelgrass, consumers, and phytoplankton. Although the presence of **eelgrass** carbon was evident in the composition of some lagoon fauna, no information was obtained on its importance to organisms outside of the lagoon.

The overall goal of this project was to describe the processes supplying nutrients to nearshore NAS waters, estimate the resulting phytoplankton production, and contrast this in situ carbon source to the importance of the allochthonous carbon inputs from **eelgrass** as energy sources to the nearshore food web.

Our specific objectives were to:

1. Measure ambient nutrient concentrations in the nearshore water column both temporally and spatially throughout the study area.
2. Conduct primary productivity measurements in the euphotic zone and obtain seasonal estimates of in situ carbon fixation in the nearshore waters.
3. Compare in situ primary productivity with estimates of **eelgrass** carbon fluxes from Izembek Lagoon to nearshore waters.
4. Collect specimens of nearshore water column and benthic fauna for isotopic analysis of radiocarbon content and $^{13}\text{C}/^{12}\text{C}$ ratios. This information was used to determine if phytoplankton production is the major source of energy and if **eelgrass** transport from the lagoon is also important as a carbon source. This information also offers insight into

the importance of deep mixing and upwelling to the nutrient supply of the coastal zone.

3.3 METHODS

3.3.1 Chlorophyll Concentrations

Water samples obtained from Niskin bottles were filtered on Gelman Type A/E 47 mm glass fiber filters with a few drops of $MgCO_3$ suspension added as a preservative. The filters were folded in half and placed in glassine envelopes. The filters were then frozen until pigment extraction was done in Fairbanks. The extraction and chlorophyll-a calculation procedures were from Strickland and Parsons (1972), and the phaeopigment calculations were from Lorenaen (1966). Chlorophyll-a and phaeopigments were measured on a Turner Designs Fluorometer (Model 10-005). For chlorophyll-a determinations, the fluorometer was periodically calibrated against a Bausch and Lomb Spectronic 2000 spectrophotometer.

Primary Production

Carbon fixation was measured at each station on the primary transects along the coast (Fig. 3.0). Light intensity profiles were obtained with a Li-cor photometer to obtain photic depths to the 1.0% light level. Water samples were then obtained from the CTD rosette at depths corresponding to the 100, 50, 25, 10, and 1% light levels. Two clear 250-ml glass bottles and one dark bottle (for non-photosynthetic uptake corrections) were filled from each sample. Each bottle was injected with 2 microcuries of ^{14}C -labelled sodium bicarbonate. All transfers and inoculations were carried out in subdued light. The bottles were then placed in an on-deck incubator cooled with flowing seawater and fitted with neutral density screens to approximate 50, 25, 10 and 1% of incident solar radiation. Incubations were 4-6 hours long and were started in early morning to minimize diurnal variations in carbon fixation rates. After incubation, samples were filtered (in subdued light) onto 25-mm Mflipore filters, dessicated, and stored in airtight containers. When ready to be counted, samples were treated according to the standard procedure described in

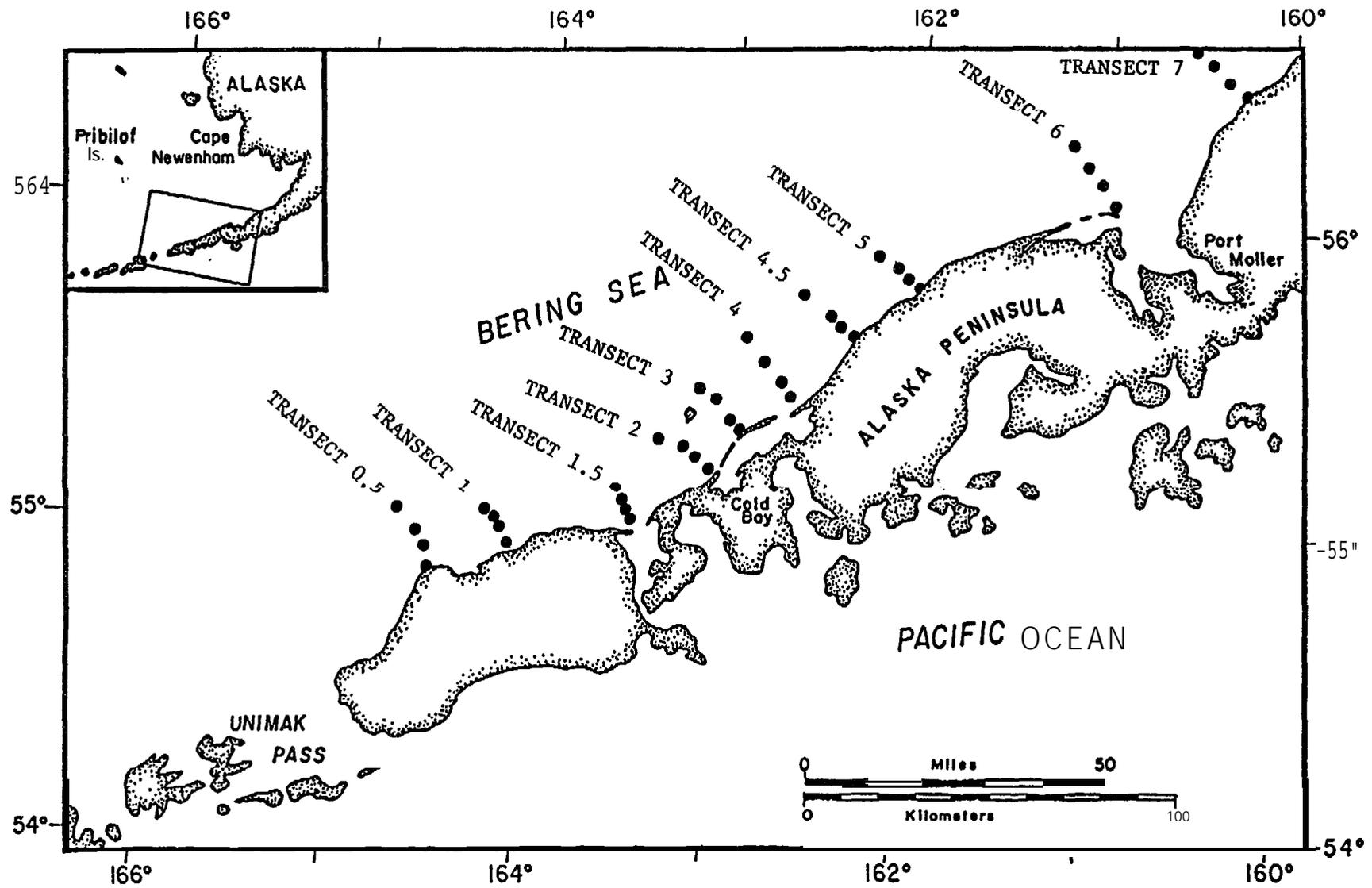


Fig. 3.0. Location of transects and stations on the NAS, Alaska, where data on nutrients and primary productivity were collected.

Strickland and Parsons (1972). Incorporated radiocarbon was determined with either a Beckman 7400 or Beckman 5801 Liquid Scintillation Counter.

Instantaneous primary productivity rates *were* extrapolated to daily fixation rates by multiplying by the integrated light intensities and average monthly day lengths. The seasonal estimates were obtained from extrapolations made with our data when available and the data obtained by PROBES (1982) when we had no comparable temporal equivalents.

3.3.2 Nutrient Concentrations

Water samples were obtained from the water column, filtered through Gelman A/E filters to remove **particulates**, transferred to 250-ml bottles, and immediately frozen. After returning to Fairbanks, these samples were analyzed for **nitrate**, phosphate, **silicate**, and ammonia concentrations using standard methods (Strickland and Parsons 1972) adapted to a Technicon Autoanalyzer. Quality assurance was maintained through the collection of random replicate samples while on station, the use of internal standards on composite samples in the laboratory and the analysis of replicates from each bottle.

3.3.3 Carbon Isotope Analyses

Samples of fishes and benthic invertebrates for isotopic analysis were collected directly from trawl-net or Marinovich trawls. Some benthic samples were collected using a rock dredge. A shotgun was used to obtain birds to collect breast muscle tissue. Plankton samples were collected with **333-micron** bongo nets and sorted to obtain the animals of interest. Phytoplankton samples were also collected with a **333-micron** bongo net and were cleaned of animals. All specimens for isotope analysis were frozen until ready to be processed.

Samples were prepared for combustion by **soaking** in 10% HCl solution to remove carbonates, rinsed with distilled water, dried at 50°C, and then ground to a fine powder **with** a mortar and pestle. In cases where organisms were very small, several animals were combined and ground together. Subsamples of the ground organisms (10-15 mg) were mixed intimately with powdered CuO and *sealed* into a glass tube while under high

vacuum. The tubes were combusted for 2 hours at 570°C to convert the organic carbon to carbon dioxide. The gas was then cryogenically purified to remove water, sulfur dioxide and nitrogen and resealed into a glass tube. The purified carbon dioxide was then analyzed on a VG Isotopes SIRA-9 mass spectrometer. These ratios are reported as $\delta^{13}\text{C}$ relative to the PDB standard where:

$$\delta^{13}\text{C} = \left\{ \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{stand}}} \right] - 1 \right\} \times 10^3.$$

Radiocarbon analyses were performed on selected samples where five grams of carbon were available for precision counting. Samples were collected and bagged immediately after bringing the trawls on board since the presence of artificial ^{14}C in the primary productivity studies presented a contamination hazard. Samples were processed in Fairbanks in a radiocarbon free lab where muscle tissue was excised from larger fish and whole specimens were used in the case of smaller animals. When necessary, samples were soaked in 10% HCl to remove carbonates. Samples were then dried under vacuum at 80°C. Dissolved inorganic carbon was obtained from the water column by stripping acidified seawater in 100 liter barrels onboard the ship and collecting the liberated carbon dioxide in 4N sodium hydroxide in a set-up similar to that used by Nydal et al. (1980). All radiocarbon analyses were performed by Beta Analytic Inc., a commercial laboratory specializing in radiocarbon determinations.

3.4 RESULTS AND DISCUSSION

3.4.1 Primary Productivity and Nutrient Dynamics

Nutrient supply processes and consequent primary production on the NAS are complex and subject to wide variations in magnitude. The advection of nutrient-rich Pacific Ocean/Bering Sea deep water onto the shelf in the vicinity of Unimak Pass is followed by intense primary production as the water moves northeastward. Since nitrate supply to the euphotic zone represents the basis for the "new" productivity of each summer season (Dugdale and Goering 1967), we have focused on its supply and consumption in the analysis of our data. In addition, the much more

detailed work of Sambrotto (1983) on the uptake of inorganic nitrogen at the PROBES station line near our study area presents a good basis for comparative interpretation. Many of the same phenomena observed by the PROBES investigators are evident in our work and allow extrapolation of productivity estimates for periods in which we have no data.

Nitrate concentrations are often as high as 10 $\mu\text{moles}/\text{m}^3$ in surface water near Unimak Island but biological consumption reduces the concentrations to levels limiting to phytoplankton growth by midsummer. Figures 3.1 to 3.12 illustrate the variations in nitrate concentrations and the increases in chlorophyll that become evident with the progression of the spring bloom. Northeast toward Bristol Bay the water column is much more depleted in nutrients during the spring and fall. Apparently the replenishment of the nitrate may not be as effective toward the northeast over the winter due to the greater cross-shelf distances. Concentrations at Transect 6 were lower than at Transects 1 and 4 in January and April. By early April the maximum amount of deep mixing has occurred and the concentrations of nitrate present in the surface waters are the highest in the annual cycle. The onset of the spring bloom was evident in the chlorophyll concentrations found at Transect 6 in April and assimilation reduces the surface nitrate available to less than 1.0 micromolar by midsummer over the study area. In contrast, a July station in Unimak Pass had surface nitrate concentrations greater than 8 micromolar, indicating effective mixing by through-pass turbulence. Also evident for much of the summer season was a zone of low salinity in the nearshore waters along the beach (see ESE, this report). This zone persists throughout much of the year and appears to establish a variable frontal system shoreward of the "inner" front, which is typically further seaward than our study area.

