

MASTER

SHELF-SEA ECOSYSTEMS¹

by

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In "Analysis of Marine Ecosystems",
ed. A.R. Longhurst, Academic Press (in press)

¹This analysis was mainly sponsored by Contract No. DE-AC02-76-CH00016 from the Department of Energy as part of the Atlantic Coastal Ecosystem (ACE) Program, with additional support by grants from the International Decade of Ocean Exploration, NSF, as part of the Coastal Upwelling Ecosystem Analysis (CUEA) Program, and by grants from the Division of Polar Programs, NSF, as part of the Processes and Resources of the Bering Sea (PROBES) Program. I wish to thank my colleagues in the ACE, CUEA, and PROBES Program for many discussions of the ideas and data presented in this chapter.

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ABSTRACT

An analysis of the food chain dynamics of the Oregon, Alaskan, and New York shelves is made with respect to differences in physical forcing of these ecosystems. The world's shelves are 10% of the area of the ocean, yield 99% of the world's fish catch, and may be a major sink in the global CO₂ budget.

INTRODUCTION

"Several years ago I climbed overboard into the clear waters of Haiti, and after a copper helmet had been lowered over my head and shoulders I slid slowly down a rope two, four, eight, ten fathoms and finally at sixty-three feet my canvas shoes settled into the soft ooze near a coral reef. I made my way to a steep precipice, balanced on the brink, and looked down, down into the green depths where illumination like moonlight showed waving sea-fans and milling fish far beyond the length of my hose. As I peered down I realized I was looking toward a world of life almost as unknown as that of Mars or Venus ... Modern oceanographic knowledge ... is comparable to the information of a student of African animals, who has trapped a small collection of rats and mice but is still wholly unaware of antelope, elephants, lions, and rhinos. The hundreds of nets I have drawn through the depths of the sea, from one-half to two miles down, have yielded a harvest which has served only to increase my desire actually to descend into this no-man's zone."

- Beebe, 1934 -

Fifty years ago, Beebe's direct observations of tropical continental shelves and Bigelow's more traditional shipboard analyses of temperate shelves marked the beginning of modern studies of this ecosystem (Allee, 1934). Today these regions, which comprise 10% of the area of the world's ocean, yield 99% of the global fish catch. The physical extent of the present shelf ecosystem is about 75 km wide reaching 130 m depth at the shelf-break (Shepard, 1963), and has a most recent origin of

about 15,000 years (Milliman and Emery, 1968; Edwards and Merrill, 1977). Glacial retreat and rising sea level are the major factors in the submergence of modern shelves (Shepard, 1963). During each of the four recent ice ages of the Pleistocene period (1.8×10^6 yr B.P.) the continental slope each time may have adjoined the coastline, without much of an intervening shelf which was then dry land (Hay and Southam, 1977).

The probable absence of most continental shelves during the 1×10^5 yr of the last Wisconsin (Würm) glaciation thus raises doubts about the evolutionary uniqueness or greater intrinsic ecological efficiency of the species of the food web of this rich coastal ecosystem. Because marine speciation takes a minimum of about 5×10^5 yr (Day, 1963), some epipelagic and benthic species of the Pleistocene coastal zone, i.e. the upper 200 m of slope waters, probably just radiated onshore during the last Holocene reappearance of the shelves. The high yield of present shelves is instead attributed to their shallow depths, which both concentrate fish for economic harvesting and allow greater nutrient recycling to the overlying water column. Seasonal wind mixing is able to reach the decomposing organic matter on the shelf bottom, with consequent rapid return of nutrients to the euphotic zone. In contrast, the widely dispersed fish of the open ocean, except for tuna, have yet to be commercially exploited and the deep permanent thermocline

inhibits rapid return of nutrients to the surface waters, which only occurs during winter overturn. As a result, both the nutrient content and daily primary production of shelf waters are usually an order of magnitude higher than surface waters of the open ocean (Table 1), e.g. the Sargasso Sea (Menzel and Ryther, 1960). In some oceanic areas such as the North Pacific (Anderson and Munson, 1972) and the equatorial divergence (Walsh, 1976) where nutrients are high, the primary production is always low because of constant grazing stress and no spring bloom occurs.

The yield of individual continental shelves (Table 1) varies as a function of their width, the duration of wind induced nutrient input and available light (Walsh, 1974), the seasonal temperature cycle which may affect the ability of planktonic herbivores to crop the primary production, the subsequent input of food to the benthos, and the utilization of these pelagic and demersal resources by the fish, through a varied number of steps in each shelf food web. Before overfishing, for example, the Peru upwelling ecosystem yielded about 20% of the world's annual fish catch as a single species yield - anchoveta (Walsh et al., 1979). At Peruvian latitudes, light and temperature are conducive to high rates of primary production throughout the year. Upwelling adds nutrients all the year to the euphotic zone off Peru to maintain a level of carbon fixation, sufficient to support

Table 1

A comparison of habitat variability and food chain productivity within shelf ecosystems at $\sim 20^\circ$, 40° , and 60° latitude

	<u>Peru (10-15°S)</u>	<u>Oregon (42-47°N)</u>	<u>New York (37-42°N)</u>	<u>Bering Sea (55-60°N)</u>
Temperature Δt of the inshore mixed layer	$5^\circ \text{C year}^{-1}$	$5^\circ \text{C year}^{-1}$	$20^\circ \text{C year}^{-1}$	$10^\circ \text{C year}^{-1}$
Cumulative nitrate within the euphotic zone (30 m)	$7.0 \text{ g-atom m}^{-3} \text{ year}^{-1}$ (1)	$2.5 \text{ g-atom m}^{-3} \text{ year}^{-1}$	$1.0 \text{ g-atom m}^{-3} \text{ year}^{-1}$	$2.5 \text{ g-atom m}^{-3} \text{ year}^{-1}$ (2)
Primary production of continental shelf	$500-1000 \text{ gCm}^{-2} \text{ year}^{-1}$	$200-250 \text{ gCm}^{-2} \text{ year}^{-1}$	$200-300 \text{ gCm}^{-2} \text{ year}^{-1}$	$200-250 \text{ gCm}^{-2} \text{ year}^{-1}$
Organic carbon content of shelf sediments	> 2.0%	< 0.5%	< 0.5% to 1%	< 0.5% to 1.5%
Fish yield of the shelf ecosystem	$\sim 100 \text{ tons km}^{-2} \text{ year}^{-1}$	$\sim 10 \text{ tons km}^{-2} \text{ year}^{-1}$	$\sim 10 \text{ tons km}^{-2} \text{ year}^{-1}$	$\sim 1-2 \text{ tons km}^{-2} \text{ year}^{-1}$

(1) Sargasso Sea cumulative nitrate = $0.1 \text{ g-atom m}^{-3} \text{ year}^{-1}$

(2) Station Poppa cumulative nitrate = $3.5 \text{ g-atom m}^{-3} \text{ year}^{-1}$

annual pelagic fish landings that used to be two orders of magnitude larger, per unit area, than the present Bering Sea demersal fishery at high latitudes.

In contrast to Peru, the Bering Sea has less annual primary production (McRoy and Goering, 1976) because ice reduces incident radiation by covering most of the shelf until March each year, when the spring bloom of phytoplankton begins, water temperatures are 10°C lower, and surface nutrients become exhausted by the end of summer as wind mixing declines. The yield of Alaska pollock (Pruter, 1973) from the Bering Sea is about 3% of the world fish catch, and the adult fish are restricted to the outer shelf (150-200 m). If the annual pollock harvest is derived only from this area of the total shelf (10-20%), however, then the fish yield km^{-2} of the Bering Sea is similar to that of other mid-latitude shelves, e.g. New York, Oregon, or the North Sea.

The annual primary production and the carbon content of the sediments (Sharma, 1974; Gross, 1968; Milliman, 1973) do not vary between these mid-latitude shelves (Table 1). Similar carbon inputs and outputs (as fish and sediment carbon) suggest that the greater width of the Bering Sea shelf (~500 km), in contrast to New York (~100 km) and Oregon (~25 km), may allow segregation of the benthic and pelagic food webs between the inner and outer parts of the high latitude shelf. With low incident radiation,

the inshore (<100 m) benthic secondary production appears to be transferred to long-lived mammals and large invertebrates in the Bering Sea rather than to demersal fish as at lower latitudes. A detailed comparison of two shelf ecosystems at about the same latitude, Oregon and New York-Georges Bank, can thus provide insight into how wind forcing and shelf width can structure the physical habitat, leading to different coupling between similar species in continental shelf systems having similar light regimes.

ENVIRONMENTAL VARIABLES

Wind Forcing

Wind events are an important source of habitat variability on the continental shelf in contrast to the open ocean (Walsh, 1976; Beardsley et al., 1976) and are responsible for both the generation of currents and for vertical mixing. Because of the north-south alignment of the North American continent, a southerly wind tends to favor offshore surface flow as a result of Coriolis force on the east coast of the United States (i.e. to the right) in contrast to a northerly wind on the west coast. Nutrient rich, cold subsurface water then moves onshore and upwells at the coast to replace the warmer, nutrient impoverished surface water transported offshore by winds favorable to upwelling (Walsh, 1975). Downwelling, (onshore flow of surface water and

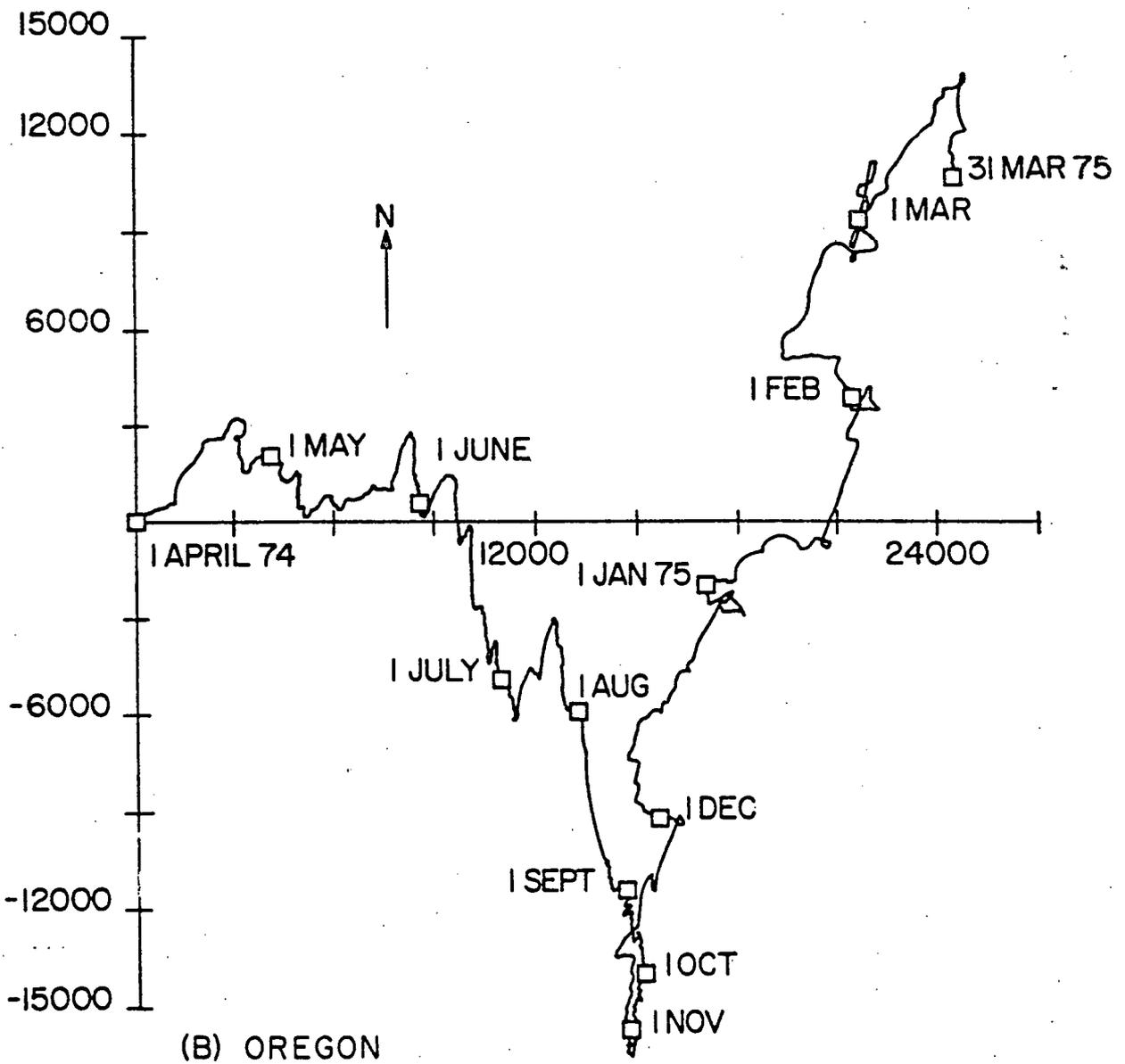
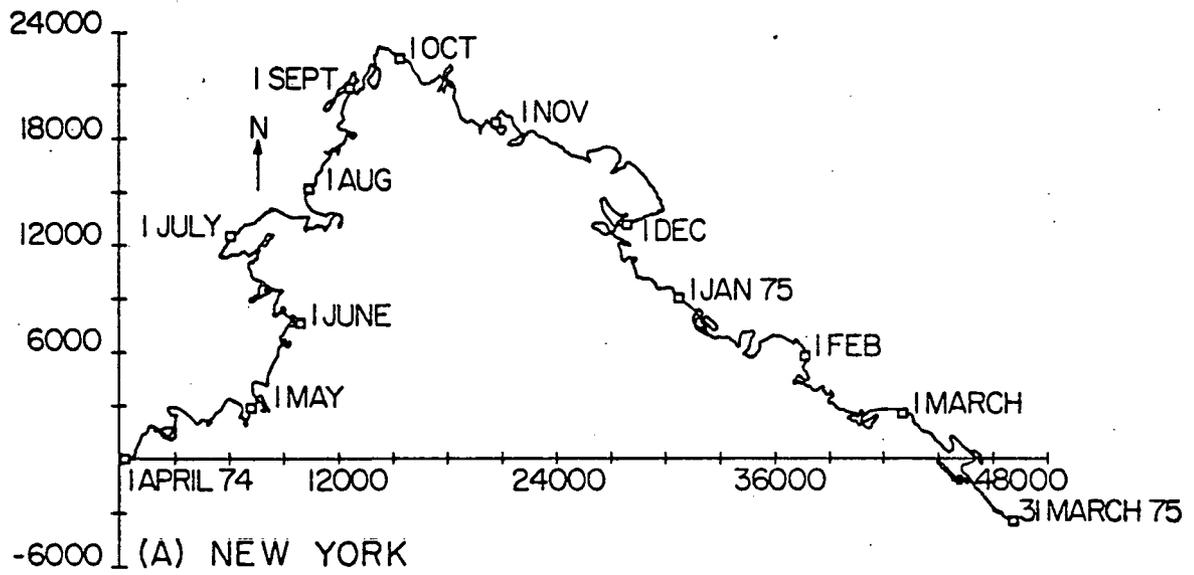


