Influences of Oceanographic Processes on the Biological Productivity of the Gulf of Maine

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I. INTRODUCTION

The Gulf of Maine is a continental shelf sea on the east coast of North America, situated between Cape Cod, MA and Nova Scotia, Canada (Figure 1). Its rich biological productivity, resulting from a suite of complex oceanographic processes, has for centuries supported a bountiful fishery. The Gulf's unusual morphometry, with deep basins and limited access to the open Atlantic Ocean, the strong tidal mixing of its shallower waters, and the seasonal cycle of intense winter cooling, springtime freshwater runoff, and summer warming, act individually and collectively to affect the physical, chemical, and biological oceanography of the Gulf, and in many ways clearly set it apart from the nation's other continental shelf ecosystems.

The purpose of this article is to review selected aspects of the oceanography of the Gulf of Maine important to biological productivity, highlighting in the process a few of the more important research questions facing scientists and environmental managers, and thus suggesting new avenues of research.

II. DOMINANT PHYSICAL PROCESSES IN THE GULF OF MAINE

A. The Influence of Slope Water

The Gulf of Maine is more of an enclosed body of water than the expose gulf its coastline implies (Figure 1). Its interior waters are to a large degree isolated from the open Atlantic Ocean to the south by Nantucket Shoals, Georges Bank, and Browns Bank, which greatly restrict flows into and out of the Gulf. The Northeast Channel, between Brown's Bank and Georges Bank, allows limited exchanges of deep waters between the Gulf and the continental slope. Influxes along the bottom of relatively warm, salty, and dense slope water replace outgoing surface and intermediate waters and spill into the three major basins inside the Gulf: Georges, Jordan, and Wilkinson. Each basin exceeds 250 m depth, but all are isolated from one another below 200 m. It is the Gulf's shape, with a deep channel and central basins, coupled with variations in pressure gradients inside and outside the Gulf, that produces this general, estuarine-like circulation patterns.[1-6] It is this influx of deep water into the basins of the Gulf of Maine that, for the most part, may represent the single most important physical process affecting the internal circulation and biological production of the entire region.[7]

As slope water flows into the Gulf of Maine through the Northeast Channel, it spills first into Georges and then the Jordan and Wilkinson Basins. The spreading of the warm, salty water responds to the Coriolis effect, as it hugs the Scotian Shelf, replacing more of the bottom water in Jordan Basin than in Wilkinson Basin in the western Gulf. Vertical profiles of temperature and salinity in these two basins show significantly more slope water in Jordan Basin as defined by the depth of the 34 ppt isohaline (Figure 2). The large-scale circulation in the Gulf of Maine is generally cyclonic, or counterclockwise, and is