Although the nutrients are depleted to near zero in the euphotic zone during midsummer, the primary productivity rates remain high, with individual values as high as 2.6 $\text{gC}/\text{m}^2\text{-day}$ during July. The summer rates are sustained by periodic inputs of deeper water nutrients, and contribute significantly to the high annual primary production. Our estimates of annual production are based on our seasonal determinations of primary productivity (Fig. 3.13) and extrapolation from PROBES data (1982) during periods when we had no comparable temporal equivalents. We conclude that

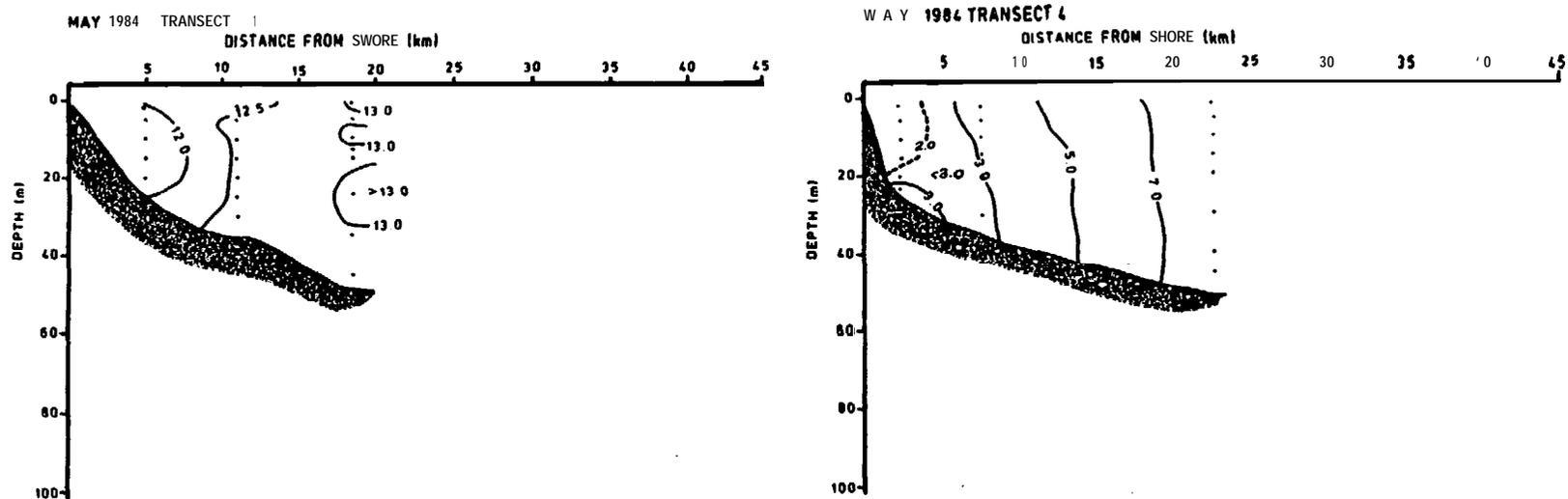


Fig. 3.1. May 1984 nitrate concentrations (μM). Stations are indicated with letters above the x-axis. Data from transects in the NE end of the study area are not contoured as not enough stations were sampled. At both Transects 6 and 7, nitrate concentrations were less than $1.0 \mu\text{M}$ at all depths.

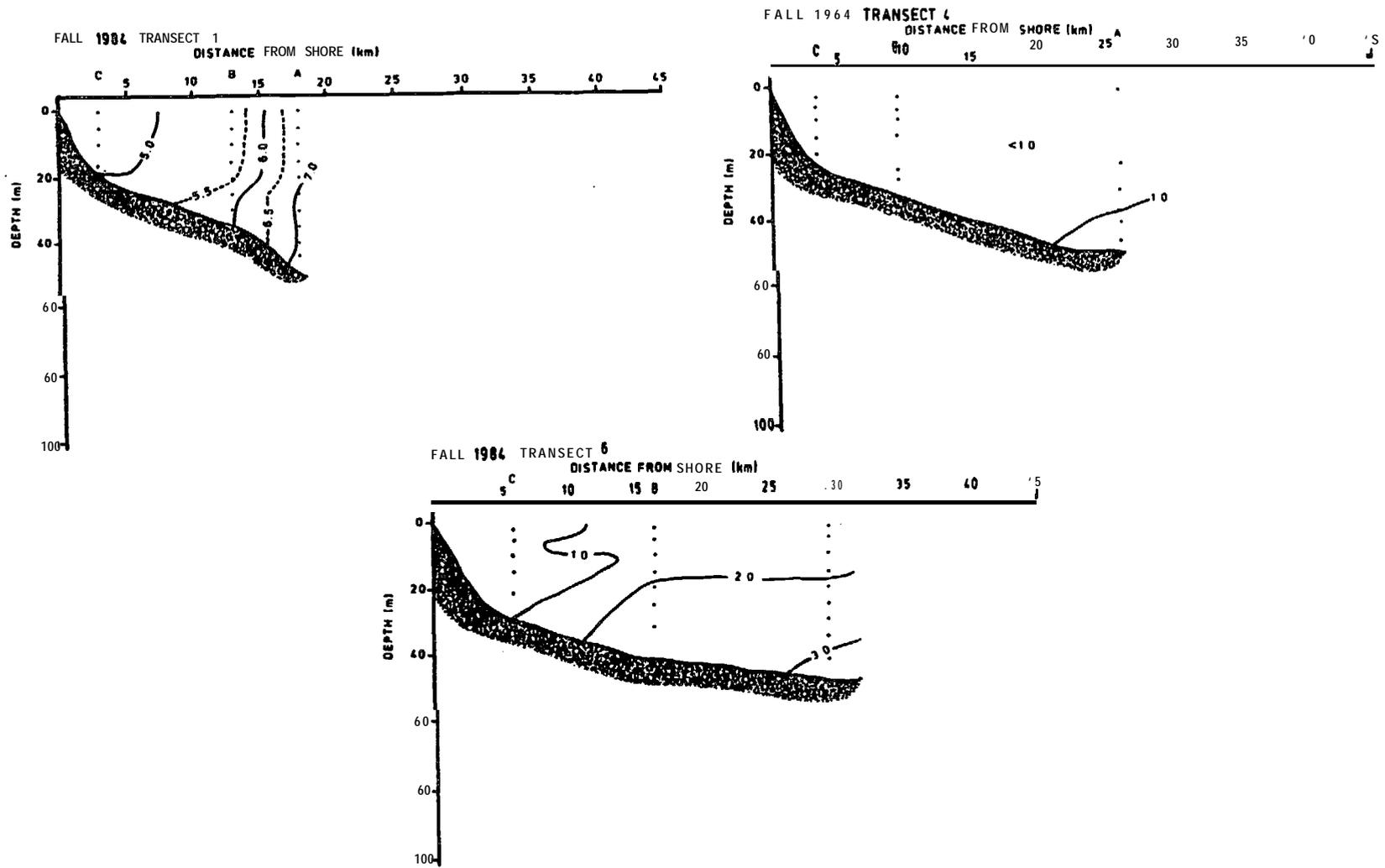


Fig. 3.2. Fall 1984 nitrate concentrations (uM). Stations are indicated with letters, above the x-axis.

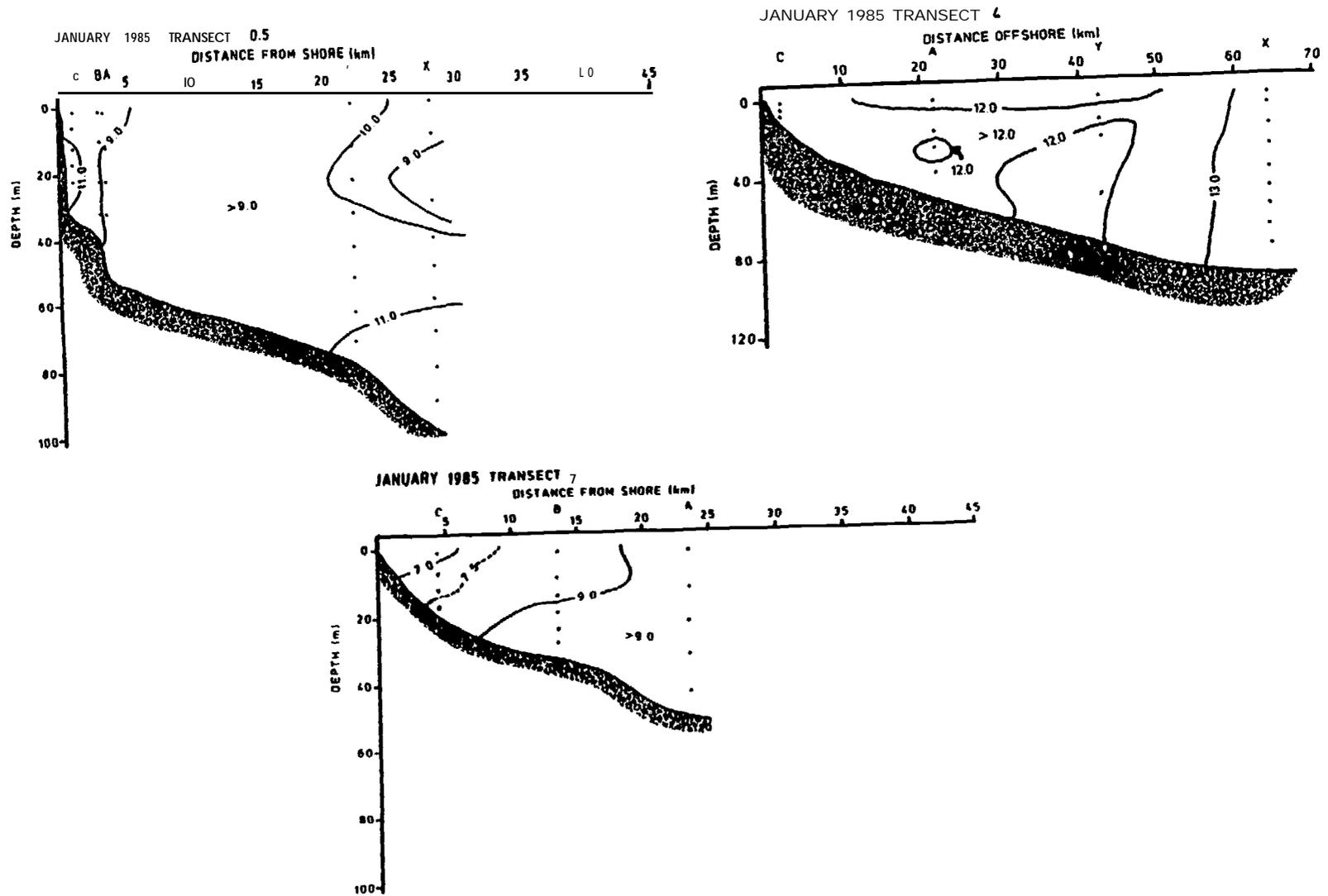


Fig. 3.3. January 1985 nitrate concentrations (μM). Stations are indicated with letters above the x-axis.