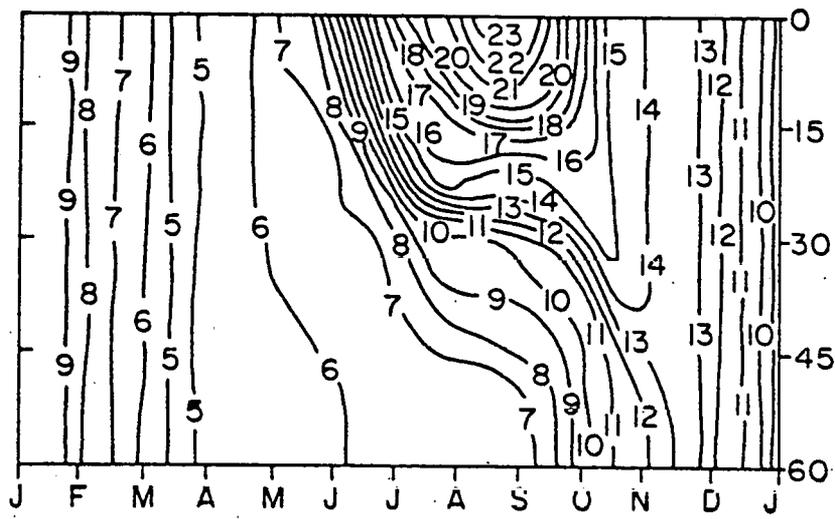
Fig. 1

sinking at the coast) occurs when winds are from the respective opposite directions off New York and Oregon. Coastal upwelling is a boundary process and most of the water is upwelled within a zone only 10-20 km from the coast, with offshore secondary cross-shelf flows set up as a function of the shelf width (Walsh, 1977). Finally, under conditions of weak stratification and strong winds, vertical mixing of the water column also occurs in addition to the upwelling/downwelling cross-shelf circulation pattern (Walsh et al., 1978).

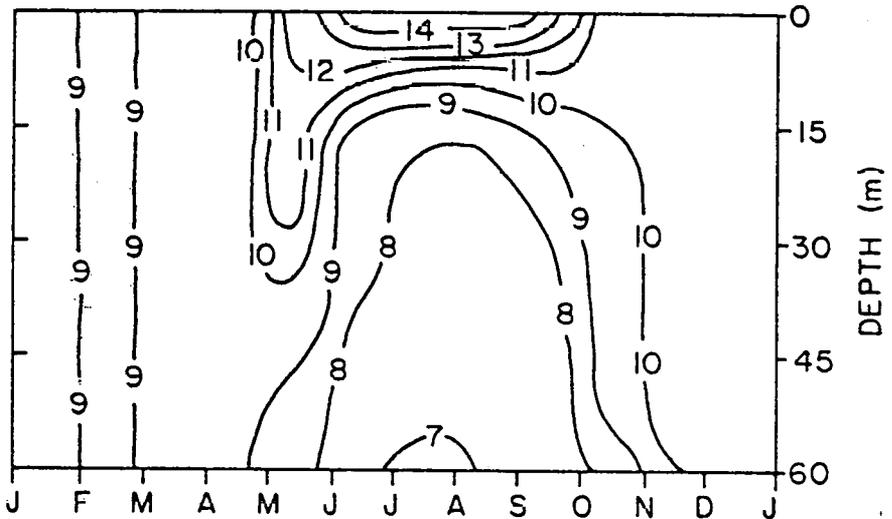
A progressive vector diagram (Fig. 1) shows wind forcing (in km) for a year at the Ambrose Light Tower off New York, and at the Newport jetty off Oregon. This analysis was compiled by plotting, head to tail, the successive vectors of wind speed and direction, every 3 h throughout April 1974-March 1975. The average offshore wind speed between Cape Hatteras and Rhode Island rises from 5 m sec^{-1} in July to 8 m sec^{-1} in January, though winds of $>20 \text{ m sec}^{-1}$ have been recorded during each month over the last 50 years at New York City (Lettau et al., 1976). Spectral analysis (O'Brien and Pillsbury, 1974) of these two sets of wind data indicates that the dominant frequencies of variability of the seasonal wind forcing within the two ecosystems are similar. Wind events, or storms, are more frequent in the winter, for example, and decline within the New York Bight

from 5-6 in January to half that number by September (Walsh et al., 1978). The cross-shelf advective input of nutrients (Table 1) also involves about the same period of 4-5 months of favorable spring-summer upwelling winds off both New York and Oregon (Fig. 1).

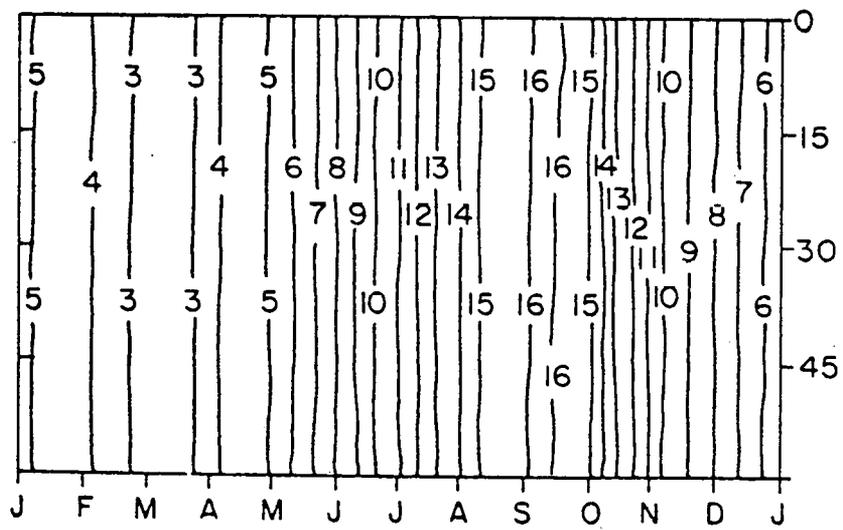
At a level of ecological complexity corresponding to trophic levels, the two shelves appear to have the same biological structure and productivity despite their differences in width. Their annual primary production is of the same order of magnitude, with a 5 year mean of $193 \text{ m}^{-2} \text{ yr}^{-1}$ at the edge of the shelf off Oregon (Small et al., 1972), in contrast to a 5 year estimate of $200\text{-}300 \text{ g C m}^{-2} \text{ yr}^{-1}$ within the whole New York Bight (Walsh et al., 1980a). The diversity of nearshore zooplankton species is also the same within 18-25 km of the coast; using a similar size of net mesh, 29 and 26 species of copepods respectively were found to be abundant in the New York Bight (Judkins et al., 1979) and off Oregon (Peterson and Miller, 1975). The abundance of estuarine-dependent fish is similar (McHugh, 1976), constituting 44.1% by weight of the U.S. commercial catch in the Middle Atlantic Bight, in contrast to 45.2% off Oregon-Washington, both in 1970. Finally, the number of common fish species on the slope and shelf is the same (~ 200) off Oregon (Pearcy, 1972; Alton, 1972) and New York (Hennemeuth, 1976), while the annual fish yield is also similar (Table 1).



(A) NEW YORK



(B) OREGON



(C) GEORGES BANK

TEMPERATURE (°C)

However, the timing of species succession and energy flow off Oregon and New York are different, because upwelling processes dominate the whole narrow west coast shelf but are confined to a relatively small region on the broad shelf off the east coast. The upwelling and downwelling responses are mainly confined to waters <30 m depth on the New York shelf, thus within 10-20 km of the coast (Scott and Csanady, 1976). A residual flow of 5 cm sec⁻¹ to the south is present at most times of year deeper on the New York shelf due to a longshore pressure gradient and thermohaline forcing. Similarly, off Oregon, the equatorward California Current flows throughout the year in deeper waters but is replaced on the shelf by the poleward Davidson Current during the winter downwelling situation.

Temperature

Consequently, the annual temperature cycle at the 60 m isobath, 60 km off New York (Fig. 2A) is that of a typical boreal shelf; 10 km off Oregon, at the 60 m isobath, it is that of a summer upwelling regime (Fig. 2B). The vernal heating cycle, river runoff, and a decline in wind events leads to stratification of surface waters by August in the New York Bight with an annual temperature range of ~20°C (Table 1) in the mid-shelf region. Because of the persistent westerly wind component in both ecosystems, temperatures of the well-mixed water on the

shelf in winter is lowered by wind off the land on the east coast and raised by wind off the ocean on the west coast. Higher winter temperatures, and the summer upwelling over most of the Oregon shelf together lead to an annual temperature range at the mid-shelf of only $\sim 5^{\circ}\text{C}$ (Table 1).

Tidal Mixing

On some shelves, tidal motion is an important factor in vertical mixing in addition to wind. Large tidal velocities of 55 cm sec^{-1} maximum amplitude, for example, can lead to roughly the same vertical mixing as a 13 m sec^{-1} wind (Pingree et al., 1978); tidal mixing energy is applied from below as opposed to the wind energy from above. Maximal tidal velocities at $>30\text{ m}$ depth are $\sim 15\text{-}25\text{ cm sec}^{-1}$ in the New York Bight and $\sim 55\text{-}110\text{ cm sec}^{-1}$ on Georges Bank. The latter velocities are similar to those of 1 m sec^{-1} around the British Isles (Simpson and Pingree, 1978), where an index of the tidal mixing (Simpson and Hunter, 1974) has been formulated as the ratio of depth (h) to the cube of the amplitude (u) of the tidal stream, i.e. $h u^{-3}$. The reciprocal of this ratio and a constant drag coefficient, $C h^{-1} u^3$, is the mean tidal energy dissipation rate per unit mass (Pingree et al., 1978). Because of the large range of values in both parameters, a log scale is used to estimate areas of stratification ($\log h u^{-3} \geq 2$ or $\log h^{-1} u^3 \leq -2$), transitional areas or fronts (1.5 or

-1.5), and tidally well-mixed areas (≤ 1 or ≥ -1). Larger tidal velocities and/or shallower depths favor increased tidal mixing.

At depths of 40-60 m in the New York Bight the tidal velocity of 0.25 m sec^{-1} suggest values of 3.41-3.59 for $\log h u^{-3}$, and stratification of the water column. A tidal velocity of 1.10 m sec^{-1} at similar depths on Georges Bank, however, suggest values of 1.48-1.65 and an area of tidal mixing. The seasonal temperature cycle at 60 m on Georges Bank does, in fact, reflect tidal mixing with an isothermal vertical structure at all times (Fig. 2C). Because of tidal and wind mixing on Georges Bank, the winter temperature minimum is about the same as that of the New York shelf but the summer temperature maximum is similar to that off Oregon.