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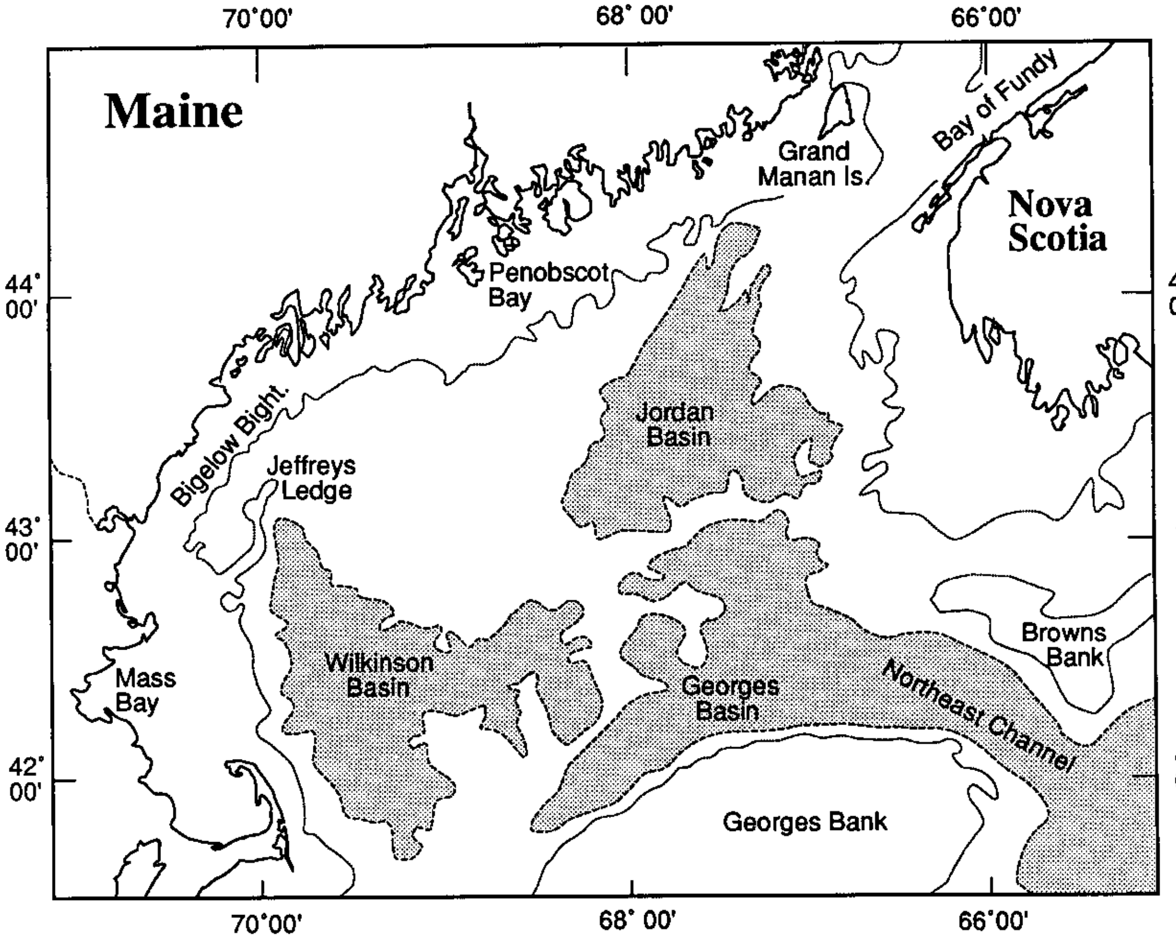

FIGURE 1. Map of Gulf of Maine showing the major features referred to in the text.

strongly baroclinic, reflecting the contrast between the dense slope water residing in the offshore basins and the fresher, tidally mixed coastal waters.[1,4] The contrast is reflected in the density field of the inner Gulf in Figure 3A where contours of dynamic topography suggest a general counterclockwise circulation pattern around the topographic lows with some evidence of separate gyres over the two northern basins, Wilkinson and Jordan. The intensity of the circulation around these lows reflects the relative volumes of slope water residing in each basin; the circulation over Jordan Basin is thus more energetic than in Wilkinson Basin. The density-driven residual circulation pattern for the region is shown in Figure 3B, as interpreted by Brooks.[4]

Although the importance of slope water to the mass balance and baroclinic circulation of the Gulf of Maine has been recognized for a long time,[1] we are gaining a greater appreciation of its variability and the resulting effects,[4] in particular the variable effects on the coastal circulation in the northeastern Gulf of Maine.[8,9] The eastern Maine coastal current represents the northern limb of the Jordan Basin gyre and transports the cooler, tidally mixed waters in the Grand Manan area down the Maine coast. A fraction of that current turns offshore as a plume of cold water in the vicinity of Penobscot Bay and enters a clockwise eddy over Jeffreys Bank (Figure 3), about halfway down the Maine coast; the remainder recirculates over Jordan Basin. This can be seen in the pattern of surface temperatures shown in Figure 4; during the warmer months,