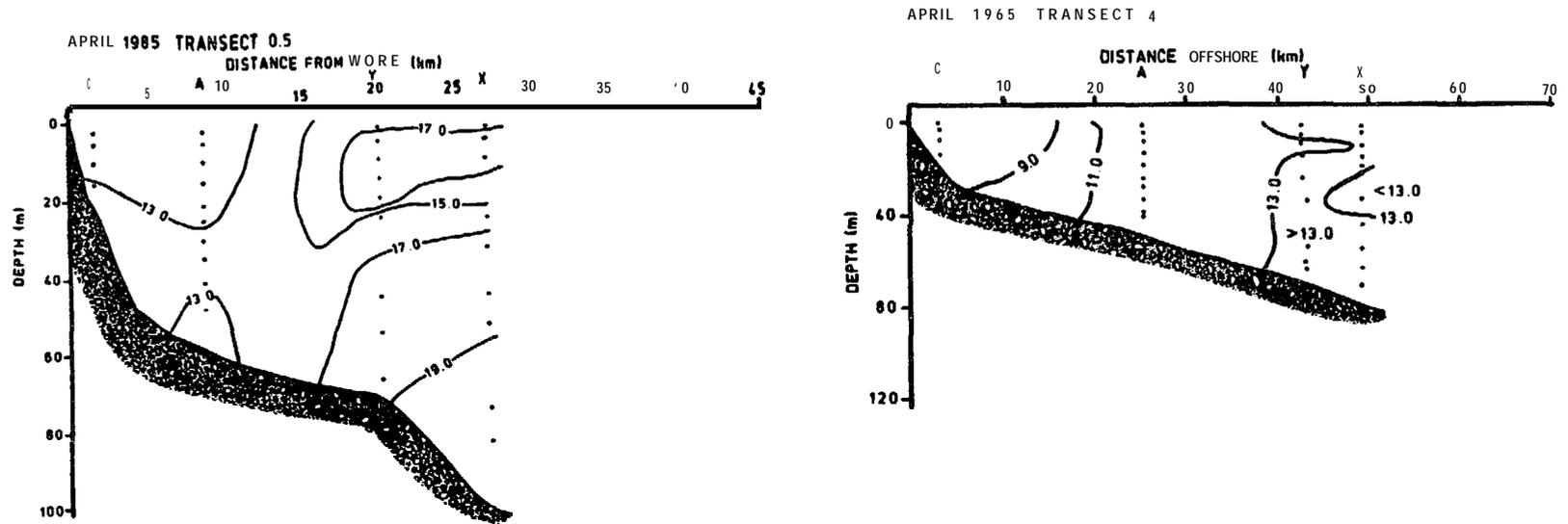


Fig. 3.4. April 1985 nitrate concentrations (μM). Stations are indicated with letters above the x-axis. Transects from the **NE end** of the study area are not included as not enough stations were sampled. At Transect 6, Station A, all nitrate concentrations were greater than 5 μM while at Station C all concentrations were less than 1 μM .

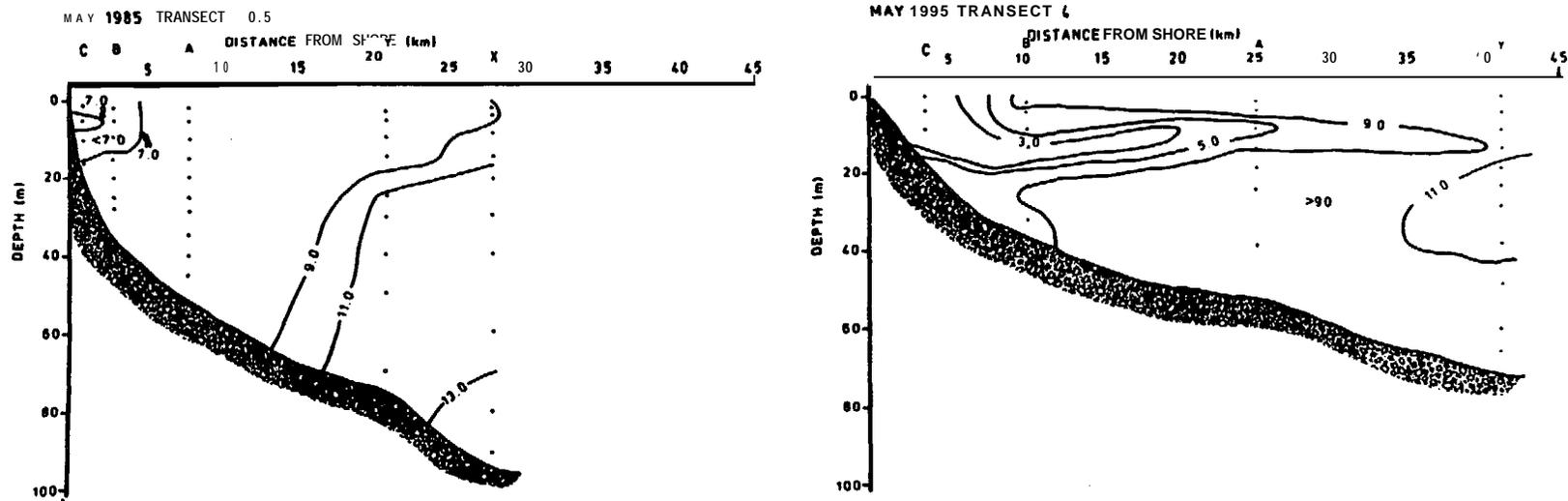


Fig. 3.5. May 1985 nitrate concentrations (μM). Stations are indicated with letters above the x-axis. Transects from the NE end of the study area are not contoured as not enough stations were sampled. At Transect 6, Station C, the concentrations were reduced to zero at all depths. At Station A the concentrations were greater than $3.7 \mu\text{M}$ at all depths.

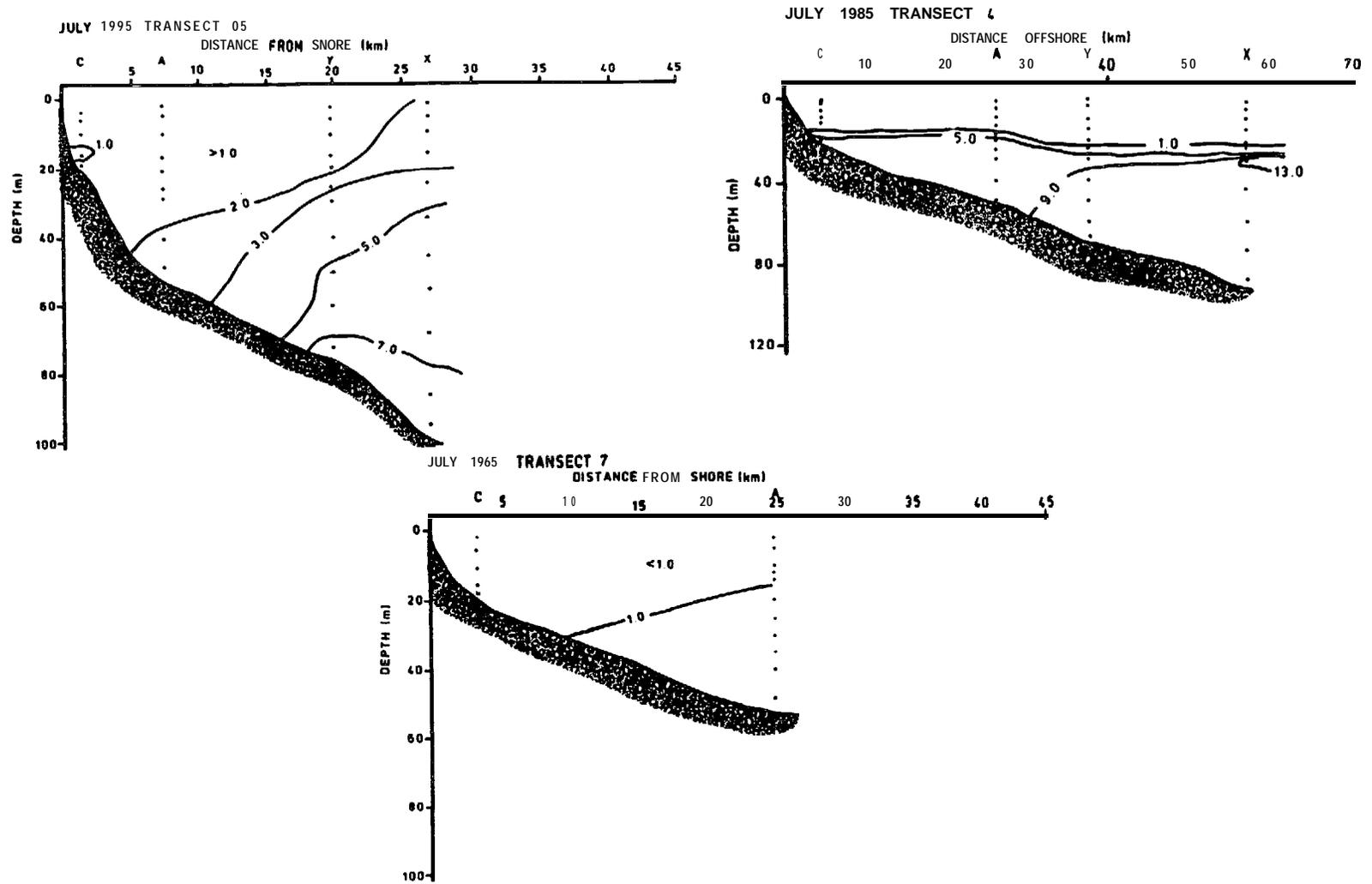


Fig. 3.6. July 1985 nitrate concentrations (μM). Stations are indicated with letters above the x-axis.

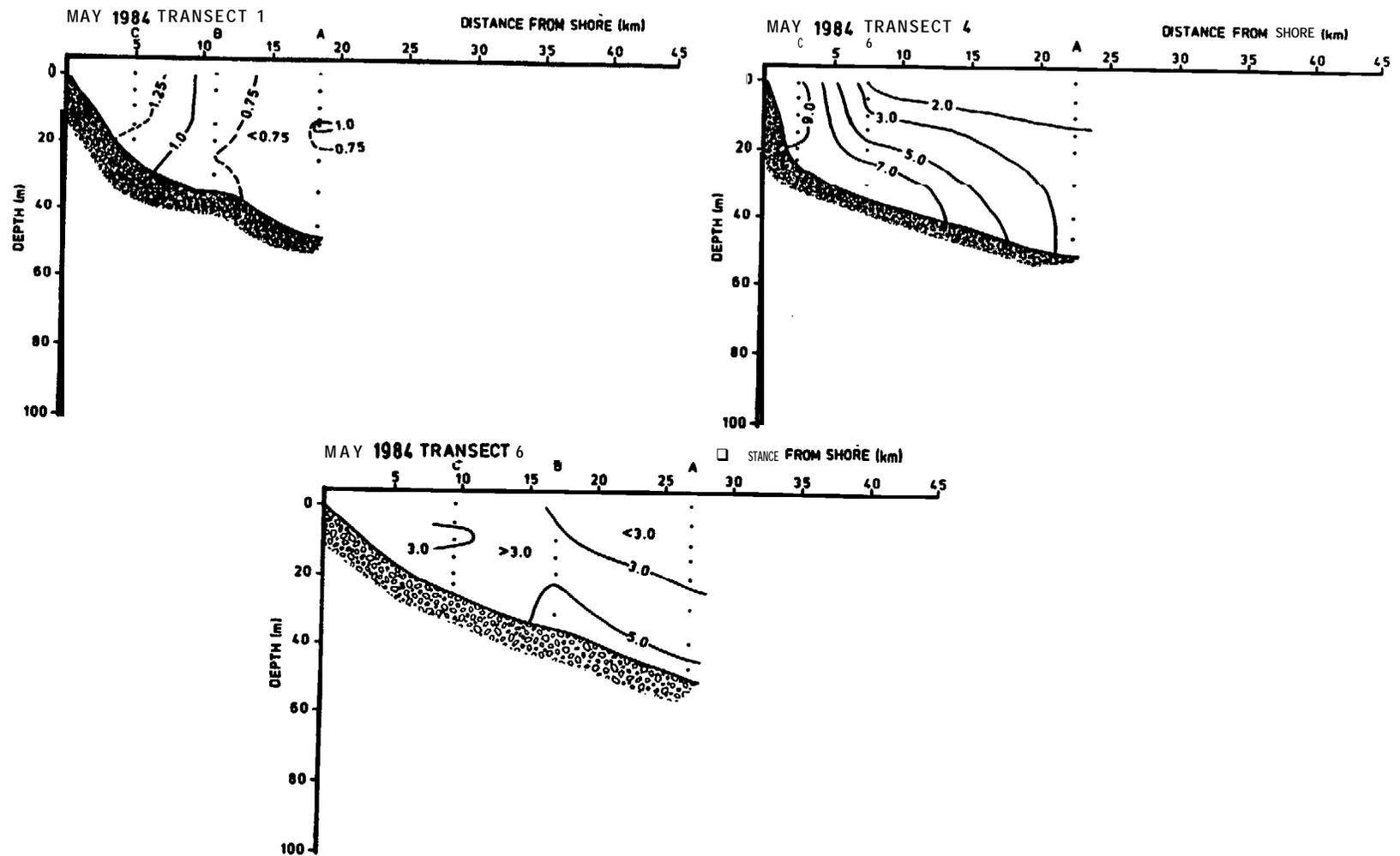


Fig. 3.7. May 1984 chlorophyll-a concentrations (mg/m^3). Stations are indicated with letters above the **x-axis**.