Light

Because light penetration decays exponentially with depth in the ocean, phytoplankton which are mixed over the whole water column on Georges Bank experience less light than those in surface layers of stratified deeper waters (Riley, 1942). Thus, less chlorophyll is found in the highly mixed shallow regions of Georges Bank despite high nutrient concentrations at the beginning of the spring bloom. Similarly on the European shelf, higher chlorophyll concentrations occur on the stratified side of a shelf front rather than on the tidally mixed side (Pingree et al.,

though higher concentrations occur at the front between two such regions.

The relation between vertical mixing, light intensity, and phytoplankton growth was quantified as a critical depth concept (Sverdrup, 1953), below which the 24 hr respiration of the water column exceeds the integrated daily photosynthesis. This critical depth is $h_c \approx 0.2 I_0 (k I_c)^{-1}$, where I_0 is the incident radiation, k is the extinction coefficient, and I_c is the compensation light intensity at which algal photosynthesis equals respiration ($\sim 0.3 \text{ ly hr}^{-1}$). Sverdrup's concept is that if $h_c < h$, the depth to which the phytoplankton are mixed as a result of wind and/or tidal stirring, no bloom will occur even in the presence of high nutrient content.

In turbid, seasonally well-mixed shelf waters with chlorophyll concentrations of $\sim 2.0 \mu\text{g chl l}^{-1}$ (Fig. 3), Secchi disk depth is $\sim 11 \text{ m}$ at the 60 m isobath in the New York Bight. Empirically, k is related to either the Secchi depth, h_s , by $k = 1.44 h_s^{-1}$ (Holmes, 1970), i.e. $1.44 (11)^{-1} = 0.131 \text{ m}^{-1}$, and/or to chlorophyll content by $k = 0.04 + 0.0088 \text{ chl} + 0.054 \text{ chl}^{2/3}$ (Riley, 1956), i.e. 0.143 m^{-1} . If the average illumination of a mixed water column $\bar{I}_h = I_0 (kh)^{-1}$, increases to an intensity at which gross phytoplankton production is greater than loss rates from respiration, grazing, and sinking, then a bloom will ensue. Riley (1967) and Hitchcock and

Smayda (1977) found that above an in situ threshold of $\bar{I}_h = 40 \text{ g cal cm}^{-2} \text{ day}^{-1}$ (1 ly day^{-1}) phytoplankton blooms occurred in Long Island Sound and Narragansett Bay.

At the beginning of March off New York and Oregon at the 60 m isobath, the incident radiation is $< 250 \text{ g cal cm}^{-2} \text{ day}^{-1}$ and \bar{I}_h is thus $32 \text{ g cal cm}^{-2} \text{ day}^{-1}$ within the well mixed 60 m water column; the critical depth is also too shallow at 53 m. However, incident illumination increases to over $300 \text{ g cal cm}^{-2} \text{ day}^{-1}$ by the end of March off New York (Walsh et al., 1978) and Oregon (Small et al., 1972), with associated increases in critical depth and average in situ light intensity. Similar changes in spring light intensity and critical depth have been calculated for the Irish Sea, with mean I_0 and h_c increasing from $250 \text{ g cal cm}^{-2} \text{ day}^{-1}$ and 60 m in mid-March to $430 \text{ g cal cm}^{-2} \text{ day}^{-1}$ and 100 m in mid-April (Pingree et al., 1976).

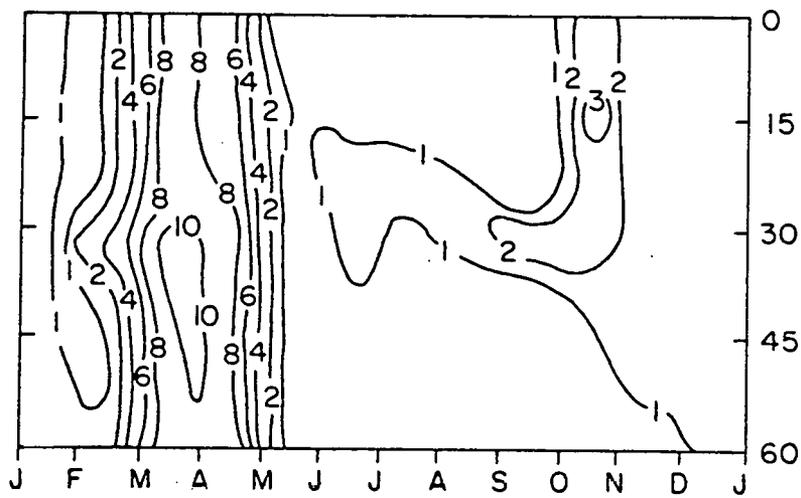
PELAGIC FOOD WEB

Phytoplankton

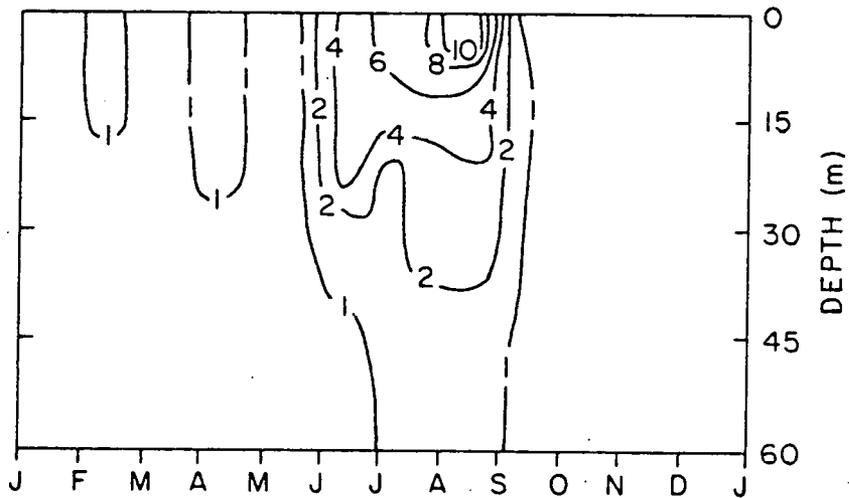
At this time of year, the isothermal March water column contains more than $4\text{-}5 \text{ } \mu\text{g-at NO}_3 \ell^{-1}$ off both New York (Walsh et al., 1978) and Oregon (Stefansson and Richards, 1964), as well as around the British Isles (Pingree et al., 1976). Having an appropriate combination of light and nutrients, the spring bloom thus begins

at the 60 m isobath in the New York Bight and on Georges Bank (Fig. 3) before the onset of seasonal stratification in the former, and despite tidal mixing in the latter (Fig. 2). Bloom conditions also occur after a surface light intensity of $300 \text{ g cal cm}^{-2} \text{ day}^{-1}$ in the Sargasso Sea (Steele and Menzel, 1962). Sporadic nearshore blooms of phytoplankton occur at the 18 m isobath, within 2 km of the Oregon coast, from March to June (Petersen and Miller, 1977); up to $6 \mu\text{g chl } \ell^{-1}$ are found even earlier at the 30 m isobath off New York in December, but these populations are relicts of the fall bloom. In contrast, mid-shelf chlorophyll concentrations, similar to the east coast spring bloom, are not found at the 60 m isobath off Oregon until July-August during the middle of the upwelling season (Fig. 3).

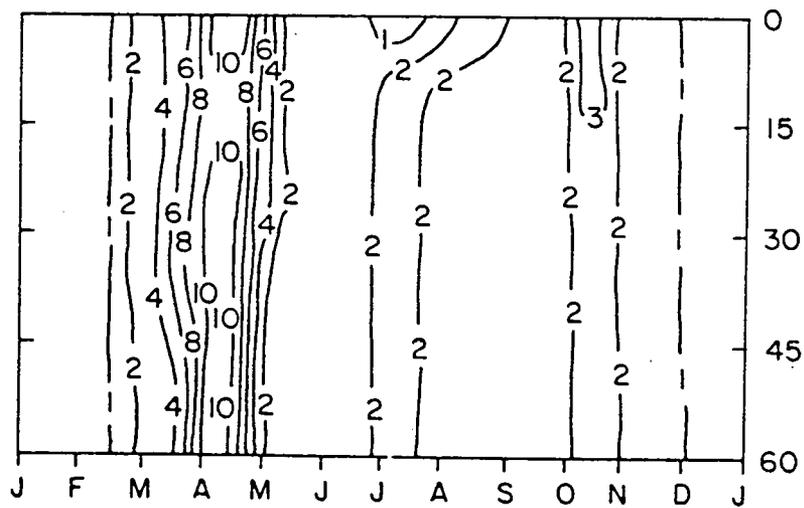
During summer stratified conditions in the New York Bight, nitrate is undetectable in the euphotic zone, while only 0.1-0.2 $\mu\text{g-at NO}_3 \ell^{-1}$ occur in tidally mixed areas of Georges Bank and the English Channel. High chlorophyll concentrations ($4-5 \mu\text{g chl } \ell^{-1}$) are then found only in subsurface maxima within the 10 km nearshore upwelling zone of the New York Bight, and on the surface, at the edge of fronts, on Georges Bank and in the English Channel. After the fall overturn in October, there is more than $2.5 \mu\text{g-at NO}_3 \ell^{-1}$ throughout the water column off New York, Georges Bank, the English



(A) NEW YORK



(B) OREGON



(C) GEORGES BANK

CHLOROPHYLL ($\mu\text{g l}^{-1}$)

Fig. 3

Channel, and Oregon. This nitrogen input is partially consumed by a small fall bloom in New York, the English Channel, and Georges Bank, but again not off Oregon. By October, incident light is less than $300 \text{ g cal cm}^{-2} \text{ day}^{-1}$ in all four areas, with the critical depths $<50 \text{ m}$: the decline in both chlorophyll and light then continues towards their winter minima.

Downwelling begins off Oregon in October and ends in May (Fig. 1), with an intervening upwelling season of varying inter-annual intensity (Petersen and Miller, 1975). Despite sufficient light and nutrients off Oregon in March and October, a bloom is not observed perhaps because the sinking water entrains phytoplankton onshore and below the euphotic zone. For example, the zooplankton species at these times suggests that the water on the shelf has come from the south as part of the downwelling circulation (Petersen and Miller, 1977). Similarly during the upwelling season off Oregon, cross-shelf distributions of phytoplankton and suspended material (Small and Ramberg, 1971) also suggest sinking within a convergence front at mid-shelf (Mooers et al., 1976). Downwelling has been observed during "northeasters" (March, July, and October storms) in the New York Bight, but phytoplankton loss is restricted to the inner part of this wider shelf. At mid-shelf depth, chlorophyll appears to be resuspended from the sediments particularly during

strong southwesterly winter-spring winds in the New York Bight (Walsh et al., 1978).

Nitrogen Demand

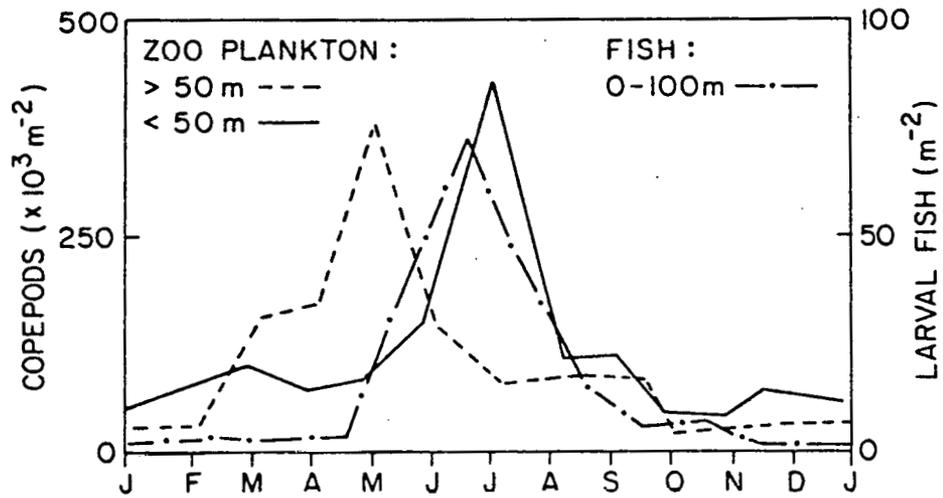
Unlike Oregon, however, nutrients limit phytoplankton population growth over most of the Mid-Atlantic Bight during summer, when nitrogen demand must be supplied by recycling by zooplankton, bacterioplankton, and benthos (Walsh et al., 1978). A phytoplankton C:N ratio of 5:1 and an annual primary production of $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ suggests an annual nitrogen demand of $60 \text{ g N m}^{-2} \text{ yr}^{-1}$, or $\sim 71 \mu\text{g-at N } \ell^{-1} \text{ yr}^{-1}$ at the 60 m isobath, part of which is supplied by biological regeneration of nitrogen as ammonium and part by physical input of nitrate.