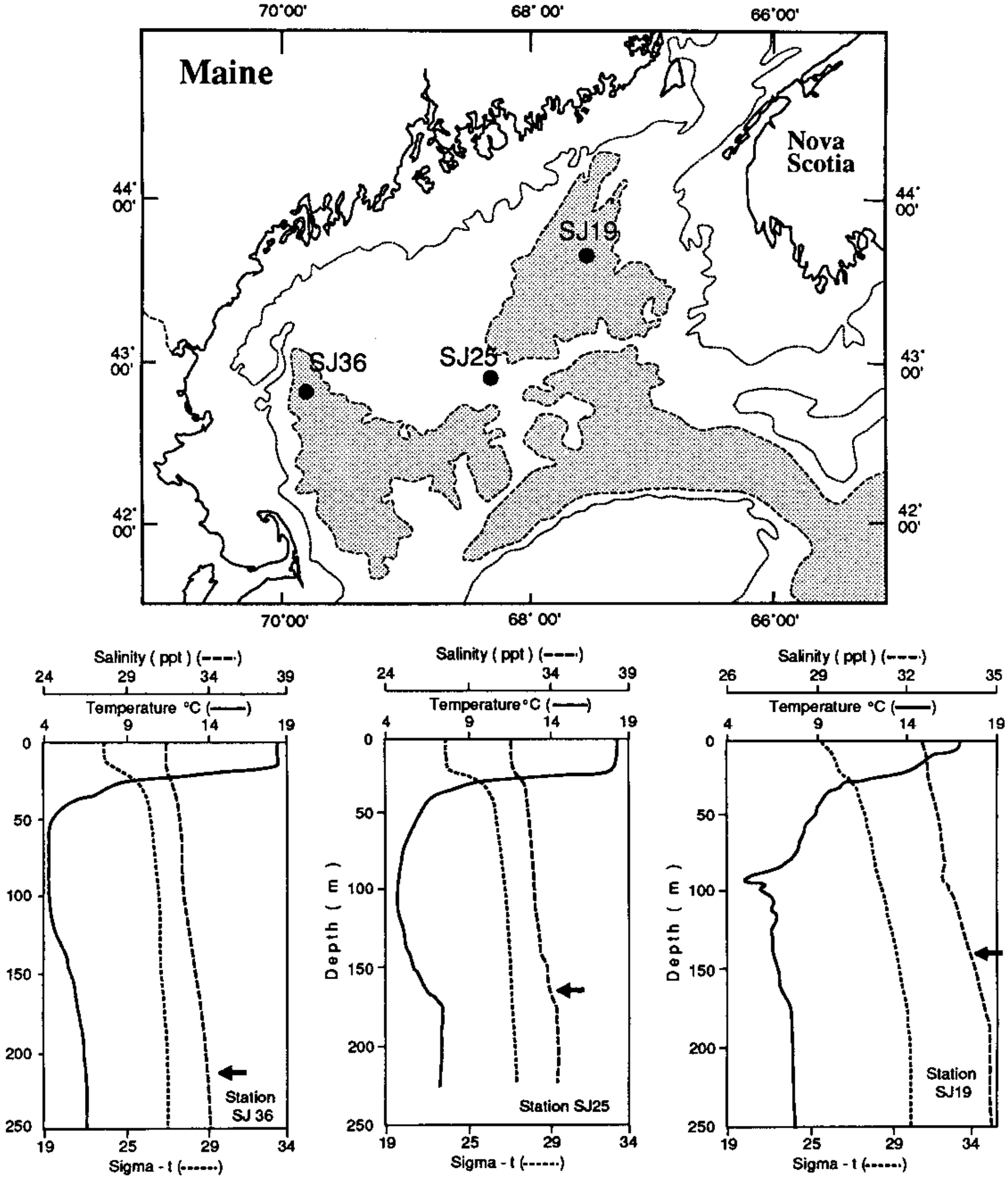

FIGURE 2. West to east differences in hydrographic structure of the offshore Gulf of Maine during summer as illustrated by vertical profiles of temperature, salinity, and density (σ_t) for three stations in the Gulf of Maine during August 1987 (data from *R/V Seward Johnson* cruise; Townsend, unpublished). The depth of the 34 ppt isohaline, which defines slope water, is indicated by an arrow; this water layer occurs closest to the surface in the eastern Gulf.