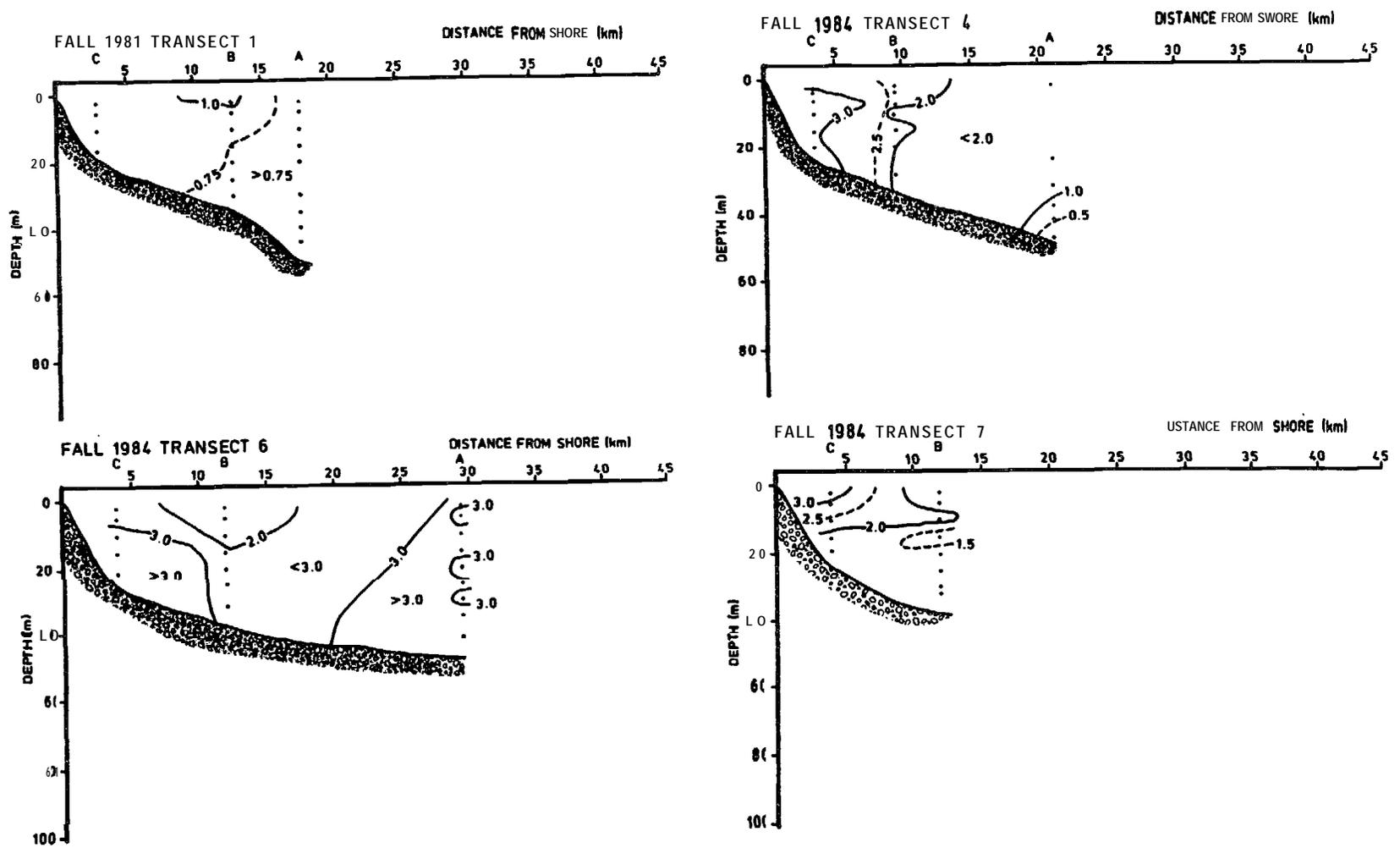


Fig. 3.8. Fall 1984 chlorophyll-g concentrations (mg/m^3). Stations are indicated with letters above the x-axis.

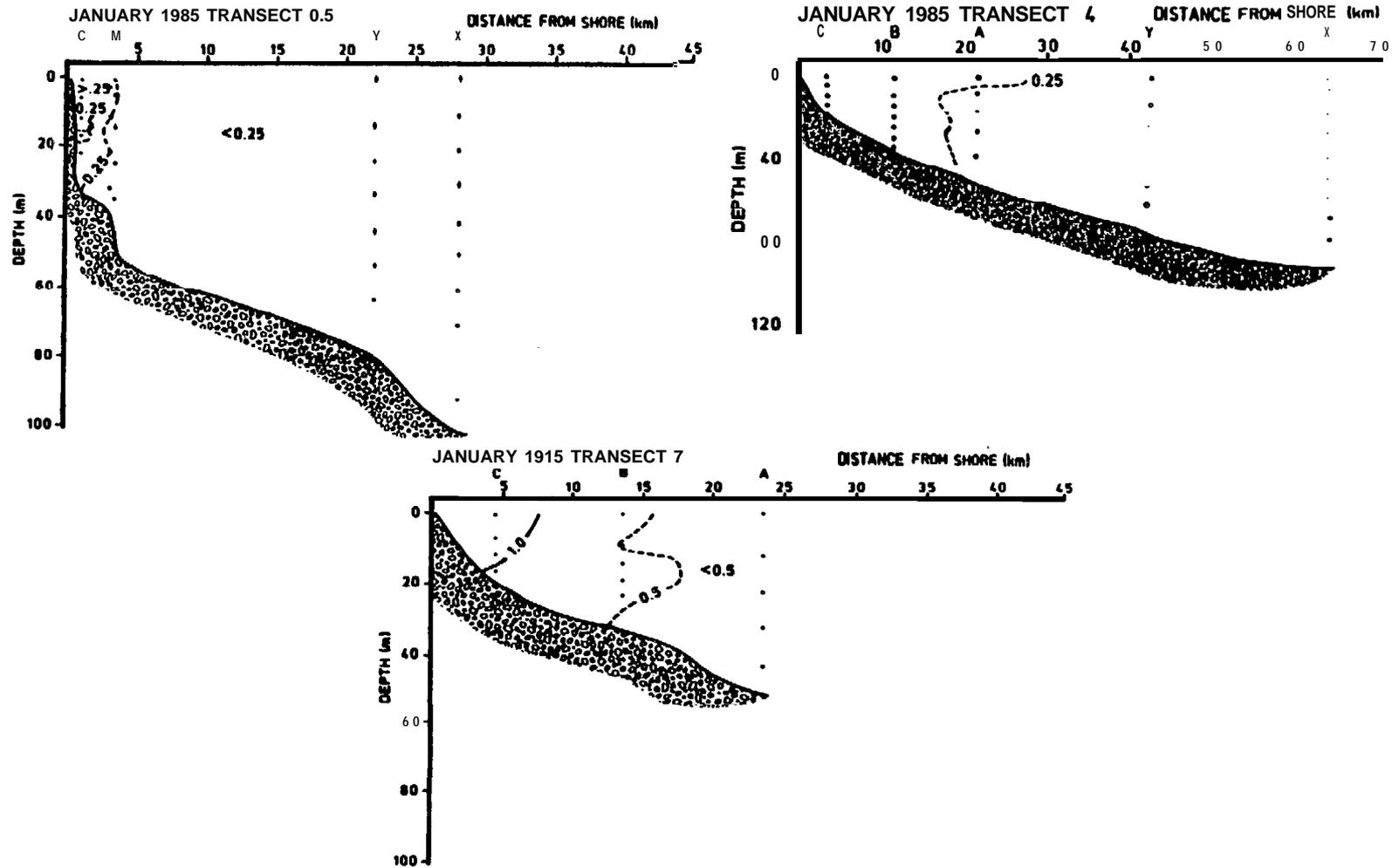


Fig. 3.9. January 1985 chlorophyll-a concentrations (mg/m^3). Stations are indicated with letters above the x-axis.

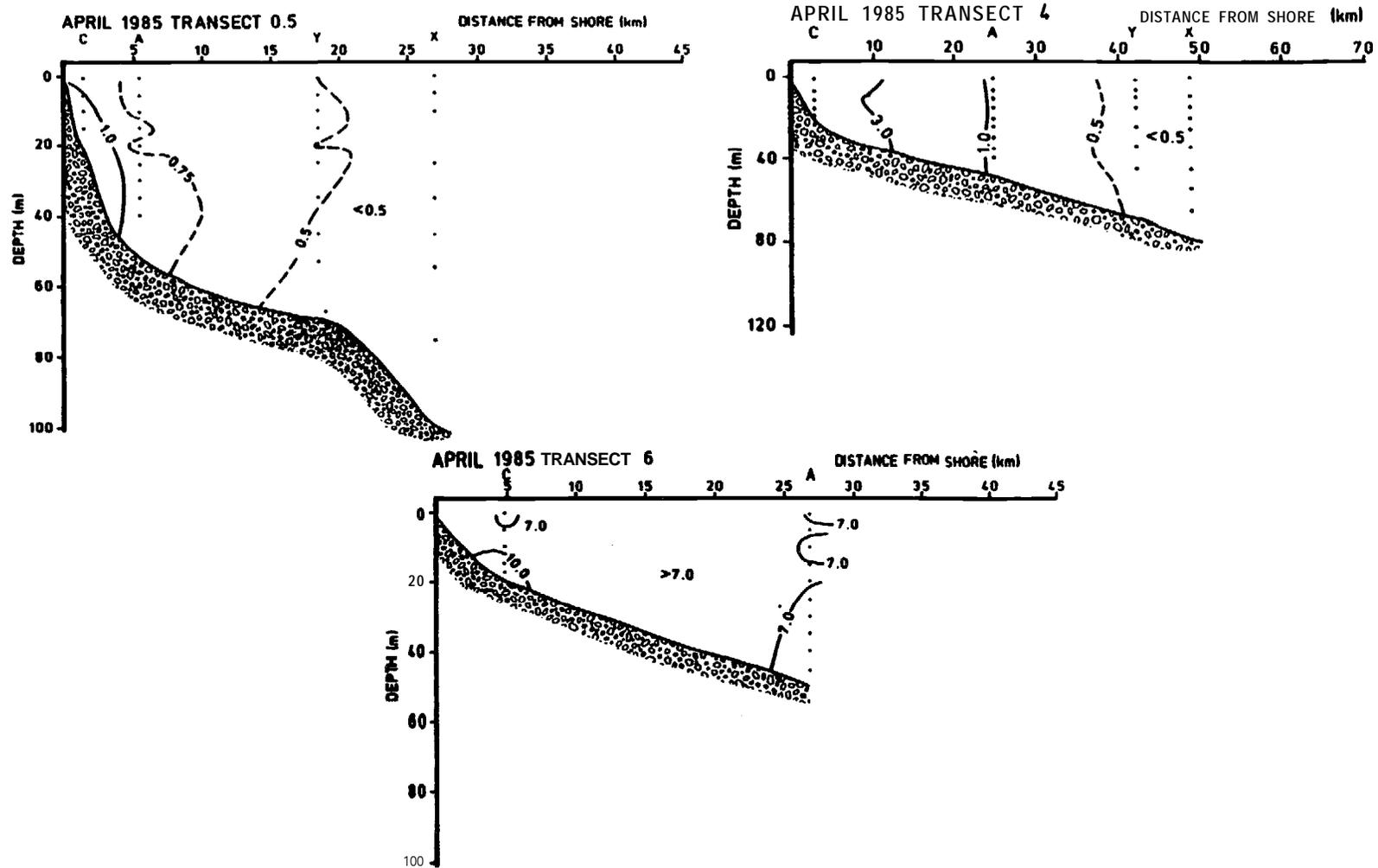


Fig. 3.10. April 1985 chlorophyll-a concentrations (mg/m^3). Stations are indicated with letters above the x-axis.