In a recent nitrogen budget (Walsh et al., 1980a) for the shelf between Cape Hatteras and Georges Bank (the Mid-Atlantic Bight), the estimated sources of nitrogen are $11.0 \mu\text{g-at N } \ell^{-1} \text{ yr}^{-1}$ from zooplankton excretion, 7.0 from bacterioplankton, 11.0 from benthos, 3.0 from nitrification, 0.5 from rainfall, 3.0 from estuarine input, 9.0 from the upstream boundary across the shelf to the north, and 26.0 from the longshore boundary at the edge of the shelf. Approximately 46% of the nitrogen demand of the annual primary production of the New York Bight may be supplied by recycling, which suggest that the pelagic food web of this shelf ecosystem may be more tightly coupled in a biological sense to the demersal food web than those of the upwelling system off Oregon.

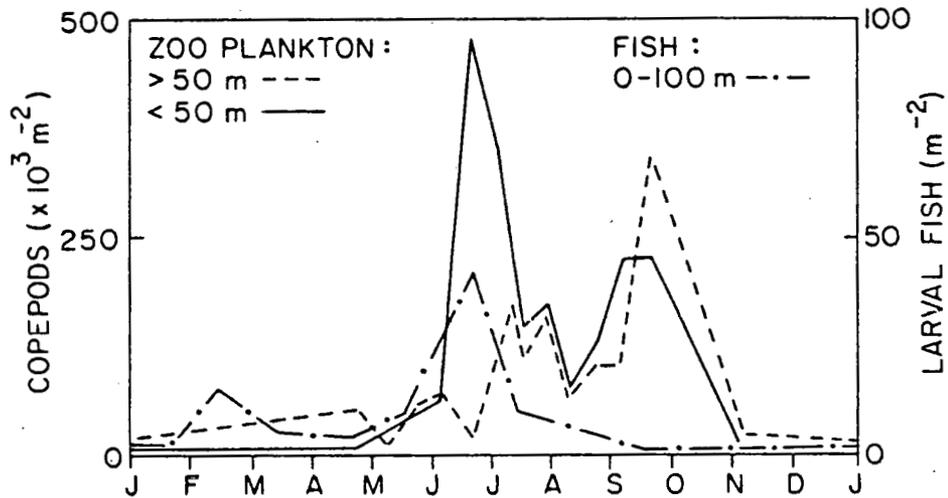
Copepods

The seasonal pulses of copepod biomass off New York, Georges Bank, and Oregon (Fig. 4) reflect regional differences in both temperature cycles and the timing of phytoplankton blooms. For example, Pseudocalanus minutus and Centropages typicus are the dominant copepods off New York and Georges Bank (Judkins et al., 1979; Sherman, 1978; Grice and Hart, 1962; Clark, 1940; Sears and Clarke, 1940; Bigelow and Sears, 1939) with the former found across the shelf in the winter-spring and the latter inshore during summer-fall; Calanus finmarchicus is also abundant offshore after the spring bloom. The New York offshore peak of these zooplankters (>50 m) occurs during May-June, as offshore waters warm about one month after the offshore phytoplankton bloom (>50 m) in March-April. Inshore zooplankton (<50 m) becomes abundant during the even warmer period of July-August, following by one month the inshore phytoplankton growth period (<50 m) of May-June (Walsh et al., 1980a).

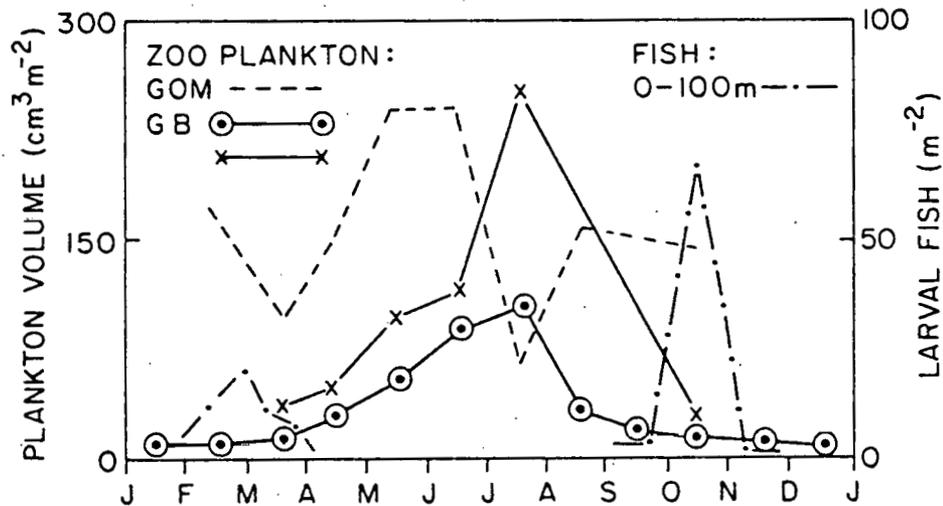
The peaks of zooplankton biomass on Georges Bank and in the Gulf of Maine (Fig. 4C) have similar spatial and seasonal patterns (Bigelow, 1926; Redfield, 1941; Riley, 1947) to the respective inshore and offshore copepod communities within the New York Bight (Fig. 4A). The cross-shelf distribution of the same genera of copepods is also similar off Oregon; Pseudocalanus sp. is found across the shelf, Calanus marshallae offshore and Centropages abdominalis inshore (Fig. 4B) during the summer upwelling period



(A) NEW YORK (1974-1975)



(B) OREGON (1970-1971)

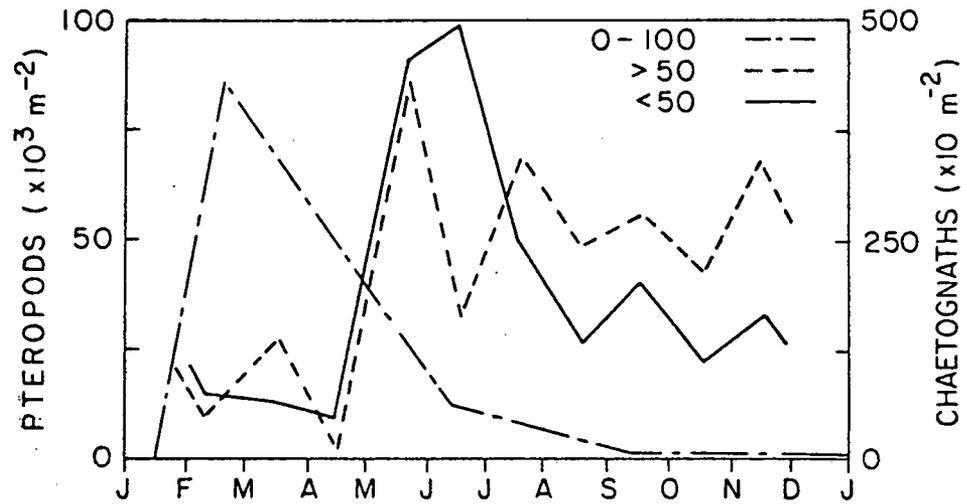


(C) GEORGES BANK : GULF OF MAINE
 (1933-34, 1939-40, 1971-78)

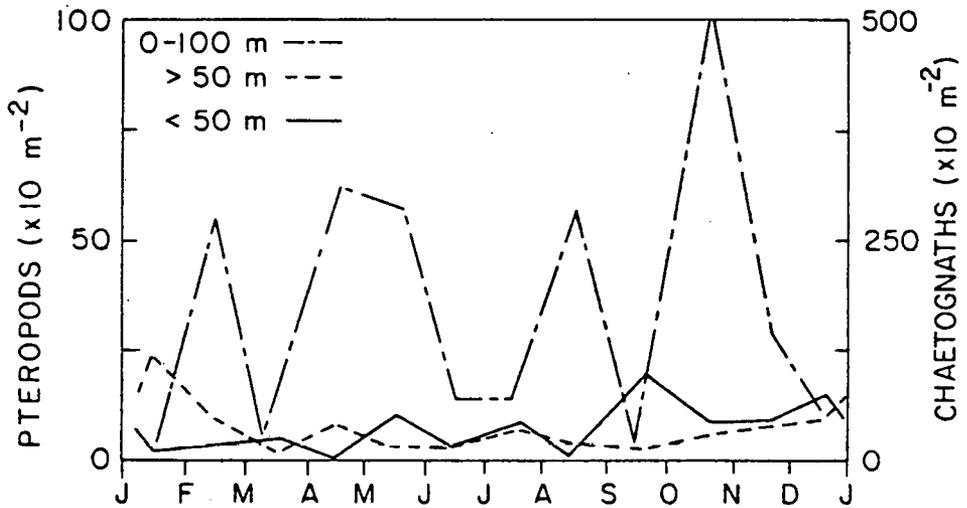
Fig. 4

(Petersen et al., 1979). However, only Pseudocalanus sp. dominates both the single offshore (>50 m) summer peak of zooplankton in July-August, that coincides with the mid-shelf phytoplankton bloom, and the smaller cross-shelf peaks of copepods that occur in the absence of high chlorophyll during October (Petersen and Miller, 1975, 1977).

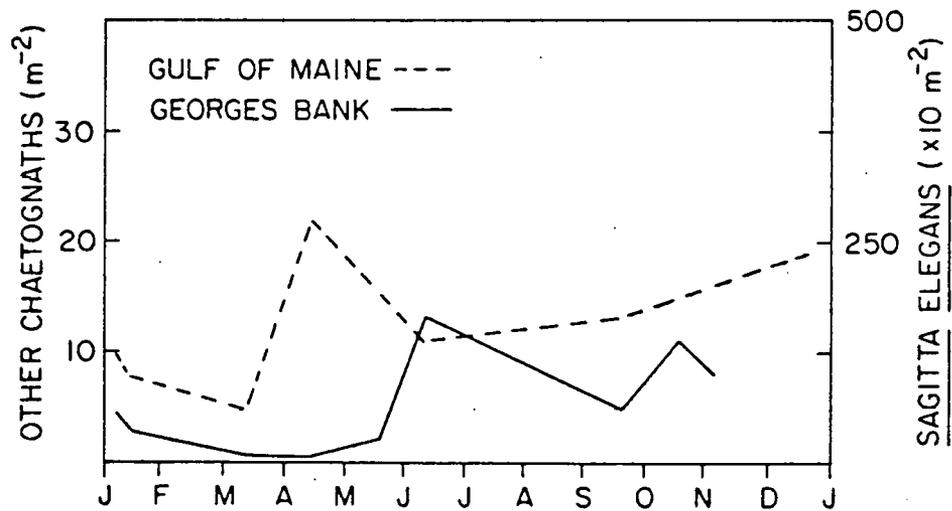
Pseudocalanus is a cold water form (Corkett and McLaren, 1978), which grows well at low temperatures (Vidal, 1978) and intermittent food supply (Dagg, 1977), in contrast to Centropages. The summer Δt between Oregon and New York is $\sim 10^{\circ}\text{C}$, a full Q_{10} range, and Pseudocalanus would thus be metabolically favored during both summer upwelling off Oregon and in the colder spring waters off New York. Pseudocalanus females also lay fewer eggs than Centropages, yet adult abundance is similar off New York (Dagg, 1979), suggesting that predation may be less during the growth phase of the cold water form. The increase (Fig. 5) of inshore (<50 m) chaetognath biomass after the spring peak of Pseudocalanus minutus may allow the slower growing Centropages to succeed Pseudocalanus off New York during the summer. Moreover, Centropages is also an omnivore, in contrast to Pseudocalanus, and may thus partially subsist on its own or other invertebrate nauplii within the summer food web off New York.



(A) NEW YORK BIGHT (1974-1975)



(B) OREGON (1970-1971)



(C) GEORGES BANK : GULF OF MAINE
(1939-41, 1974) (1933-1934)

Fig. 5

Invertebrate Predators

Clarke et al. (1943) have suggested that two to three generations of chaetognaths are produced each year on Georges Bank. There are, in fact, indications of maturation in May-June, September-October, and November-December of three broods, or cohorts, of these predators in all three systems (Fig. 5). The main chaetognath peak is smaller and later in the year off Oregon, however, in contrast to those off New York and Georges Bank (Redfield and Beale, 1940). Similarly, major pulses of ctenophore predators occur in the fall off both California (Hirota, 1974) and New York (Malone 1977), after the peak of Centropages typicus, compared to the summer bloom of ctenophores off Oregon (Petersen and Miller, 1976). The low temperature, lack of fall bloom, and different timing of predator stress may thus all act to prevent Centropages from succeeding Pseudocalanus as the dominant copepod off Oregon. Conversely, the continued existence of a herbivore off Oregon during summer and fall may not allow a fall bloom to develop in October, similar to the manner in which the lack of a spring bloom in the North Pacific is due to constant grazing pressure of Calanus cristatus (McAllister et al., 1960).