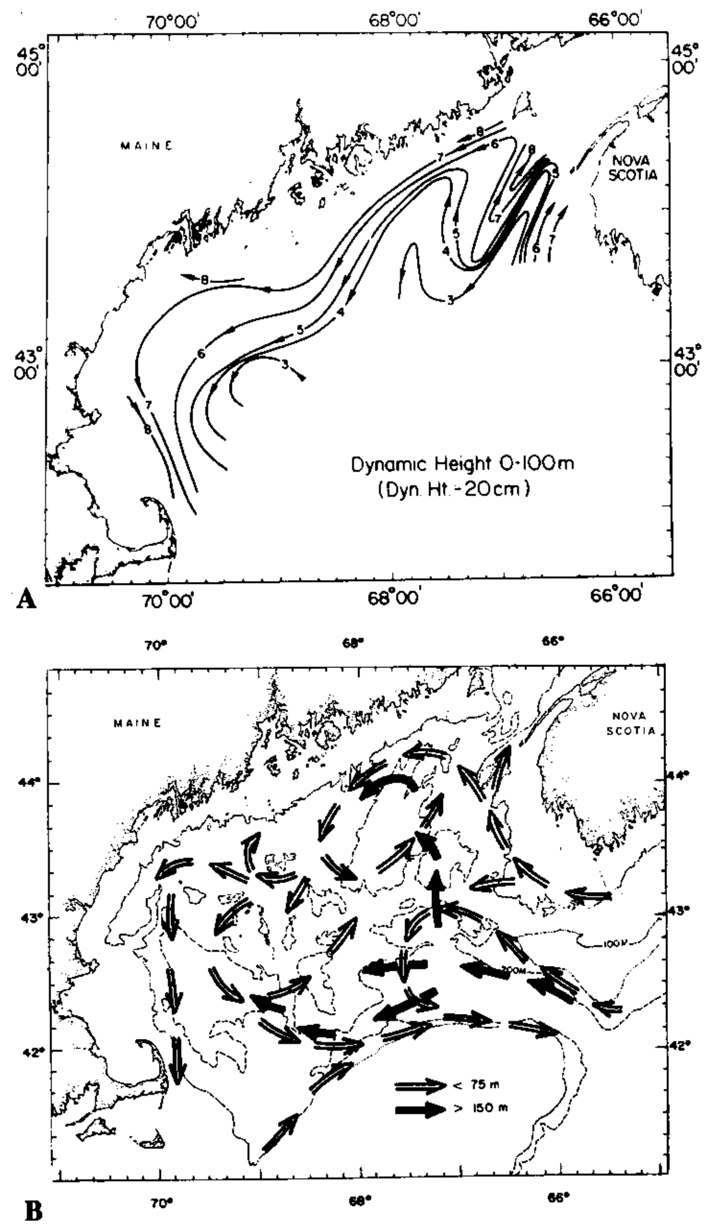

FIGURE 3. (A) Contours of dynamic height (calculated relative to a reference depth of 100 m) for the Gulf of Maine in July 1985 (from Townsend et al.[8]) and (b) the inferred residual circulation during the spring-summer period at the surface and at depth (from Brooks[4]).

this cool-water feature is clearly seen in satellite infrared images of sea surface temperature (Figure 5).

The influx of slope water through the Northeast Channel between 75 m and the bottom occurs in pulse-like events that may be correlated with the winter winds, but when time averaged, the transport appears to be seasonal, from a late-winter low to a maximum in early summer.[5] Reports of these inflow events have been few and anecdotal. Townsend and Spinrad[10] observed what appeared to be an anomalously greater volume