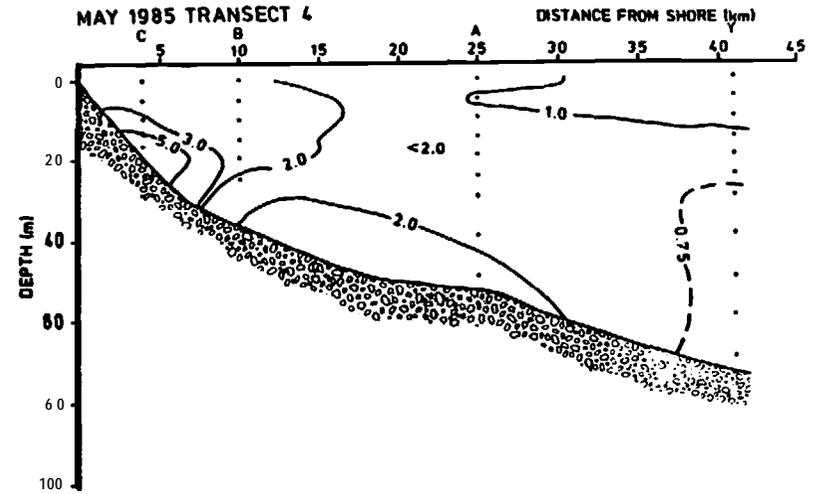
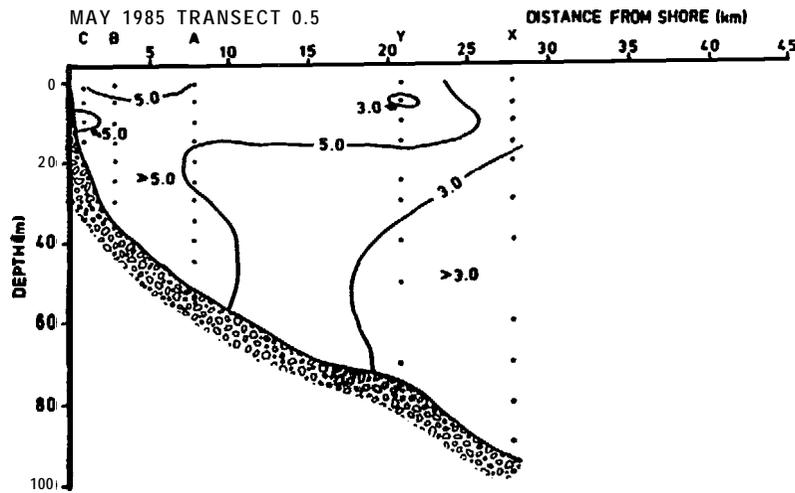


Fig. 3.11. May 1985 chlorophyll-a concentrations (mg/m^3). Stations are indicated with letters above the x-axis. Data from transects in the NE end of the study area were not contoured as not enough stations were sampled. At Transects 5 and 6 the chlorophyll-a concentrations were all higher than $4 \text{ mg}/\text{m}^3$ in the photic zone, and were as high as $12.7 \text{ mg}/\text{m}^3$.

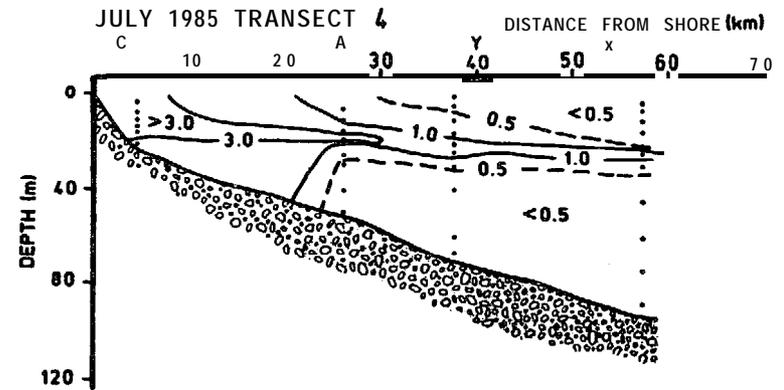
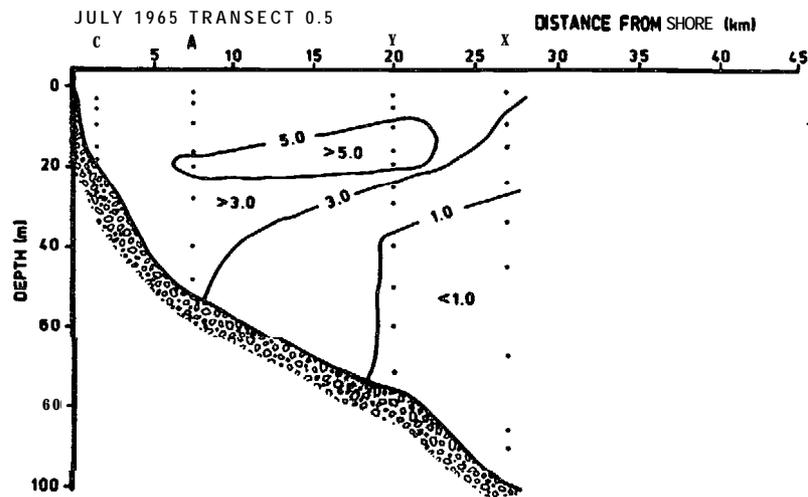


Fig. 3.12. July 1985 chlorophyll-a concentrations (mg/m^3). Stations are indicated with letters above the x-axis. Transects in the NE end of the study area are not contoured as not enough stations were sampled. At both Transects 6 and 7 the chlorophyll-a concentrations were less than $1 \text{ mg}/\text{m}^3$ at Station A and greater than $1 \text{ mg}/\text{m}^3$ at Station C.

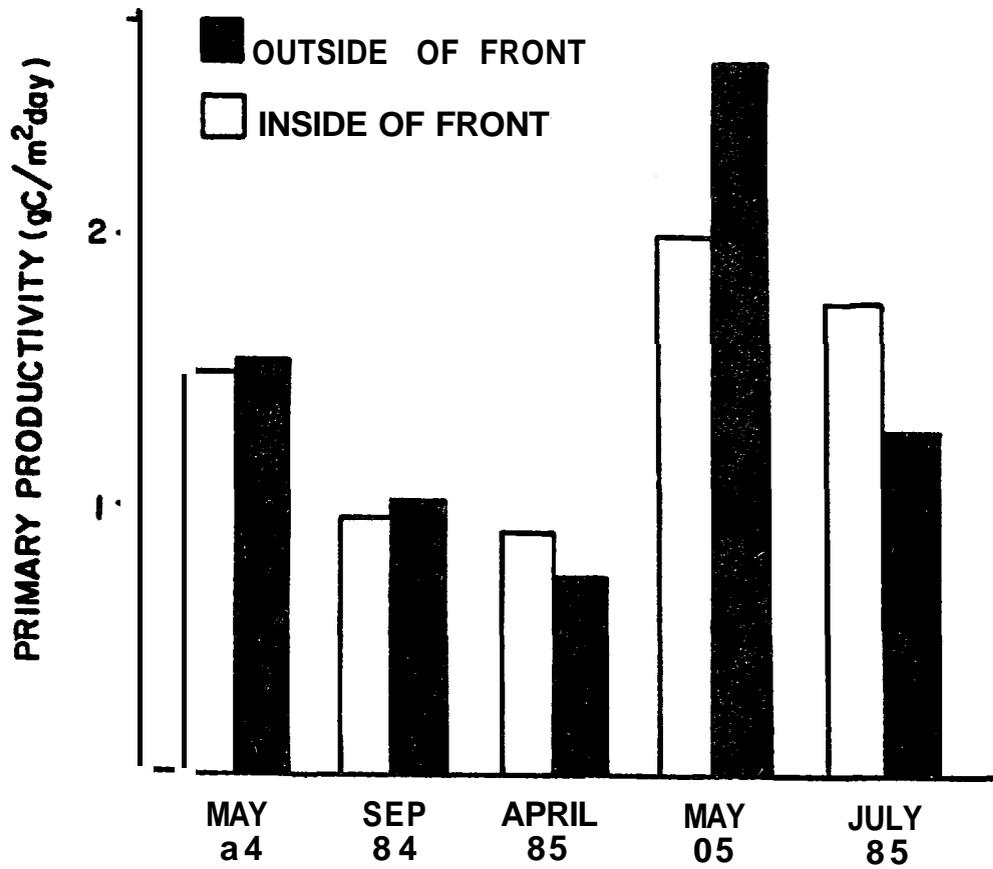


Figure 3.13. Primary productivity over the seasonal cycle during an *ice-free* year. Productivities are integrated for the water columns shoreward and seaward of the nearshore low salinity boundary.

carbon fixation amounts to 220-240 gC/m²-yr in the study area. This is higher than the estimate by Sambrotto (1983) of 188 gC/m²-yr based on nitrogen uptake for the PROBES area further offshore, but similar to the estimate communicated to him by Iverson based on the ¹⁴C method. Also similar to the PROBES data are our findings that the seasonal maximum productivity occurs in late spring. One measurement of over 6.7 gC/m²-day at Transect 4, Station C on 14 May 1984 is among the maximum rates observed anywhere in the world oceans and approaches the high fixation rates of the dense Zostera beds of Izembek Lagoon. Although the chlorophyll data and the nutrient concentrations often show marked changes and pronounced structure in moving offshore, these differences are not reflected in our measurements of primary productivity. When we compared productivity rates of waters shoreward of the lowered salinity boundaries with rates offshore we found no significant difference. Indeed, given the variability and uncertainties in the techniques for measuring primary production, no significant difference (see Fig. 3.13) is noted in moving either up the coast or perpendicular to it within the study area. The differences undoubtedly do exist but the temporal and spatial coverage does not allow a quantitative statement on the possible magnitude of the variation.

The water column productivity within the lagoon is sometimes a significant fraction of the eelgrass productivity, but only during high tides. During the remaining time eelgrass production greatly exceeds that by phytoplankton. But the inefficiencies in the trophic transfer of eelgrass carbon to higher levels result in generally lower secondary and tertiary productivities in the lagoon than in waters outside (excluding some birds and crabs which feed directly on eelgrass). This premise is substantiated by the stable carbon isotope data on the fauna collected from both within the lagoon and immediately outside.