Ichthyoplankton

Seasonal cycles of larval fish (Fig. 4) tend to follow those of the invertebrate herbivores and carnivores. The May-June peak

of larval fish in the New York Bight comprises mainly yellowtail flounder and mackerel, while the smaller winter peak on Georges Bank is of cod, haddock, and sand lance following the herring maximum; data were not available for the summer period on Georges Bank but yellowtail and mackerel spawn in this area as well (Colton et al., 1979). Similarly off Oregon, the winter peak of larval fish represents sand lance, butter sole, and english sole, while the summer maximum comprises capelin (Richardson and Pearcy, 1977).

Although the larval survival of fish may be the critical factor in determining fluctuations of adult abundance (Lasker, 1975; Walsh, 1978), ichthyoplankton probably have little direct impact on energy flow through lower trophic levels. For example, daily respiration within the summer water column of the New York Bight of peak larval fish populations represents a maximum oxygen demand of only $1.6 \text{ ml } O_2 \text{ m}^{-2} \text{ day}^{-1}$ in contrast to $48 \text{ ml } O_2 \text{ m}^{-2} \text{ day}^{-1}$ for the chaetognaths, $360 \text{ ml } O_2 \text{ m}^{-2} \text{ day}^{-1}$ for the benthos, and $500 \text{ ml } O_2 \text{ m}^{-2} \text{ day}^{-1}$ for the copepods (Walsh et al., 1980b). Furthermore, a nitrogen budget for the New York shelf (Walsh et al., 1978) suggests that 53% of the nearshore phytoplankton biomass in August is consumed daily by the copepods, whereas only 6% of the inshore bloom is grazed in May, and 7% of the mid-shelf bloom (Fig. 3) in March, when few chaetognaths and larval fish are present.

Pteropods

With an incident radiation of $150 \text{ g cal cm}^{-2} \text{ day}^{-1}$ at the end of January, the critical depth is 32 m and the average light intensity of the well-mixed water column at the 30 m isobath is $38.5 \text{ g cal cm}^{-2} \text{ day}^{-1}$. Without downwelling, an inshore phytoplankton bloom at the 30 m isobath should occur in the New York Bight after the February increase of incident radiation. In fact, phytoplankton blooms ($\sim 10 \text{ } \mu\text{g chl } \ell^{-1}$) are then observed nearshore (Evans et al., 1979) despite the presence of the herbivorous pteropods (mainly Limacina retroversa). These are the third most abundant zooplankters, with a peak occurrence (Fig. 5) before Pseudocalanus minutus in February-March (Judkins et al., 1979) within 60 km of the Long Island coast (Walsh et al., 1978).

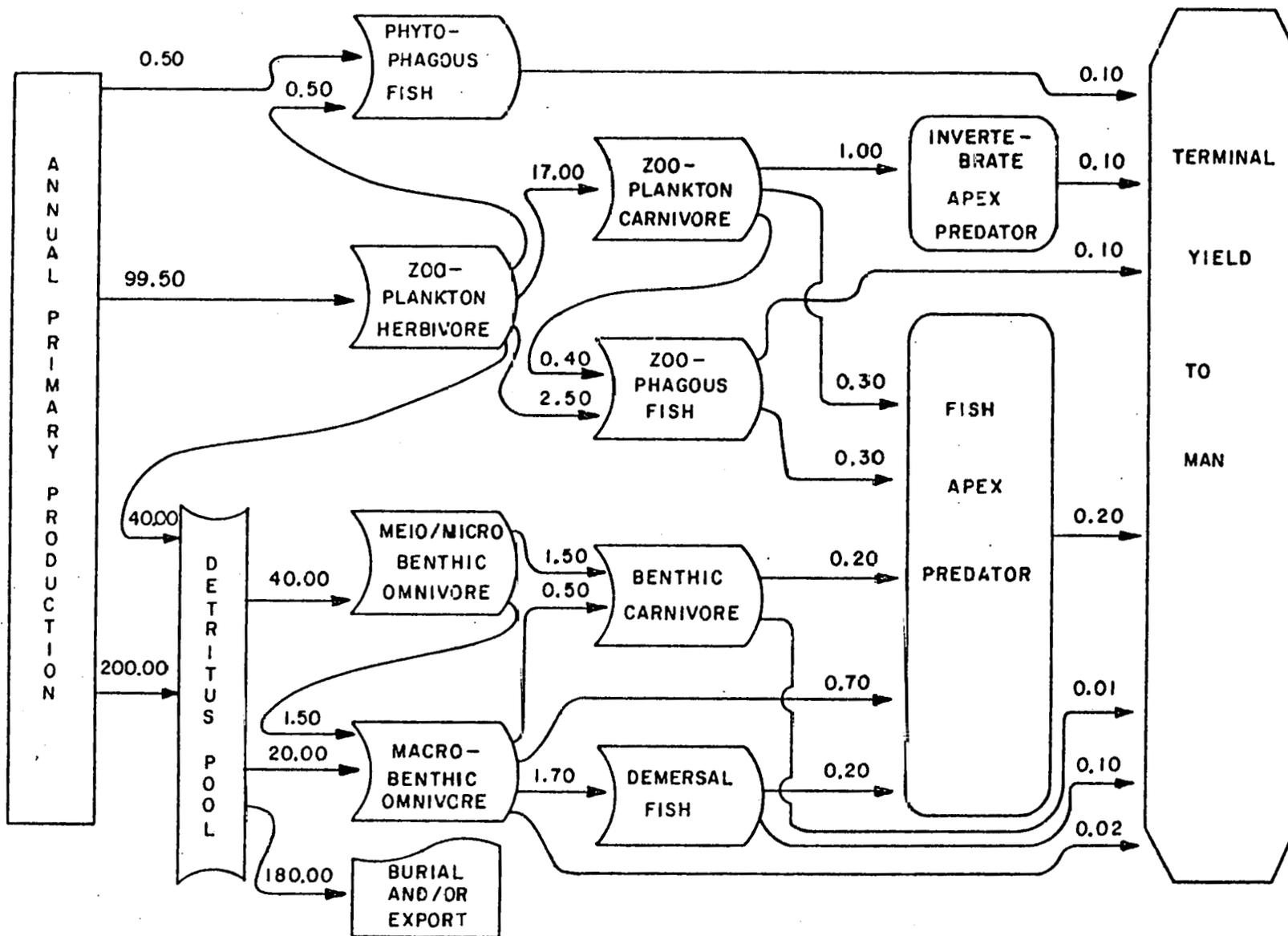
These pteropods are as ubiquitous as calanoid copepods within the Mid-Atlantic Bight. Redfield (1939) described the growth of a population of Limacina retroversa during a 7 month drift from its possible winter spawning area on the Nova Scotian shelf until it was entrained southward within the gyre around the Gulf of Maine, and pteropods have also been used to delimit long-shore shelf habitat changes at Cape Hatteras (Myers, 1967). Although abundance within the copepod maxima off Oregon and New York are of the same order (Fig. 4), the Oregon pteropod maximum of Limacina helicina is only 2% of that off New York and occurs

during October (Fig. 5) at the same time as the Pseudocalanus sp. fall peak. Thus downwelling appears to prevent a winter bloom of phytoplankton and zooplankton off Oregon, whereas off New York the February inshore primary production is cropped before mid-March by both pteropods and tintinnids: This is indicated by diatom chain length, fo:fo ratios, and PN:chl ratios (Walsh et al., 1976).

DEMERSAL FOOD WEB

Benthos

As a result of different shelf width and similar wind forcing, an inshore zooplankton species succession of Limacina retroversa, Pseudocalanus minutus, and Centropages typicus occurs in the New York Bight, while Pseudocalanus sp. remains the dominant shelf herbivore off Oregon. The nearshore winter and summer primary production ($\sim 100 \text{ g C m}^{-2} \text{ yr}^{-1}$) is thus transferred to protozoa and zooplankton off New York, while the production of the March-May spring bloom at mid-shelf ($\sim 200 \text{ g C m}^{-2} \text{ yr}^{-1}$) is apparently transferred instead to the bottom (Fig. 6). A regression of benthic macrofaunal biomass on average chlorophyll of the March-May euphotic zone, in fact, yields an r^2 of 0.80 for other areas in the Canadian coastal zone, the North Sea, and Long Island Sound (Mann, 1976). In contrast, the lack of a spring bloom on most of the Oregon shelf, suggests that little transfer of carbon to the bottom occurs at this time of year.



A CARBON BUDGET ($g\ C\ m^{-2}yr^{-1}$) OF YIELD TO MAN ON THE NORTHEAST CONTINENTAL SHELF

Fig. 6

In the preliminary carbon budget for Cape Hatteras-Georges Bank already discussed, the utilization of the primary production by the herbivorous zooplankton (growth efficiency 20% and assimilation efficiency 60%) leads to an annual secondary production of $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ available for consumption by the pelagic food web and a fecal pellet flux of $40 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the demersal food web (Fig. 6). Flux of fecal pellets and phytodetritus to the bottom ($\sim 240 \text{ g C m}^{-2} \text{ yr}^{-1}$) can be partitioned into the larger macrobenthic invertebrates (detritivores, herbivores and omnivores) and the smaller more abundant heterotrophic organisms, the meiofauna and microbiota (Fig. 6). Finally, the food requirements of the pelagic and demersal fish and the yield to man from all commercial living resources, are independent estimates (Edwards and Bowman, 1978; Sherman et al., 1978) at the output side of this carbon budget.

The number of meiobenthic organisms in some areas, south of Martha's Vineyard ($0.1-1.0 \times 10^6$ animals m^{-2} ; Wigley and McIntyre, 1964) for example, far outnumber the macrobenthos (1.4×10^3 animals m^{-2} ; Wigley and Theroux, 1979). They appear to be responsible, along with the bacteria and protozoa, for remineralization of material on the bottom rather than serving as much of a pathway to higher trophic levels (Fenchel, 1969; McIntyre et al., 1970;

Coull, 1973; Tenore, 1977). The detritus flux is thus assumed to be either buried, exported, or mineralized by both the meiobenthos and the microbenthos in this carbon budget. It is possible that meiobenthos production is consumed by brittle stars and polychaetes, as well as by other deposit feeders. An inverse spatial distribution has been observed between the meiofauna and macrofauna biomass in the New York Bight, with perhaps as much as 50% of the meiobenthic production consumed by the macrobenthos (J. Tietjen, personal communication). A similar budget of benthic interactions has been constructed for the Baltic Sea (Ankar and Elmgren, 1976).

Some phytodetritus and fecal matter would be used as an energy source by all three size categories of benthos, and several studies have estimated total community metabolism off New York; for example, Thomas et al. (1979) measured nearshore bottom oxygen utilization by incubating cores aboard ship at in situ temperatures. Their results of $360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (or $54 \text{ g C m}^{-2} \text{ yr}^{-1}$ with an R.Q. of 0.75) were similar to seasonal oxygen demand of the bottom biota (Smith et al., 1974), within in situ bell-jar incubations. Florek and Rowe (in prep.) have recently made core incubations over a broader area of the shelf of the Middle Atlantic Bight, and their data suggest levels of infaunal utilization of organic carbon in different parts of the shelf:

Nearshore (<30 m depth)	-	70 g C m ⁻² yr ⁻¹
Central shelf depths	-	43 g C m ⁻² yr ⁻¹
Georges' Bank	-	27 g C m ⁻² yr ⁻¹
Outershelf margin	-	20 g C m ⁻² yr ⁻¹

If an average value for inner shelf respiration measurements of $\sim 50 \text{ g C m}^{-2} \text{ yr}^{-1}$ is assumed to be representative of all the Middle Atlantic Bight, only about 25% of the total direct loss (about $240 \text{ g C m}^{-2} \text{ yr}^{-1}$) from the water column can be attributed to utilization by microfauna, meiofauna, and macrofauna. If this is the case, either the fecal pellets and phytoplankton carbon produced during the winter-spring bloom is buried and exported, or it must be utilized by organisms not considered in these assumptions. Another approach to this enigmatic carbon loss is independently to estimate carbon utilization from known macrofaunal biomass (Wigley and Theroux, 1979).