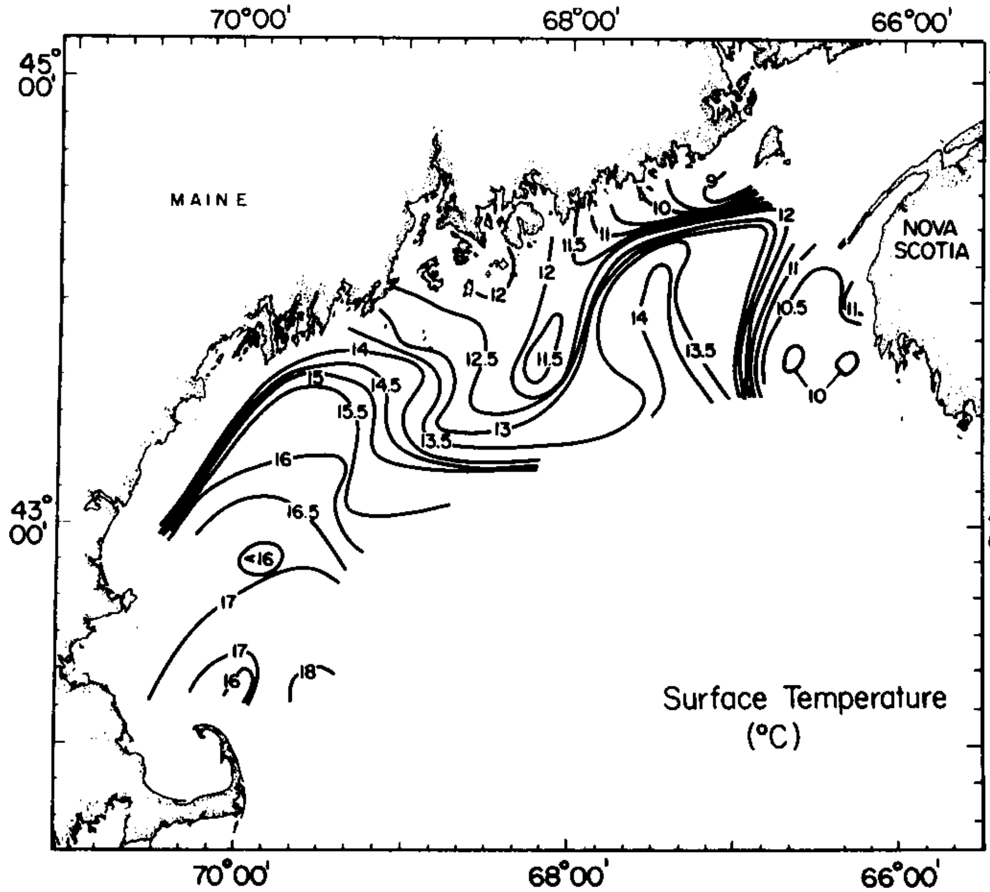

FIGURE 4. Cruise results from July 1985. (A) Contours of surface temperatures showing the advection of cooler, tidally mixed waters from the Grand Manan area down the Maine coast as part of the eastern Maine coastal current. The cooler water can be seen to turn offshore as a plume-like feature off Penobscot Bay. (B) Surface nitrate concentrations. (C) Nitrate concentrations per square meter integrated to 35 m. (From Townsend et al.[8])

of slope water in Jordan Basin in late March-early April 1984. The 34 ppt isohaline domed to within 116 m of the surface and produced a pycnocline between 90 and 100 m, which was shallower than the critical depth, and thus triggered an early spring phytoplankton bloom there. Citing a similar observation of enhanced doming of slope water in Jordan Basin by Cain,[11] and the concurrent observation by Fitzgerald and Chamberlain[12] of a large warm-core Gulf Stream ring just off the Northeast Channel, Townsend and Spinrad[10] suggested that Gulf Stream rings may be important in the episodic pumping of slope water into the Gulf. Brooks[13] provided the first account of the mechanism of Gulf Stream-slope water interactions by documenting a major inflow event apparently triggered when a ring streamer brushed against the mouth of the channel, forcing streamer-modified slope water to enter the Northeast Channel.

Brooks and Townsend[9] presented further evidence of the importance of episodic slope water intrusions in controlling the circulation in Jordan Basin and the coastal waters of the northern Gulf of Maine when they witnessed a redirecting of the eastern Maine coastal current, steered by the increase in baroclinicity caused by a greater influx of slope water into Jordan Basin. The influx of slope water and the resultant increased doming in the basin displaced the offshore departure point of the coastal current toward the east by about 100 km; the coastal current returned to its "nor-