The eelgrass constitutes a large fraction of the total inputs of carbon to the biota immediately outside of the lagoon, assuming that it is consumed within the area. This probably is quite unlikely, for eelgrass is observed floating several tens of miles from the nearest sources (Fig. 3.14) and anecdotal evidence indicates it may float for over a hundred miles. Nevertheless, we can use a scenario of near maximum consumption near the lagoon to illustrate the potential for eelgrass support of the

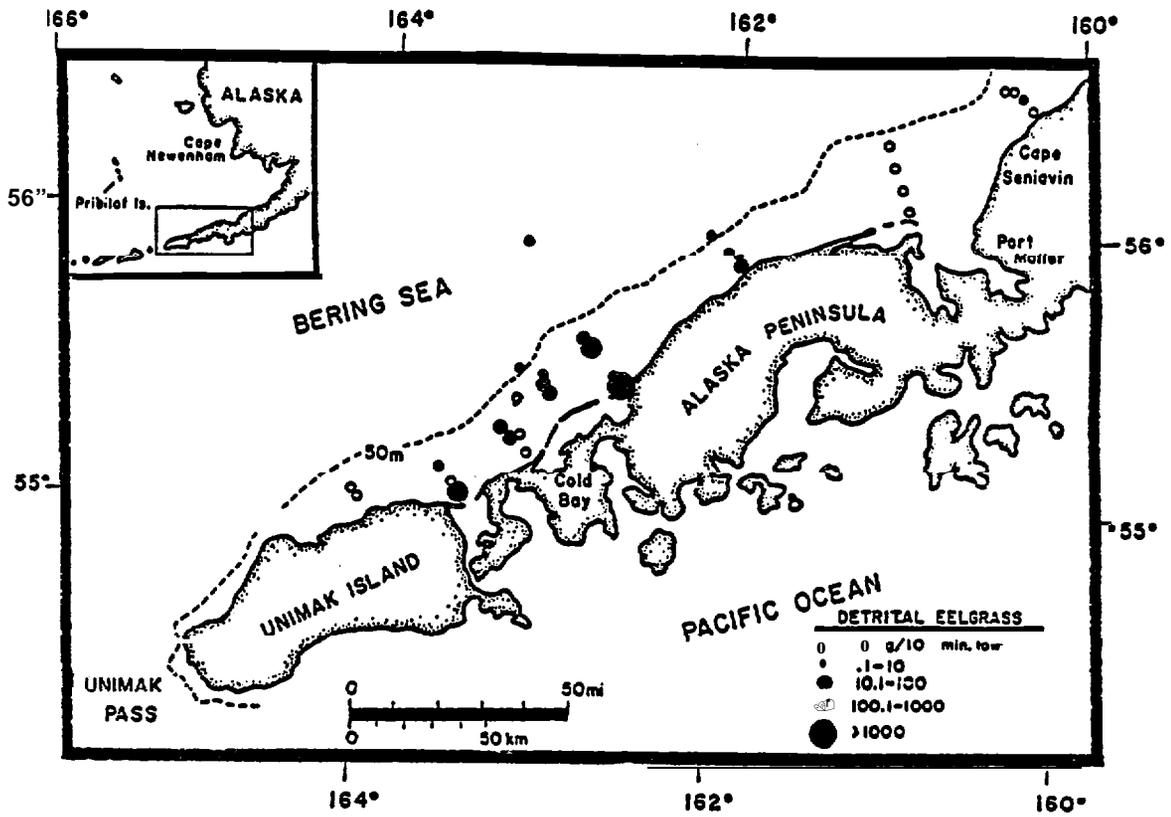


Fig. 3.14. Distribution of detrital eelgrass, 1-3 October 1984. Samples were collected by a **neuston net** which was towed for 10 min. and filtered approximately 770 m².

nearshore ecosystem. Using our primary productivity estimates and the estimates of Barsdate et al. (1974) on eelgrass transport, the following approximation can be made:

Eelgrass transport from lagoon	161 x 10 ⁶ kg/yr
Phytoplankton production	0.25 kg/m ² -yr
Assumed area of consumption = shoreward of 50-m contour, between Bechevin Bay and 50 km NE of Moffet Lagoon entrance	26 x 10 ⁸ m ²

Calculation of the relative inputs reveals that the eelgrass would contribute about 62 gC/m²-yr or an amount equivalent to 28% of the annual phytoplankton crop. Thus the possibility exists that eelgrass is a significant energy source either if concentrations accumulate in seafloor depressions or if a grazer is well adapted to use this resource.

3.4.2 Carbon Isotope Studies

3.4.2.1 Stable Carbon Isotope Results

Table 3.1 lists the $\delta^{13}\text{C}$ values of the organisms analyzed from the study area. It is important to note that the variation in the $\delta^{13}\text{C}$ values of these animals is not due solely to the presence or absence of eelgrass carbon, but also reflects biochemical fractionation resulting from the position of carbon in the trophic levels. Offshore studies have shown that a trend toward less negative $\delta^{13}\text{C}$ values occurs from primary producers to benthic consumers (Eadie 1972, Mills et al. 1983, McConnaughey and McRoy 1979a, Fry et al. 1983, Fry 1977, Fry and Parker 1979, Gearing et al. 1984, Thayer et al. 1983). From laboratory experiments, DeNiro and Epstein (1978) estimated that each trophic step enriches an organism 0.8 ± 1.1 $\delta^{13}\text{C}$ units and field studies have estimated trophic step enrichments ranging from 0.4 (Gearing et al. 1984) to 1.5 (McConnaughey and McRoy 1979a). Although trophic enrichments are not always consistent with increasing trophic levels, they offer insight into the trophic transfers of carbon necessary to support the organism. The $^{13}\text{C}/^{12}\text{C}$ ratio of eelgrass collected in the study area and in Izembek

Table 3.1. Del ^{13}C values for plants and animals collected in lagoon and nearshore waters of the NAS. Sample numbers differing only by a number in parentheses at the end represent separate organisms collected from the same trawl. Sample numbers differing by a letter at the end represent replicates of the same organism. Middle digits represent the month and year of cruise.

Sample Number	Sample Identification	Transect/Station	del ^{13}C (ppt)
PLANKTON			
AS-585-1A	Phytoplankton	0.5C	- 25.0
AS-785-9	Phytoplankton	0.5C	- 22.9
AS-785-13	Phytoplankton		- 22.6
AS-785-27	Phytoplankton	6A	- 23.8
AS-785-28	Zooplankton	B85-2725	- 22.5
M-785-24	Zooplankton	7A	- 23.7
AS-785-7	Zooplankton	0.5A?	- 21.8
M-785-25	Zooplankton	0.5 (70 m)	- 23.7
AS-785-40(1)	Jellyfish (<i>Chrysaora</i> (?) sp.)	B85-728	- 21.1
AS-785-40(2)	Jellyfish (<i>Chrysaora</i> (?) sp.)	B85-728	- 20.3
AS-785-41	Jellyfish (J-1)	B85-785, 4X	- 21.6
AS-584-15	<i>Thysanoessa raschii</i>	4B-6	- 19.5
EELGRASS			
AS-185-18	<i>Zostera marina</i>	4 c	- 10.6
AS-1084-1	<i>Zostera marina</i>	4.5C	- 10.0
AS-1084-2	<i>Zostera marina</i>	1.5C	- 9.9
AS-1084-3	<i>Zostera marina</i>	3C	- 11.5
AS-1084-4	<i>Zostera marina</i>	7B	- 11.5
AS-1084-5	<i>Zostera marina</i>	4.5A	- 9.4
AS-286-1(2)	<i>Zostera marina</i>	Grant Pt.	- 13.0
BENTHIC CRUSTACEANS			
AS-584-1	<i>Crangon dalli</i>	1D	- 18.2
AS-584-8	<i>Crangon dalli</i>	4D	- 18.8
AS-1084-10	<i>Crangon dalli</i>	2D	- 16.4
AS-185-18	<i>Crangon dalli</i>	6C	- 16.8
AS-185-17	<i>Crangon dalli</i>	4 x	- 19.8
AS-185-22	<i>Crangon dalli</i>	6A	- 16.9
AS-185-20	<i>Crangon dalli</i>	0.5C	- 17.3
AS-185-21	<i>Crangon dalli</i>	4 c	- 16.5
AS-785-10	<i>Crangon dalli</i>	0.5C	- 17.5
AS-785-14	<i>Crangon dalli</i>	043 (50 m)	- 17.7
AS-785-16	<i>Crangon dalli</i>	6A	- 17.2

Table 3.1 [Continued]

Sample Number	Sample Identification	Transect/Station	$\delta^{13}\text{C}$ (ppt)
BENTHIC CRUSTACEANS (Continued)			
AS-785-19	Crangon dalli	093 (30 m)	- 17.7
AS-785-18	Crangon dalli	7D (10 m)	- 17.5
AS-785-12	Crangon dalli	0.5 (70 m)	- 19.0
AS-785-17	Crangon dalli	086	- 17.9
POLYCHAETES			
AS-585-7a	Ophelia limacina	4Y	- 19.0
AS-585-5b	Ophelia limacina	0.5Y	- 17.4
AS-585-6	Ophelia limacina	2A	- 17.1
AS-585-7(2)	Ophelia limacina	4Y	- 19.1
AS-585-8	Ophelia limacina	4A	- 16.3
AS-585-2	Nephtys caeca	4 c	- 16.0
AS-585-10	Nephtys caeca	2A	- 16.0
AS-585-3	Nephtys caeca	2 c	- 15.8
AS-585-4	Nephtys caeca	5A	- 16.8
AS-585-1	Nephtys caeca	0.5A	- 17.0
BIVALVES			
AS-585-14	Astarte borealis	0.5A	- 18.9
AS-585-15	Astarte borealis	4Y	- 20.4
M-585-1 7	Astarte borealis	2 c	- 19.3
AS-585-18	Cyclocardia crebricostata	2A	- 19.8
AS-585-19	Cyclocardia crebricostata	6A	- 17.9
AS-585-20	Cyclocardia crebricostata	4A	- 18.2
AS-585-26	Cyclocardia crebricostata	0.5C	- 18.3
FISH			
AS-984-1	White-spotted Greenling	4E	- 17.3
AS-984-1(2)	White-spotted Greenling	4E	- 16.5
AS-785-37	White-spotted Greenling	4F	- 15.9
AS-584-2 1	White-spotted Greenling	7 c	- 16.2
AS-784-7	Masked Greenling	—	- 15.6
AS-984-10	Masked Greenling	5D	- 16.4
AS-185-1	Staghorn Sculpin	1C	- 14.5
AS-785-5	Staghorn Sculpin	0.5 Nearshore	- 15.9
AS-785-5b	Staghorn Sculpin	0.5 Nearshore	- 15.8
AS-785-33	Staghorn Sculpin	4F	- 14.6

Table 3.1 (Continued)

Sample Number	Sample Identification	Transect/Station	$\delta^{13}\text{C}$ (ppt)
FISH (Continued)			
AS-984-12	Sculpin	4E	- 14.6
AS-584-3	Rainbow Smelt	6E	- 17.1
AS-584-3(2)	Rainbow Smelt	6E	- 17.2
AS-784-12	Rainbow Smelt	—	- 16.6
AS-984-3	Rainbow Smelt	4E	- 17.6
AS-984-8	Pacific Cod	4B	- 18.3
AS-984-6	Pacific Cod	4c	- 18.1
AS-984-7	Pacific Cod	5C	- 17.4
AS-185-26	Pacific Cod	4D	- 16.0
AS-185-4	Pacific Cod	4D	- 16.7
AS-785-8	Pacific Herring	0.5C	- 21.2
AS-785-8(2)	Pacific Herring	0.5C	- 20.6
AS-985-3	Pacific Sand Lance	5C	- 20.0
M-584-2	Pacific Sand Lance	1D (3 m)	- 17.5
AS-984-1	Pacific Sand Lance	4c	- 20.5
AS-984-3	Pacific Sand Lance	5D	- 19.2
AS-984-7	Pacific Sand Lance	1C	- 19.7
AS-984-7(2)	Pacific Sand Lance	1C	- 18.6
AS-785-44	Pacific Sand Lance	4c	- 19.7
AS-584-14	Pacific Sandfish	—	- 17.2
AS-185-14	Pacific Sandfish	4D (10 m)	- 17.7
AS-785-2	Pacific Sandfish	0.5E	- 17.7
AS-785-2(2)	Pacific Sandfish	0.5E	- 17.7
AS-984-5	Prickly Snailfish	5B	- 17.9
AS-784-4	Chum Salmon		- 21.5
AS-784-8	Chum Salmon (juv.)		- 18.2
M-785-46	Chum Salmon (juv.)*		- 17.2
AS-785-43	Chum Salmon (juv.)*		- 20.9
AS-784-6	Sockeye		- 21.6
AS-785-21	Sockeye	4E	- 21.9
AS-785-22	Sockeye	2E	21.1
AS-785-23	Sockeye	5E	- 21.2
AS-785-42	Coho (juv.)	3.5 mi. off Port Moller*	- 19.1
AS-785-42b	Coho (juv.)	3.5 mi. off Port Moller*	- 19.3
AS-784-5	Dolly Varden		- 19.5
AS-784-9	Walleye Pollock (juv.)		- 16.9
AS-984-4	Walleye Pollock (juv.)	2A	- 18.4
AS-984-5	Walleye Pollock (juv.)	5B	- 17.3
AS-185-2	Walleye Pollock (juv.)	2C	- 18.3
AS-185-2(2)	Walleye Pollock (juv.)	2C	- 18.4