Large areas of the Mid-Atlantic shelf have a wet weight benthic biomass of more than 100 gm m^{-2} ($\sim 6 \text{ g C m}^{-2}$), most of which is composed of the long-lived macrobenthos with low rates of secondary production (Warwick and Price, 1975; Buchanan and Warwick, 1974). If the average macrofaunal biomass on the shelf is on the order of 100 g m^{-2} and a P/B of 0.5 is assumed, then their production would be about $50 \text{ g m}^{-2} \text{ yr}^{-1}$, or $3 \text{ g C m}^{-2} \text{ yr}^{-1}$. With a

growth efficiency of 15%, total carbon consumption by the macrofauna would be about $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 6). This is reasonable, because attempts to partition carbon flow through benthic communities in the past have shown that only a small portion is used by larger organisms (Smith et al., 1973; Smith, 1973). If the benthic fluxes of the carbon budget ($40 \text{ g C m}^{-2} \text{ yr}^{-1}$ to small organisms and $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ to macrofauna, see Fig. 6) are in fact reasonable estimates, then the benthic community on the shelf of the Middle Atlantic Bight does not consume much of the annual carbon flux to the bottom, and there must be burial or carbon export.

Sediments

Most of the sediment on the Mid-Atlantic shelf is relict sand with <0.5% carbon (Emery and Uchupi, 1972), however, deposited during or soon after the last Wisconsin glaciation, when the shelf was dry land 15,000 years ago. Seaward of the 60 m isobath, the sediments contain more silt (Freeland and Swift, 1978), and, beyond the shelf-break, the organic content finally increases to 1-2% carbon, but still lower in organic content than the >4% carbon muds (Table 1) off the Peru coast (Rowe, 1971). The Hudson Canyon, areas of Georges Bank (Hathaway et al., 1979), and the "mud hole," a region of $4 \times 10^3 \text{ km}^2$ southwest of Martha's Vineyard between the 50-100 m isobaths, are the exceptions where 1-2% carbon

muds are found on the Mid-Atlantic shelf. In these areas, ^{14}C and ^{210}Pb dating suggest modern deposits with a sedimentation rate of at least 50-100 cm 1000 yr⁻¹ (Drake et al., 1978; Bothner et al., 1980) in contrast to about 15 cm 1000 yr⁻¹ on the slope (MacIlvaine, 1973) and 3 cm 1000 yr⁻¹ on the rise (Milliman, 1973).

The C:N ratio (Fig. 7) of Mid-Atlantic shelf sediments (Milliman, 1973) can be used as an index of areas of modern carbon deposition and possibly also of the fate of particles during transport in this ecosystem (Fig. 6). The average C:N ratio of marine bacteria, phytoplankton, copepods, polychaetes, other zooplankton and benthic organisms, as well as fish are all less than 6, while land plants and aquatic vascular plants, e.g. Zostera and Thalassia, are greater than 15 (Müller, 1977). Sediments with C:N content <6 may indicate a marine origin if also rich in carbon (Müller, 1977) and those >10 would indicate a terrestrial or marine vascular plant source. The carbon content of the shelf sediments with a C:N ratio <6 in the Middle Atlantic Bight (Fig. 7) is, in fact, twice those with a >10 C:N ratio, while $\delta^{13}\text{C}$ measurements (Hunt, 1966) suggest the surface sediments with a C:N <6 south of Martha's Vineyard (Fig. 7) are of marine origin. Similar $\delta^{13}\text{C}$ measurements are not available for the >10 C:N sediments off New York and New Jersey (Fig. 7), but the N-alkane hydrocarbon fraction of the sediment carbon pool in this region

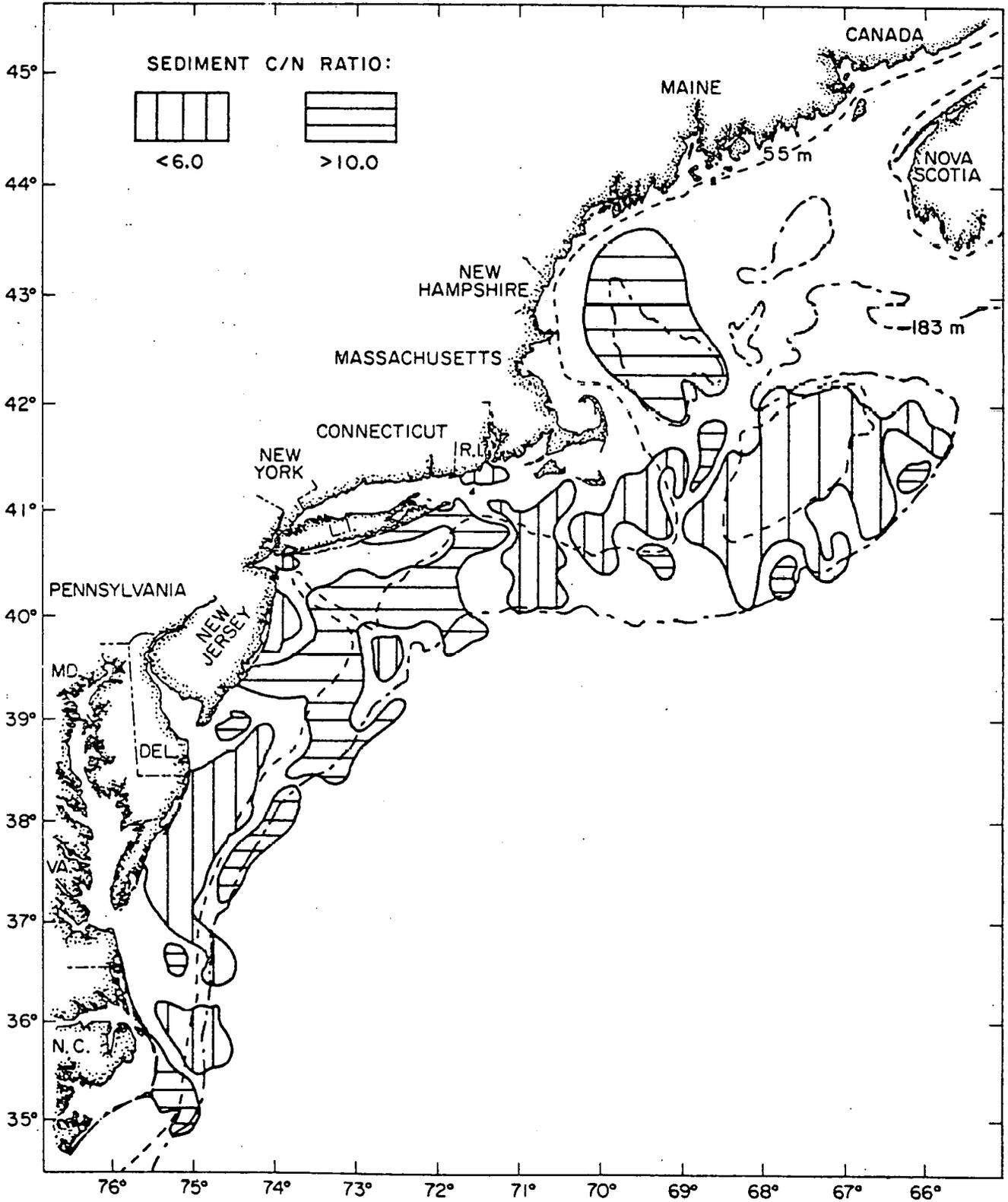


Fig. 7

suggests that this material instead had both terrestrial and petrochemical origin (Farrington and Tripp, 1977). In contrast off South Carolina, the shelf sediments have a C:N ratio <6 (Emery and Uchupi, 1972) and an N-alkane hydrocarbon fraction that suggests a marine origin (Hathaway et al., 1979).

The C:N ratio of the shelf edge sediments (Fig. 7) thus suggests terrestrial or vascular plant carbon deposition, presumably when relict sands were deposited during both the last Wisconsin and previous glaciations. The depth of Pleistocene sediments on the upper slope is ~ 300 m in contrast to only ~ 100 m on the shelf (Hathaway et al., 1978), i.e. average accumulation rates of respectively $15 \text{ cm } 1000 \text{ yr}^{-1}$ and $5 \text{ cm } 1000 \text{ yr}^{-1}$. As the river mouths, marshes, and sea grass beds retreated towards the present shore line during the Holocene transgression, sediments of >10 C:N content were continually laid down and are still observed across the shelf in some areas, e.g. south of Montauk Point and east of Atlantic City (Fig. 7). In other areas, e.g. Georges Bank (Hathaway et al., 1979), Nantucket Shoals, the "mud hole", Hudson Canyon, and at the mouth of estuaries, a surface layer of modern (Holocene) biogenic <6 C:N sediments may now overlay the relict sediments with their >10 C:N ratios. For example, after a sea

level stand still of ~ 1500 yr at -40 to -45 m of the present coastline (Jansen, 1976), an "allochthonous" sediment of 15-17 C:N ratio was deposited 8700 B.P. in the northern North Sea (Jansen et al., 1979). This terrestrial or vascular plant material is overlain by a surface layer 1.5 m thick with a C:N ratio between 4 to 10, suggesting a biogenic deposition rate of $17 \text{ cm } 1000 \text{ yr}^{-1}$ in a system where most of the primary production is consumed by the zooplankton (Steele, 1974). In contrast, recent dating of cores on northern Georges Bank (Hathaway et al., 1979) suggested that the deposition rate of diatoms and organic matter in this region may be $363 \text{ cm } 1000 \text{ yr}^{-1}$.

PELAGIC-DEMERSAL COUPLING

Input

A longshore drift of 5 cm sec^{-1} occurs in the Mid-Atlantic Bight, and regions of <6 C:N content in the surface sediments may either be downstream of the areas where primary production is not consumed, or be the sites of deposition near estuaries, as a result of entrainment within sub-surface onshore flow of water. During an April spring bloom of $\sim 4 \mu\text{g chl } \ell^{-1}$ at the 65 m isobath near 55°N in the Baltic Sea, long chains of diatoms were observed (Smetacek et al., 1978), despite the presence of Pseudocalanus elongatus with few carnivores, thus with low grazing loss as during spring

in the New York Bight. The C:N content of particulate matter in sediment traps within this water column varied from ~5 to 10, with lower values mainly observed during the first 18 days of active sedimentation. Because of plankton patchiness and a current of 15 cm sec^{-1} within the euphotic zone, these sediment traps may have underestimated the local detrital flux, but an average downward carbon input to the shelf of $0.2 \text{ g C m}^{-2} \text{ day}^{-1}$, or 15% of the mean primary production, was found above sediments containing 3% carbon. During upwelling at 700 m on the upper slope off California, a similar carbon flux of $0.1 \text{ g C m}^{-2} \text{ day}^{-1}$ was also estimated from sediment traps (Knauer et al., 1979), but a flux of only $0.01 \text{ g C m}^{-2} \text{ day}^{-1}$ occurs in the deep ocean (Rowe and Gardner, 1979). If only 15% of the annual primary production off New York also sinks directly on the shelf, i.e. $45 \text{ g C m}^{-2} \text{ yr}^{-1}$, this is close to the benthic flux of $60 \text{ g C m}^{-2} \text{ yr}^{-1}$ obtained in the preliminary carbon budget (Fig. 6).

Longshore Structure

Assuming sinking velocities of $1-10 \text{ m day}^{-1}$ (Smayda, 1970) for live phytoplankton, and a longshore current of 5 cm sec^{-1} ($\sim 4 \text{ km day}^{-1}$), a bloom could travel for 6-60 days, over 25-250 km along the 60 m isobath, before sinking to the bottom in the Mid-Atlantic Bight. The latter is the downstream distance of the