Table 3.1 (Continued)

Sample Number	Sample Identification	Transect/Station	del ¹³ C (ppt)
FISH (Continued)			
AS-185-6	Walleye Pollock (juv.)	5A	- 18.5
AS-185-6(2)	Walleye Pollock (juv.)	5A	- 18.0
AS-185-9	Walleye Pollock (juv.)	4B	- 18.5
AS-185-9(2)	Walleye Pollock (juv.)	4B	- 19.0
AS-785-35(1)	Walleye Pollock (juv.)	4A	- 19.9
AS-785-31	Walleye Pollock (juv.)	0.5C	- 18.4
AS-785-35(Z)	Walleye Pollock (juv.)	4A	- 20.0
AS-785-11	Halibut	0.5D	- 16.9
AS-185-3b	Rock Sole	4Y	- 18.1
AS-185-3	Rock Sole	4Y	- 17.8
AS-185-15	Rock Sole	4Y	- 16.7
AS-185-7	Rock Sole	4A	- 17.5
AS-185-10	Rock Sole	6A	- 15.6
AS-185-19	Rock Sole	4c	- 15.4
AS-584-4	Yellowfin Sole	6E	- 15.6
AS-185-13(2)	Yellowfin Sole	2C	- 16.4
AS-185-5	Yellowfin Sole	0.5C	- 17.4
AS-185-8	Yellowfin Sole	6C	- 15.6
AS-185-12	Yellowfin Sole	4c	- 15.8
AS-785-45	Yellowfin Sole	2E	- 18.0
AS-785-20	Yellowfin Sole	6D	- 15.9
AS-785-46	Yellowfin Sole	6A	- 15.5
AS-185-13	Yellowfin Sole	2C	- 16.8
AS-785-38	Yellowfin Sole	4D (10 m)	- 17.1
AS-784-2	Starry Flounder		- 14.4
AS-785-3	Starry Flounder	0.5E	- 16.5
AS-785-3(2)	Starry Flounder	0.5E	- 16.2
AS-785-3(3)	Starry Flounder	0.5E	- 16.0
AS-785-34	Starry Flounder	0.5E	- 17.9
AS-785-36	Starry Flounder	4F	- 14.3
AS-785-1	Alaska Plaice	0.5 (10 m)	- 15.7
BIRDS AND MAMMALS			
AS-984-1 1	Steller's Eider	Port Moller Area	- 17.9
AS-785-44	Steller's Eider	5 Nearshore	- 17.0
AS-785-45	Steller's Eider	Nelson Lagoon	- 18.1
AS-685-1	Harbor Seal†	Port Heiden	- 17.0
AS-685-2	Harbor Seal†	Port Heiden	- 16.8
AS-685-3	Harbor Seal†	Port Heiden	- 16.9

* Samples collected by Dames and Moore.

† Samples provided by Alaska Department of Fish and Game.

Lagoon ranged from -9.4 to -13.0. The phytoplankton in the Bering Sea water column had a $\delta^{13}\text{C}$ value of -23.6 ± 1.1 . This is similar to the value reported by McConnaughey and McRoy (1979a) of -24.4 ± 0.3 ppt for Bering Sea phytoplankton. With few exceptions, all other organisms have values ranging between phytoplankton and eelgrass and are less than 9 ppt enriched with ^{13}C compared with phytoplankton. Integrating our data into the compilation of Gearing et al. (1984) of average $\delta^{13}\text{C}$ values for organisms in phytoplankton-based ecosystems worldwide (Table 3.2), our ^{13}C enrichments match closely those of the other authors.

A food web based heavily on eelgrass, however, would be much more enriched in ^{13}C . McConnaughey (1978) found that the Izembek Lagoon benthic community depended on eelgrass detritus for some of its carbon. A value of -22.3 ppt was used for lagoon phytoplankton. His isotopically lightest lagoon copepod had a $\delta^{13}\text{C}$ value of -18.8, enriched by 3 $\delta^{13}\text{C}$ units relative to our most enriched zooplankton sample. His detritus feeders in the lagoon were also enriched relative to detritus feeders analyzed in our study. The bivalve Macoma inconspicua had a $\delta^{13}\text{C}$ value of -14.4 in Izembek Lagoon. We found an average value for filter feeding bivalves in the Bering Sea of -19.0, considerably more depleted in ^{13}C . Eelgrass is contributing a substantial amount of carbon to these organisms in the lagoon, but not in the nearshore Bering Sea, since the Bering Sea samples compare closely with values for phytoplankton-based food webs.

To quantify the amount of eelgrass carbon in even the lagoon bivalves is difficult although an approximation can be made. If the food ingested by bivalves in the lagoon undergoes the same metabolic fractionation as that in pelagic food webs, (a major assumption) then a pure eelgrass diet should yield a clam with a $\delta^{13}\text{C}$ of about -7 ppt (a 3 ppt enrichment). If the -19 ppt value represents no eelgrass, then the -14.4 bivalve contains 40% eelgrass carbon. McConnaughey (1978) performed similar calculations on several resident faunal in the lagoon and found eelgrass carbon fractions ranging from undetectable to over 50% in the crab Telmessus, but our data indicate that the eelgrass contribution to faunal nutrition is quickly diluted to insignificant amounts outside of the lagoon.

DeNiro and Epstein (1978) reported that in the laboratory different species of animals fed the same diet had similar $\delta^{13}\text{C}$ values. In field

Table 3.2. Average $\delta^{13}\text{C}$ values for organisms in plankton-based ecosystems worldwide (Ph = phytoplankton, Z = zooplankton, S = shrimp, B = bivalve, NP = non-carnivorous polychaete, CP = carnivorous polychaete, CG = carnivorous gastropod). From Gearing et al. (1984).

Location	Ph	Z	S	B	NP	CP	CG
Bering Sea ^a	-24.4	-22.1	-17.8	-18.6	—	-17.8	-16.4
Off Maine ^b	—	—	—	-17.7	—	—	—
Narragansett Bay ^c	-21.3	-20.8	-17.9	-18.5	-18.7	-16.5	-16.7
Off California ^d	—	—	—	-16.2	-17.2	-16.1	—
Gulf of Mexico ^e	-20.0 ^g	—	-16.0	-18.4	—	-17.7	—
Off Malaysia ^f	-21.0	—	-16.5	-18.1	—	-17.3	-15.3
AVERAGE	-21.7	-20.9	-17.1	-17.9	-18.3	-17.1	-16.1
This Study	-23.6	-23.0	-17.7	-19.0	-17.8	-16.4	—

^a McConnaughey and McRoy (1979)

^b Incze et al. (1982)

^c Gearing et al. (1984)

^d Spies and Desmarais (1983)

^e Fry and Parker (1979)

^f Rodelli et al. (1984)

^g Fry (1977)

studies, organisms with similar feeding behaviors are often treated as a group when estimating isotopic enrichments with trophic level (Gearing et al. 1984, Fry et al. 1984). Figure 3.15 shows histograms and average values of $\delta^{13}\text{C}$ for organisms with similar feeding patterns. The shifts toward higher ^{13}C concentrations with increasing trophic level are apparent and follow the trend expected for a phytoplankton-based food web. Walleye pollock were separated into two groups for plotting in Figure 3.15, those less than 50 mm and those 50 mm or larger. This separation reflects the shift from pelagic feeding to demersal feeding when the juveniles reach 35-50 mm (see Section 5 on Fishes). The two pollock less than 50 mm in length had $\delta^{13}\text{C}$ values of -19.9 and -20.01 ppt while those larger had an average of -18.2 ± 0.6 ppt ($n=10$). The change from pelagic feeding on isotopically lighter zooplankton to more enriched benthic invertebrates in their demersal existence is indicated in these $\delta^{13}\text{C}$ values.

Detritus-feeders are probably the major link between eelgrass and large demersal and benthic organisms (McConnaughey and McRoy 1979b). Eelgrass should be evident in organisms such as crangonid shrimp and deposit feeding polychaetes such as Ophelia limacina if it was a major energy source to the food web. The average for these two detritivores is -17.7 ± 1.0 ppt, close to the value given by McConnaughey (1978) for Bering Sea Crangon dalli of -16.9 ppt. The lagoon samples of Crangon which he collected had an average $\delta^{13}\text{C}$ value of -14.1 ppt, and he estimated that eelgrass contributed 17% of the carbon to the shrimp. Therefore, even for crangonid shrimp in the lagoon, eelgrass is not contributing a large fraction of carbon to the organisms. From our isotopic evidence, we cannot detect eelgrass in crangonid shrimp outside of the lagoon.

3.4.2.2 Radiocarbon Studies

The ^{14}C contents of the organisms sampled provide indirect evidence that the nutrients needed for primary production are being supplied by upwelling of deep Pacific Ocean water. After a deep mixing event occurs, phytoplankton growth fixes the marine carbon dioxide before complete equilibration can occur with the radiocarbon background in the atmosphere. The ^{14}C activity of the atmospheric pool is currently about 122% of the

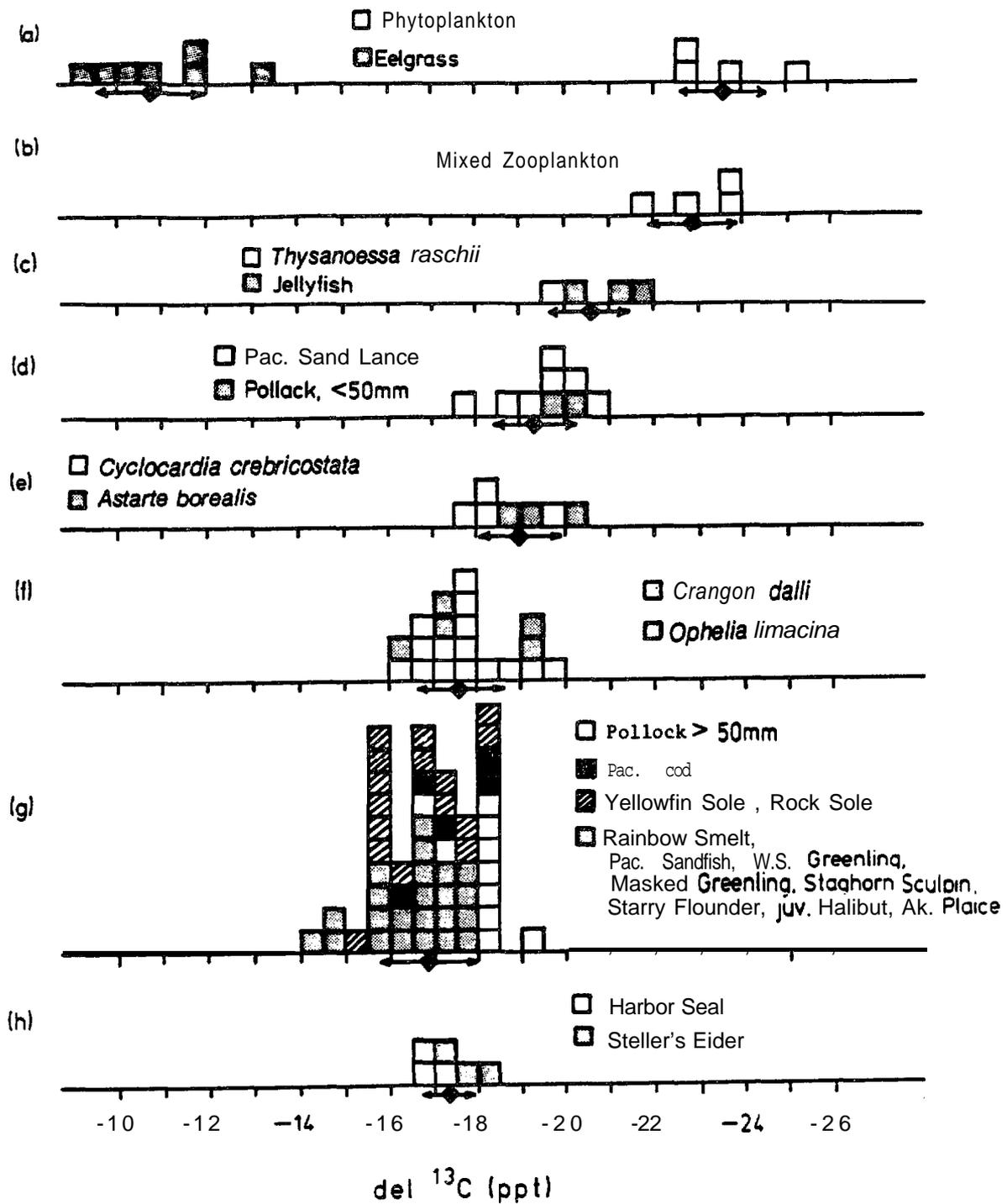


Figure 3.15. Histogram showing $\delta^{13}\text{C}$ values of the plants and animals listed in Table 1. -Organisms collected within the lagoon are not included except for the Steller's Eiders. Organisms with similar feeding habits were grouped together: primary producers (a), zooplankton, mostly copepods (b), omnivorous zooplankton (c), pelagic forage fish (d), filter feeding bivalves (e), detritivores (f), demersal/benthic fishes (g), and marine mammals and birds (h). The black diamonds and bars show the average and standard deviation of each group.

1950 standard activity (100%). If the organisms were feeding on phytoplankton growing in a stable or well ventilated water column, the expected radiocarbon content would yield activities of about 112-118% modern, values typical of surface water bicarbonate in more temperate latitudes (Ostlund and Stuiver 1980). The ^{14}C activities of the animals listed in Table 3.3 are all depressed by at least 2% from the lower limit of this range showing that the nearshore waters of the NAS are not as equilibrated with atmospheric carbon dioxide and must have been recently upwelled from the deep Pacific. Even within Izembek Lagoon eelgrass radioactivities are indicative of plants growing in water not fully equilibrated with atmosphere. The chronologically old Pacific deep water is influencing the lagoon before complete equilibration with atmosphere can occur. The radioactive content of the dissolved inorganic carbon (DIC) in surface waters agree well with radiocarbon activities from the GEOSECS Stations 218 and 219 (Ostlund and Stuiver 1980) which show the shallowing of the radiocarbon gradients in the North Pacific (Fig. 3.16). This shallowing of the gradient is caused by the surfacing of older, deep Pacific water in areas of upwelling and deep winter mixing in high latitudes. There is insufficient difference in radiocarbon activity between Izembek eelgrass and nearshore fauna to use radiocarbon to quantify the eelgrass contribution to nearshore food webs.

3.5 CONCLUSIONS

With the determination of temporal and spatial nutrient concentrations and primary productivity rates in NAS waters, we have acquired insight into the principal environmental and biological processes controlling the productivity of this region. Specifically, we note:

Primary productivity along the NAS coastal zone is higher than the values reported by PROBES investigators for areas further northeast and offshore. This may be due to the advection of nitrate-N rich deep-mixed water into the study area. Productivities are very high and by July the nutrient supply has been depleted to limiting concentrations in the euphotic zone. Our annual production estimate is 220-240 $\text{gC}/\text{m}^2\text{-yr}$ for the study area.

Table 3.3. Radiocarbon activities of fishes, eelgrass, and dissolved inorganic carbon collected from NAS waters. Activities are normalized and reported to 1950 atmospheric ^{14}C 100%.

Sample	Identification	^{14}C Activity (percent modern)
BIOCARBONATE		
Surface Water,	4A, 19 Sep 84	99.0 \pm 0.9
Surface Water,	4Y, 23 May 85	107.3 \pm 0.9
Surface Water,	4E, 21 May 85	109.8 \pm 0.9
Surface Water,	Unimak Pass, 1 Aug 85	104.1 \pm 0.9
EELGRASS		
Glazenap Pass,	29 Sep 84	111.0 \pm 0.9
Grant Point,	Feb 86	107.9 \pm 0.9
FAUNA		
Rainbow Smelt,	399-6C1, 29 Sep 84	107.7 \pm 1.1
Pacific Sandfish,	340-1C, 24 Sep 84	105.4 \pm 1.2
Pacific Cod,	399-6C1, 29 Sep 84	104.0 \pm 0.7
Pacific Sand Lance,	350-5C, 25 Sep 84	108.5 \pm 0.9
Pacific Sand Lance,	B85-340, 1C, 24 Sep 84	105.7 \pm 0.8
Pacific Sand Lance,	4C, Jul 85	109.1 \pm 0.6
Walleye Pollock,	399-6C1, 29 Sep 84	109.6 \pm 0.8
Yellowfin Sole,	317-2A, 21 Sep 84	104.6 \pm 0.7
Yellowfin Sole,	2C, 1 Feb 85	108.0 \pm 0.7
Yellowfin Sole,	B85-742, 2E, 22 Jul 85	108.4 \pm 0.7
Yellowfin Sole,	6A, 27 Jul 85	106.4 \pm 0.8
Flathead Sole,	317-2A, 29 Sep 84	109.5 \pm 0.8
Rock Sole,	0.5A, 21 Jul 85	106.3 \pm 0.8
Rock Sole,	B85-522, 4Y, 26 Jan 85	103.4 \pm 0.7

C = 14, PERCENT MODERN

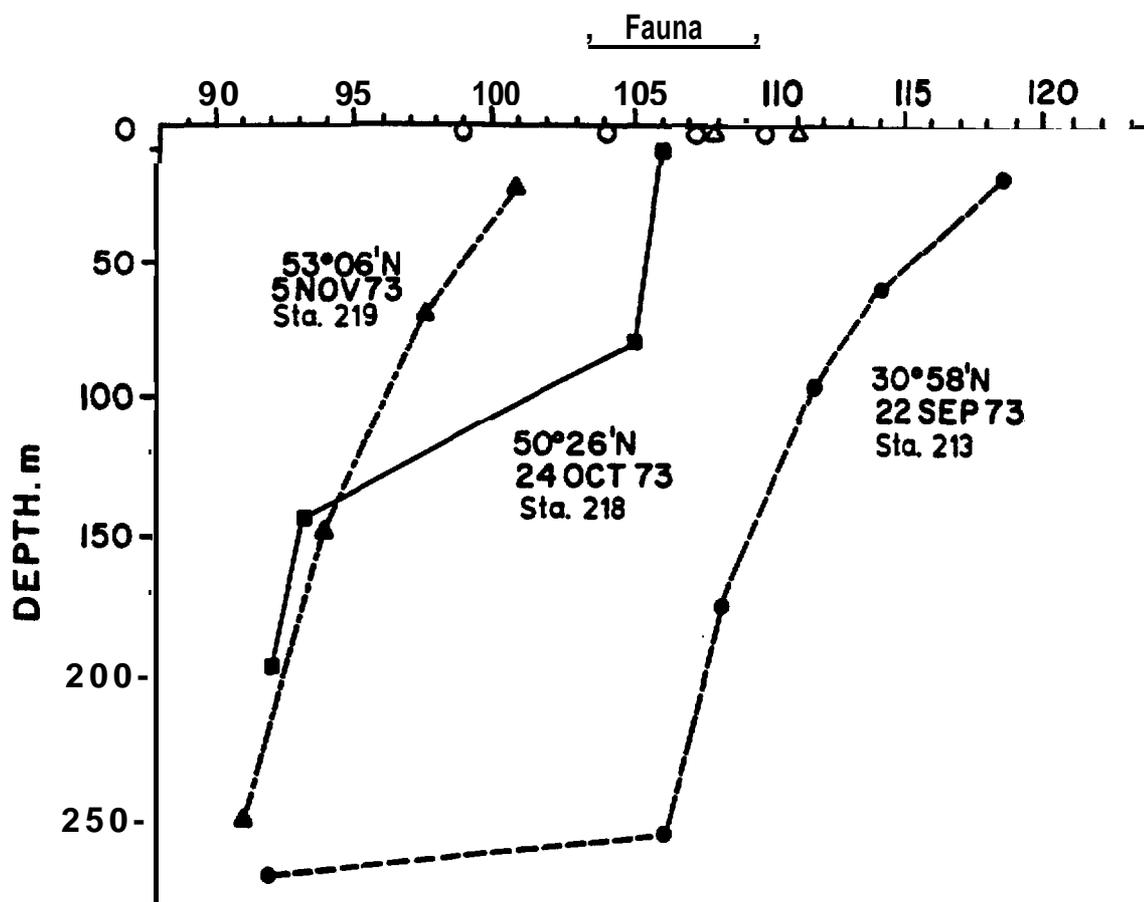


Fig. 3.16. Radiocarbon activities from the GEOSECS stations 213, 218, and 219 (Ostlund and Stuiver 1980). Fauna (shown on x-axis), DIC (o), and eelgrass (A) activities are also included from Table 3.

Nutrient supply to the coastal waters occurs in the vicinity of **Unimak** Island and represents deep Pacific Ocean/Bering Sea water **advected** onto the shelf. Nitrate concentrations in the southwestern portion of the study area reach 20 micromolar in surface waters and account for the high primary production. Replenishment of the nitrate in the **euphotic** zone is accomplished by storm and tidal mixing during the summer months and high rates of primary productivity are possible at any time in the summer depending upon the recent history of mixing events and water column stability.

In spite of the large inputs of **eelgrass** carbon to the coastal zone, equivalent to about one-quarter to one-third of the local in situ production, the isotopic compositions of the sessile benthos and the forage fishes resident in the area show that very little of the **eelgrass** carbon enters the food web. This is attributed to losses of carbon in inefficient transfers to higher **trophic** levels and, perhaps, dispersal of the **eelgrass** over a much larger region than the study area.

Radiocarbon abundances in the animals of the coastal zone are markedly depressed from the concentrations expected for a food web in a water column equilibrated with atmospheric carbon dioxide. North Pacific/Bering Sea deep water is known to be the chronologically oldest water in the world oceans (**Ostlund** and **Stuiver 1980**). The radiocarbon depression in the animals indicates that the uptake of inorganic carbon by phytoplankton occurs before water-column carbon dioxide can equilibrate with the atmosphere. This presents prima facie evidence that deep mixing of Bering Sea water supplies nutrients to the nearshore community.

3.6 RECOMMENDED FURTHER RESEARCH

There are many questions left unanswered as to the interactions between the environmental variables and the organisms in the nearshore zone. We have identified the following tasks as useful toward clearing up the roles of the terrestrial and **lagoonal** inputs versus oceanic inputs to the nearshore **zone**:

1. Samples of forage fishes and commercially-important fishes are needed from the lagoon environment for both radiocarbon

and stable carbon isotope analyses. Trawls for benthic species would be very desirable from inside the lagoon. Neither the literature data nor the sampling efforts so far have provided information on many of these species.

2. Early stabilization of the water column associated with sea ice melt may extend phytoplankton production to include the early spring. Data collected during the spring of a heavy ice year would give information on the effects of ice on primary productivity.
3. More information is needed on the composition of the phytoplankton community--diatom versus blue-green algae versus dinoflagellate production. Phytoplankton floristics may regulate the carbon available to primary consumers and control the species succession and recruitment.
4. Synoptic collection of nutrient and chlorophyll samples would help to determine whether the large concentration gradients we see during much of the year between the SW and NE boundaries of the study area are due to temporal effects or to physical factors such as the advection of nutrient rich water from the vicinity of Unimak Pass.

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