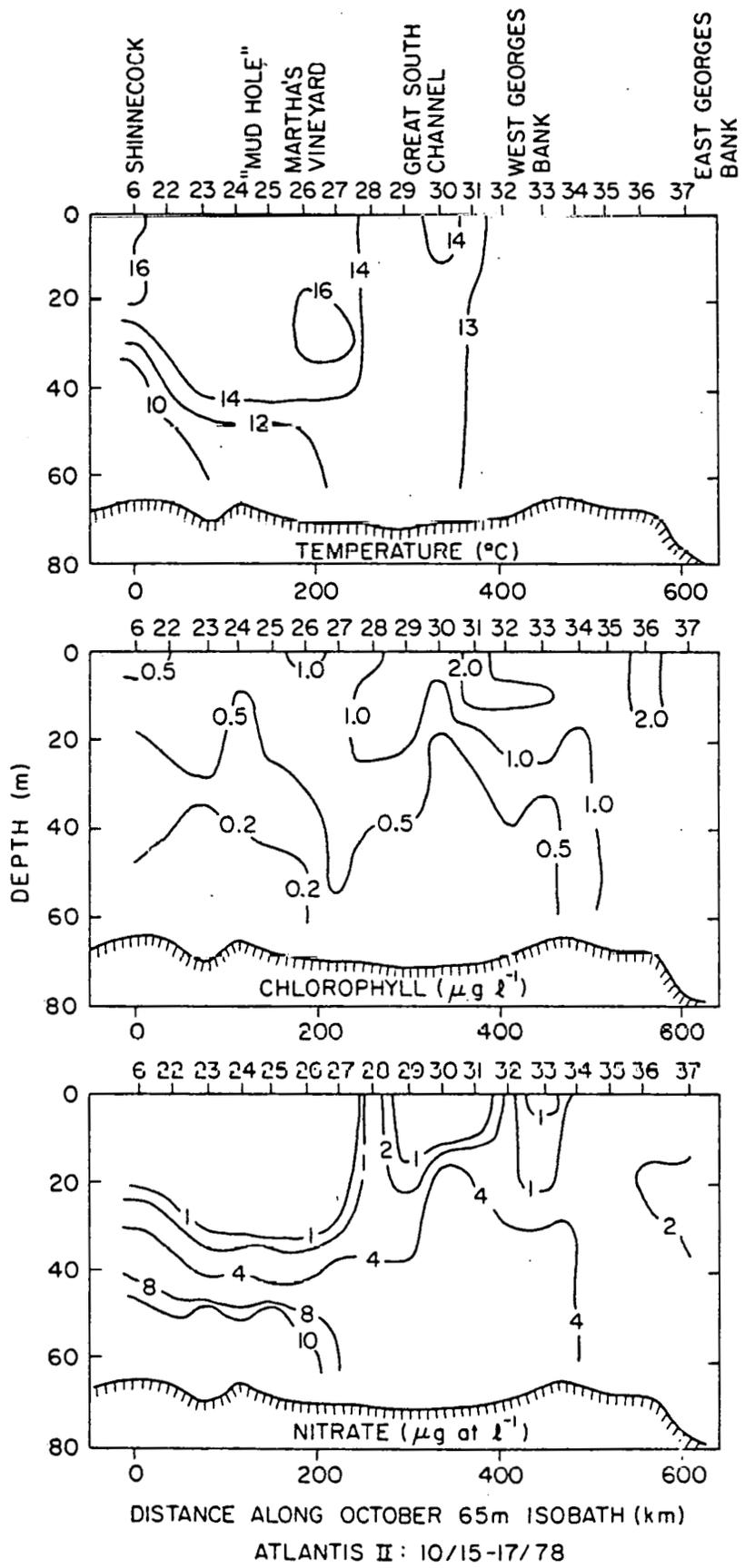


Fig. 8

"mud hole" from Georges Bank (Fig. 8), while the former is close to the separation distance between the "mud hole" and Nantucket Shoals. Both upstream areas have high chlorophyll in the water column at all times of year in addition to low C:N ratios in the sediments (Fig. 7). Longshore studies in May at the 60 m isobath show that vertical isopleths of chlorophyll do, in fact, slope downstream from the surface towards the bottom, to intersect the sediments at both the Hudson Shelf Valley and the "mud hole".

Before the fall overturn in October, however, little chlorophyll remains above the bottom of the water column in the New York Bight. Sub-surface nitrate concentrations along a transect at the 65 m isobath instead increase near the "mud hole" (Fig. 8). The longshore difference in integrated chlorophyll between the eastern tip of Georges Bank and New York Bight (Fig. 8) was $\sim 70 \text{ mg chl m}^{-2}$ in October 1978, or about $40 \text{ mg-at N m}^{-2}$ (assuming a C:chl of 35:1 and a C:N of 5:1) in contrast to the dissolved nitrate change of $130 \text{ mg-at NO}_3 \text{ m}^{-2}$. If the difference in particulate nitrogen represented by the phytoplankton in the water column ($40 \text{ mg-at N m}^{-2}$) is subtracted from that of the dissolved stocks, an estimate of $90 \text{ mg-at NO}_3 \text{ m}^{-2}$ is obtained for nitrate increase by nitrification during drift from Georges Bank to New York (Walsh et al., 1980a). In contrast, ammonium concentration at each end of the 65 m isobath transect was $192 \text{ mg-at NH}_3 \text{ m}^{-2}$ in

the north and $105 \text{ mg-at NH}_3 \text{ m}^{-2}$ in the south. This ammonium decrease independently suggests that $87 \text{ mg-at NH}_3 \text{ m}^{-2}$ may have converted to NO_3 during the southwesterly drift along the shelf. This longshore nitrogen budget thus implies that particulate matter on the bottom must also be remineralized to ammonium and then to nitrate with a C:N ratio of $\sim 5:1$ within the bottom water.

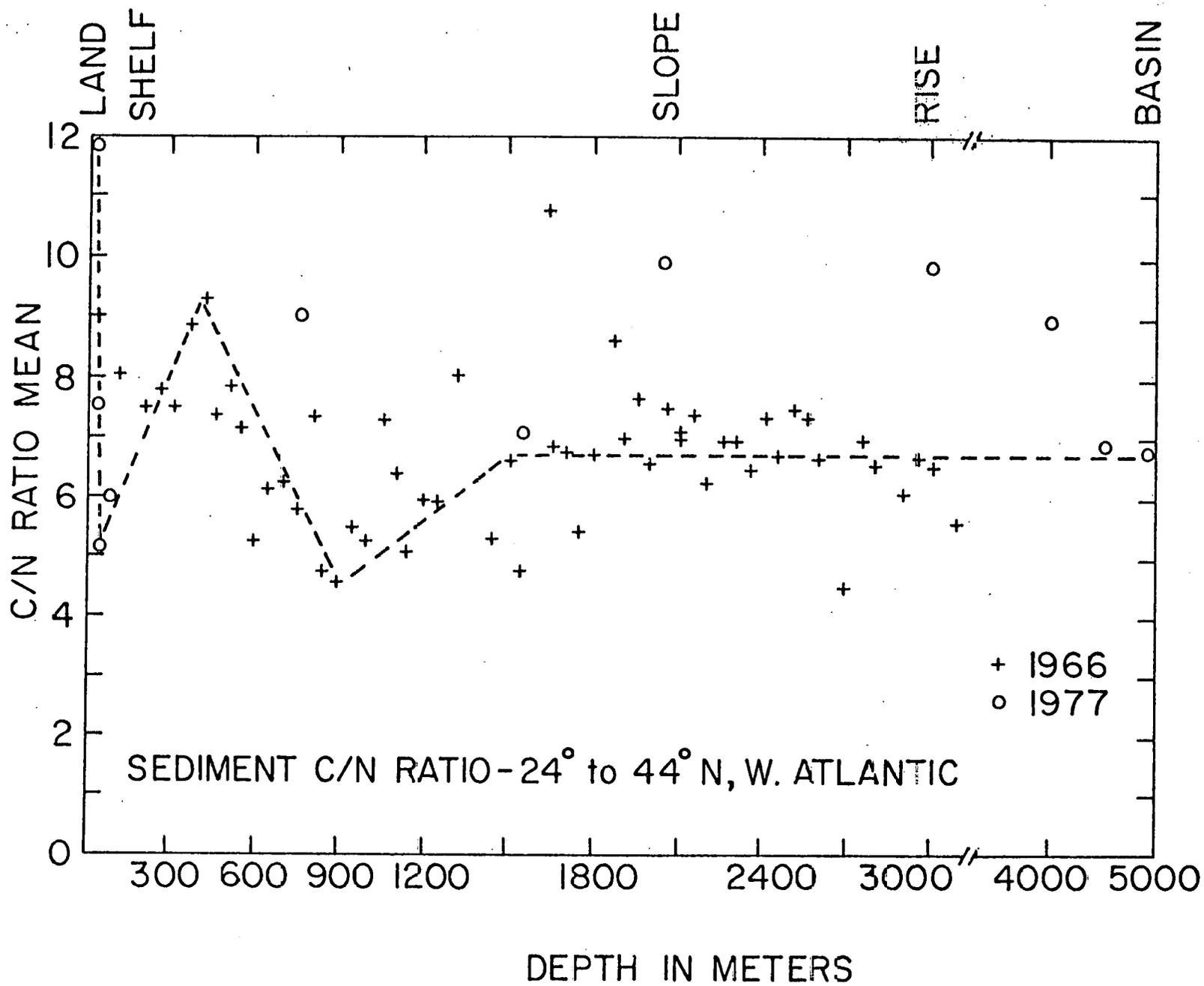
Direct observations of a bottom flux of $21 \text{ mg NH}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Rowe et al., 1975) and an oxygen consumption of $360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Thomas et al., 1979), suggest a benthic carbon respiration of $148 \text{ mg C m}^{-2} \text{ day}^{-1}$, and a C:N ratio of <7 for carbon respiration:nitrogen regeneration in the New York Bight. The areas of sediment C:N content >10 may thus indicate regions where marine biogenic deposition has not overlain relict sediments on the shelf, that is to say the southern and offshore boundaries of present carbon deposition and decomposition (Fig. 7). Presumably high C:N values do not indicate areas of the shelf where differential nitrogen recycling on the bottom might occur with respect to carbon mineralization. The implication is that during longshore transport that carbon which sinks to the bottom is assimilated by the benthos with little accumulation in the sediments; in fact, there is a suggestion of a declining downstream gradient in sediment carbon and macrobenthos populations from

Georges Bank to Cape Hatteras (Walsh et al., 1980a). What then is the fate of the seasonal spring pulses of phytoplankton input to the bottom (Fig. 6), if the "mud hole" and northern Georges Bank are the only major downstream (offshore) consequences of continuous detrital input from the tidally mixed parts of this shelf ecosystem?

Cross-Shelf Exchange

Away from the "mud hole", a composite transect of C:N sediment content from land to the deep ocean basin of the North Atlantic (Fig. 9) suggests two areas of low C:N ratios. The nearshore region is located off the estuaries (Fig. 7) and reflects sinking and onshore entrainment of phytoplankton beneath surface offshore river plumes (Malone and Chervin, 1979). The second region of low C:N values is at 800-900 m, beyond the high C:N zone at the shelf-break (i.e. the presumed area of relict deposition of terrigenous and/or vascular plant material) and represents offshore transport of biogenic material from the shelf to the slope (Schubel and Okubo, 1972; Hay and Southam, 1977). Off North Carolina, half as many meiofauna are found at 400 m as at 800 m (Coull et al., 1977), at which depth the offshore transition from sandy to muddy sediments occurs (Tietjen, 1971). This organic matter at 800-900 m has either bypassed the natural

Fig. 9



sedimentary traps at the mouths of estuaries or has originated at mid-shelf; we recall that estimates of particle flux to the bottom of the shelf and the upper slope are similar (Smetacek et al., 1978; Knauer et al., 1979), but accumulation of pleistocene sediments is greater on the upper slope.

The vertical distribution of particulate and dissolved organic carbon in the sea is, in fact, homogeneous below 200-300 m in the Atlantic and Pacific Oceans (Menzel and Ryther, 1970). The entire biochemical cycle of organic matter, including production, decomposition and solution, thus appears to occur mainly above these depths: beyond the shelves there may be little amount of direct input of carbon to the bottom from the water column above. For example, little change occurs in C:N ratio of the sediments from 1500 to 5000 m (Fig. 9), and this intermediate C:N ratio of the deep sediment reflects the long residence time of open ocean source material and thus slow reworking of nitrogen compounds in the overlying waters (Müller, 1977; Knauer et al., 1979). Any lowering of the C:N ratio of sediments on the upper slope (Fig. 9) would thus require a modern biogenic shelf source and some mechanism for relatively fast lateral seaward transport past the shelf-break.

As a result of upwelling and low salinity water influx at the coast (Ketchum and Keen, 1955), there is a continual transport

of surface water seaward in the New York Bight. Seabed drifters (Bumpus, 1974) and a simple physical model (Csanady, 1976), also suggest a bottom layer flow seaward of the 60 m isobath. Hence, there may be offshore flow at the bottom as well as at the surface on the outer part of the shelf, with a return onshore flow in the middle of the water column to maintain the salt balance. Organic matter tends to be co-transported with finegrain sediment fractions (Gross, 1968). A simple advection-diffusion model of the transport of finegrain inorganic matter across the northeast continental shelf (Schubel and Okubo, 1972) thus provides insight into the origin of low C:N values on the upper slope (Fig. 9). For example, with an offshore advective and diffusion "velocity" of 2 cm sec^{-1} and a fine grain sinking velocity of $\sim 1 \text{ m day}^{-1}$, their calculations suggest that any fine grain sediment which had escaped the estuaries would bypass the shelf and be deposited on the upper slope, within 100 km of the shelf edge.

The mid-shelf bloom during March off Long Island occurs between the 60 m isobath, $\sim 60 \text{ km}$ from shore, and the shelf-break (Walsh et al., 1978). Assuming an offshore flow of 2 cm sec^{-1} , an average depth of 250 m and a sinking velocity of $1-10 \text{ m day}^{-1}$, algal cells within the bloom would travel seaward 40-400 km, or 0-360 km past the shelf-break before reaching the bottom. With weaker offshore flow, of 0.5 cm sec^{-1} , which is 1/10 of the

longshore flow, and a sinking velocity of 2 m day^{-1} , a phytoplankton could sink to the bottom at only 10 km seaward of the shelf-break. In this area, the bottom topography decreases from 200 to 2000 m within ~ 40 km of the New York shelf, and, in fact, the lowest C:N ratios are found at 800-900 m (Fig. 9), while 2-3% carbon sediments are observed at the head of the Hudson Canyon in waters of 200-300 m depth. Off Oregon, the shelf width is $\sim 1/4$ that of New York, and deposits with 2-3% organic carbon occur at 1000-2500 m (Gross, 1968), roughly the same distance (125 km) as off the coast at New York.

In contrast, the Bering Sea shelf is about five times wider than that off New York with a similar weak flow regime ($\sim 1-5 \text{ cm sec}^{-1}$) which is dominated by tidal mixing (Coachman and Charnell, 1979). The pleistocene sediments are generally less than 100 m thick on the Bering Sea shelf, with little quarternary (Pleistocene + Holocene) deposits found nearshore (Nelson et al., 1974). After a sea level stand still at -40 to -45m of the present coastline $\sim 10-12,000$ B.P. in the Chukchi (Creager and McManus, 1965) and Laptev (Holmes and Creager, 1974) Seas, the holocene sedimentation rate of nearshore Bering Sea areas, e.g. Norton Sound, has been less than $20 \text{ cm } 1000 \text{ yr}^{-1}$ (Nelson et al., 1974). The C:N content of the surface sediments in the tidally mixed nearshore areas (<50 m) is >10 in contrast to a C:N ratio of <6

for the middle and outer shelf areas (Lisitzin, 1966; R. Iversen, personal communication). Within a 200 km wide area of the middle shelf where Pseudocalanus is the major herbivore, a carbon budget for the southeast Bering Sea (McRoy, Walsh, and Iversen, in prep.) suggests that 50% of the annual primary production is buried within or exported from this region. Less than 0.5% carbon is found within surface sediments of the middle shelf (Lisitzin, 1966; Sharma, 1974), however, whereas >1% carbon is found ~125 km seaward in the <6 C:N sediments of the outer shelf (Gershanovitch, 1962; R. Iverson, personal communication). Because of a greater shelf width, the carbon export of the Bering Sea appears to be deposited on the outer shelf rather than on the upper slope off New York and on the lower slope off Oregon.

CONSEQUENCES

These examples suggest that the ocean's continental shelves, with an average width of 75 km, may represent a major carbon sink from the water column, and source for the export of phytodetritus and fecal pellets to the present adjacent slopes. An important aspect of carbon export to the slope from the New York Bight, however, is that a mass balance of the elements must presumably be maintained, in an annual steady state. If CO₂ does not limit

plant production in the ocean, the same amount of nitrogen (Ryther and Dunstan, 1971) must be returned each year to the shelf as is lost in the proposed detrital flux, i.e. $\sim 180 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 6), or $\sim 36 \text{ g N m}^{-2} \text{ yr}^{-1}$ assuming a C:N ratio of 5. The fact that our independent nitrogen budget (pg. ___) indicated that about $33 \text{ g N m}^{-2} \text{ yr}^{-1}$ must be supplied from the upstream, offshore, and coast boundaries, suggests that a mass balance of nitrogen is apparently maintained on the New York shelf.

The nitrate-rich pool of upper slope water at the shelf-break is large and seasonally constant at $\sim 9500 \text{ mg-at N m}^{-2}$ down to 500 m, the maximum depth of the winter mixed layer (Leetma, 1977). In comparison, the whole shelf water column has a maximum winter nitrate content of $400 \text{ mg-at N m}^{-2}$ at the 60 m isobath, over an order of magnitude less than the offshore source water. Nitrate may thus be supplied to the shelf from intermediate offshore depths, while particulate nitrogen is lost to the slope bottom, with a significant time delay (years to decades; Broecker et al., 1979) between nutrient remineralization on the bottom of the slope (1000-2000 m) and replenishment of nitrate stocks to the offshore surface layer by vertical mixing or diffusion through the deep thermocline. In this mass balance, carbon could also be removed from the shelf in the form of fixed CO_2 , and stored deep on the

the slope as detrital carbon, forming a CO₂ sink in the ocean without nitrogen limitation.

The flux of CO₂ from past fossil fuel burning, cement production, and deforestation, its present storage pools (in the atmosphere, on land, or in the sea), and the impact of our future use of fossil carbon are poorly understood processes. At the present rate of increase in fuel consumption of 4.3% yr⁻¹, a doubling of the atmospheric CO₂ and a 2-3°C increase in temperature from the "greenhouse" effect (Chamberlin, 1899) could occur by 2035; present ocean temperatures are, in fact, only ~2.3°C warmer than during the last Wisconsin glaciation (CLIMAP, 1976). Up to 1950, most of the CO₂ emitted from fossil fuel burning and from the use of limestone for cement was thought to have been absorbed in the ocean with little accumulation in the atmosphere (Revelle and Suess, 1957). Although the amount of CO₂ in the atmosphere has steadily increased since the industrial revolution from many sources, the cumulative addition of 70-80 x 10⁹ tons C to this pool is only equivalent to about half of the CO₂ produced by burning fossil fuel, a great deal of which has occurred in just the last two decades (Bolin, 1977). Finally, though land biota were at one time thought to be a sink for CO₂, the terrestrial ecosystem now instead may be a source of CO₂ as a result of deforestation. The rate of carbon flux from the land to the

atmosphere or ocean is a subject of some controversy, (Woodwell et al., 1978; Ralston, 1979; Broecker et al., 1979), comparable to earlier disagreements about the amount of harvestable carbon from the sea (Ryther, 1969; Alverson et al., 1970).

Without consideration of marine photosynthesis as a net loss term, a global budget for the inorganic storage of CO_2 in the ocean from 1850 to 1950 (Stuvier, 1978) overestimated the initial amount of carbon in the pre-industrial atmosphere by $\sim 50 \times 10^9$ tons (Keeling, 1978), suggesting that at least 0.5×10^9 tons C yr^{-1} might have been lost to a biotic sink. Models of abiotic storage of CO_2 in the ocean by vertical mixing over just the last few decades can account for only 37% of the CO_2 emitted from fossil fuel burning and similarly ignored biological fixation of carbon in the sea; they also cannot account for the missing CO_2 presumably emitted from deforestation (Siegenthaler and Oeschger, 1978). Furthermore, chemical considerations (Bacastow and Keeling, 1973) of the buffer capacity of surface sea water suggest that with an increased CO_2 content leading to more acidic conditions, the upper mixed layer might become an increasingly effective barrier to CO_2 absorption by the deep ocean. Specific considerations of CO_2 emitted from just wood burning (Wong, 1978) suggests, in fact, that almost all of this CO_2 source, i.e. 1.2×10^9 tons C yr^{-1} could be

lost in the form of detrital carbon deposition on the continental shelves.

Of the three major inorganic nutrients utilized by marine phytoplankton, nitrogen is most likely to be limiting. Despite its low concentration in sea water, phosphate recycles very rapidly in the marine environment, and does not appear to limit significantly the productivity of the world's oceans. Silicate recycles slowly, but is not required by all marine phytoplankton; when it is limiting, the primary effect is probably on phytoplankton species composition rather than total primary production.

Current theory suggests that it is the rate of supply of nitrogen to the euphotic zone which limits primary production, with the input rate of nitrate as an estimate of the "new" production of the system (Chapter). Since CO_2 presumably does not limit marine primary production, although it has been observed to stimulate photosynthesis in lakes (Schindler et al., 1972), the extent to which marine food chains may act as a sink for atmospheric CO_2 thus depends upon the rates of nitrogen recycling and the removal of carbon which is not associated with respiratory costs of the nitrogen recycling.

From an early CO_2 model of the atmosphere and an ocean without continental shelves (Keeling and Bolin, 1967), approximately

2.7×10^9 tons C yr⁻¹, or about 10% of the global marine primary production ($\sim 25 \times 10^9$ tons C yr⁻¹; Woodwell et al., 1978) was estimated to sink to the sediments. Based on a more recent nitrogen budget for "new" production of offshore waters (Eppley and Petersen, 1980) and again ignoring the coastal zone, the same flux of carbon was assumed to occur in the open ocean. Most of this carbon apparently does not leave the upper 300 m of the sea (Menzel and Ryther, 1970), however, and below 300 m, sediment trap studies of the oceanic detrital carbon flux suggest a loss of $0.005-0.010$ g C m⁻² day⁻¹ (Wiebe et al., 1976; Rowe and Gardner, 1979; Knauer et al., 1979); over the whole 2.6×10^8 km² of open ocean, this is equivalent to a yearly carbon sink of only $0.5-1.0 \times 10^9$ tons C yr⁻¹.

The major organic carbon sink in the global CO₂ budget (Keeling and Bolin, 1967) probably occurs instead on the continental shelves. With a minimum primary production of 200 g C m⁻² yr⁻¹ (Table 1), a total shelf area of 2.6×10^7 km² (Hay and Southam, 1977), and a 60% ratio of carbon export to production (i.e. 180/300 g C m⁻² yr⁻¹, see Fig. 6), 5.2×10^9 tons C yr⁻¹ would be fixed and 3×10^9 tons C yr⁻¹ lost to the continental slope. Current CO₂ budgets require a presently unknown sink, in fact, of $\sim 3 \times 10^9$ tons C yr⁻¹ during the last decade (Bolin, 1977) to account for the

missing CO₂, which must have been released by increased fossil fuel burning and deforestation, but not observed in the atmosphere or apparently mixed to the deep sea in such a short time.

The sedimentation rate at the head of the Hudson Canyon has doubled over the last few thousand years (Drake et al., 1978), and nitrogen content of rain has doubled in recent decades, largely by the combustion of fossil fuel (Hall et al., 1978). Rainfall contributed less than 1% of the annual nitrogen demand of primary production in the New York Bight, however; more importantly the amount of organic carbon to be exported from the shelf is fixed during the spring bloom when nutrients are not limiting. The total yield to man as commercial fish from the New York continental shelf over the last 10 years has been only $\sim 0.63 \text{ g C m}^{-2} \text{ yr}^{-1}$, while the carbon export may be at least $180 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 6); the former provides food, but the latter may, by reducing the "greenhouse" effect, actually be of greater importance to us. This chapter presents a preliminary, but a reasonably consistent proposal for steady state carbon fluxes which could both support the 99% of the global fish catch which is produced by the shelf ecosystem and, at the same time, serve as a major sink in the global CO₂ budget.

Major alteration of carbon flow through any one of the shelf food web components (Fig. 6) can be attributed to interannual changes of species survival patterns as a function of external perturbations. For example, because of their proximity, the continental shelves have tended to become the refuse pit of industrialized maritime nations. We are coming to realize, however, that dilution of waste material in the sea can no longer be considered a permanent removal process in either the open ocean or nearshore waters. The increasing utilization of the continental shelf for oil drilling and transport, cooling of nuclear power plants, planned and inadvertent waste disposal, as well as for food and recreation, require careful management of man's future activities in this ecosystem. Certainly as we continue to learn more about the organisms and control functions of the shelf-sea ecosystem, man will be able to more rationally manage the coastal zone by avoiding overfishing and carefully selecting sites of industrial activity. The assimilatory capacity of this ecosystem to store toxicants must now be considered, however, with respect to its present resiliency (Holling, 1973) to withstand perturbations at much shorter time scales than either glacial or evolutionary events.

Figure Legends

- Fig. 1. Progressive vector diagram (km) of the seasonal wind forcing off A) New York and B) Oregon.
- Fig. 2. Annual cycle of temperature ($^{\circ}\text{C}$) at the 60 m isobath off A) New York, B) Oregon, and C) Georges Bank.
- Fig. 3. Annual cycle of chlorophyll ($\mu\text{g l}^{-1}$) at the 60 m isobath off A) New York, B) Oregon, and C) Georges Bank.
- Fig. 4. Annual cycle of copepods and larval fish on the inner (<50 m) and outer (>50 m) continental shelf off A) New York, B) Oregon, and C) Georges Bank: Gulf of Maine.
- Fig. 5. Annual cycle of pteropods and chaetognaths on the inner (<50 m) and outer (>50 m) continental shelf off a) New York, B) Oregon, and C) Georges Bank: Gulf of Maine.
- Fig. 6. A carbon budget of both yield to man and a biological sink for atmospheric CO_2 on the northeast continental shelf.
- Fig. 7. The distribution of relict (C/N >10) and modern (C/N <6) sediments between Cape Hatteras and Georges Bank (modified from Milliman, 1973).

Fig. 8. The October longshore distribution of temperature ($^{\circ}\text{C}$), chlorophyll ($\mu\text{g } \ell^{-1}$), and nitrate ($\mu\text{g-at } \ell^{-1}$), at the 65 m isobath between New York and Georges Bank.

Fig. 9 . A composite of sediment C/N ratios on 1) the north-east continental shelf away from the "mud hole" and 2) from the continental slope to the ocean basin between 24° to 44°N in the western Atlantic.

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