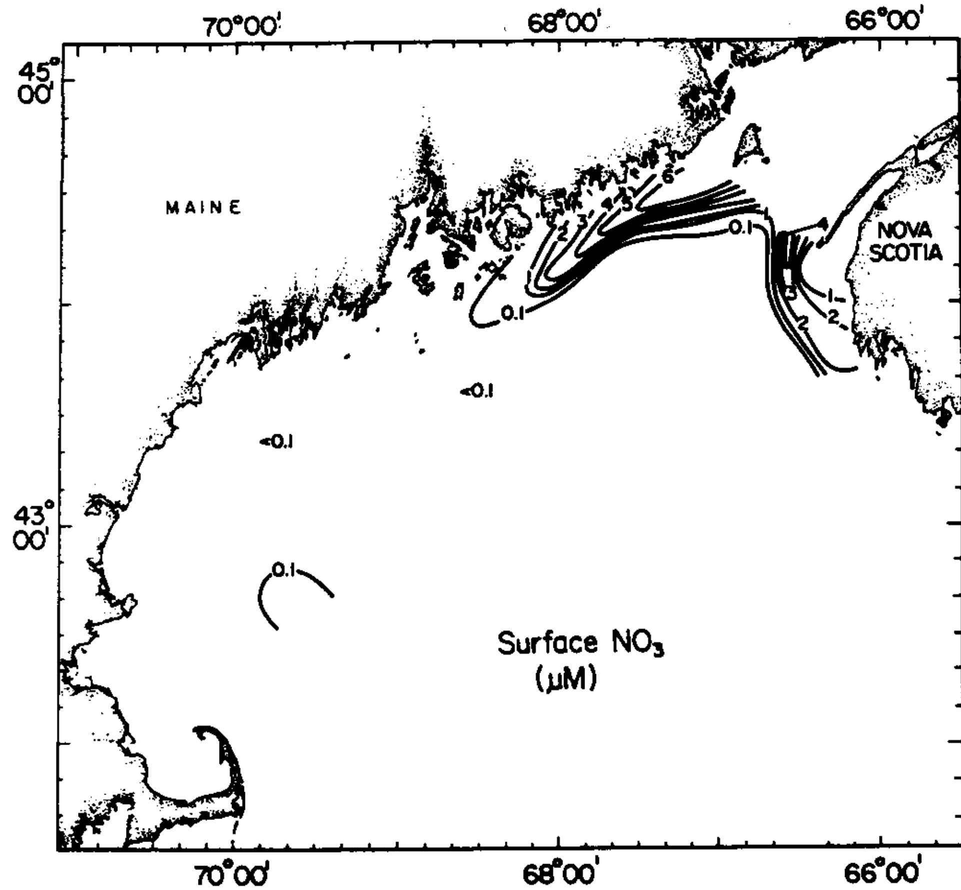

FIGURE 4B

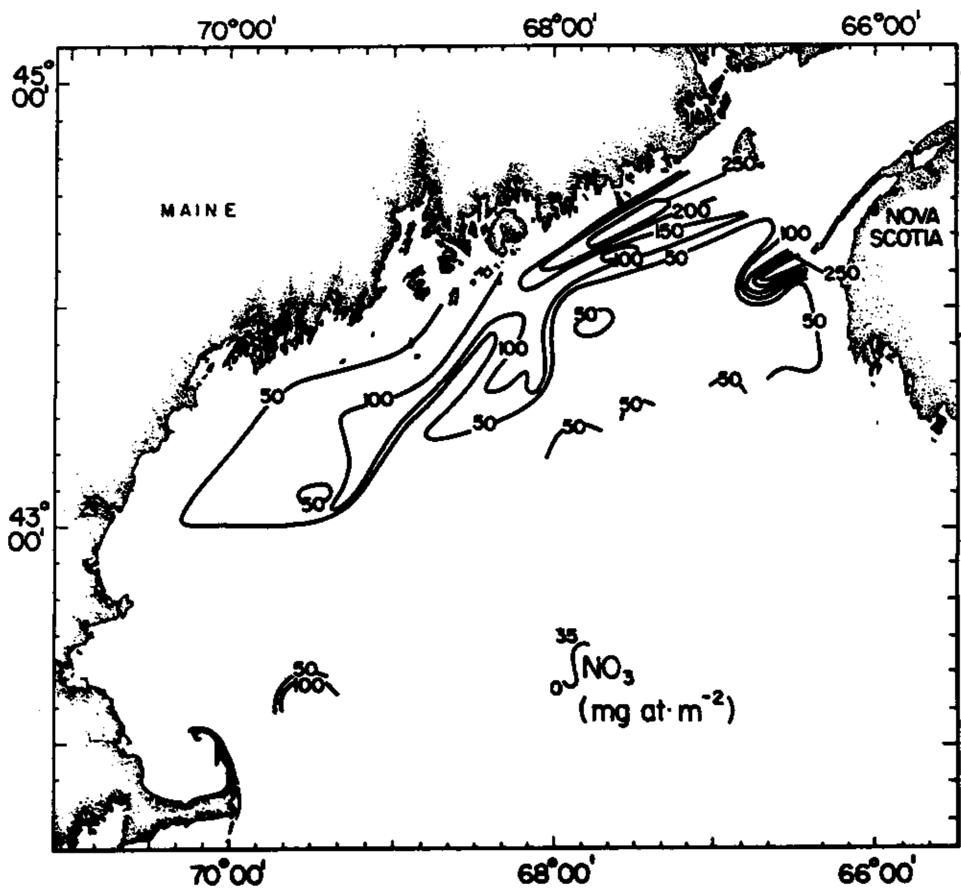

FIGURE 4C

FIGURE 5. AVHRR thermal satellite image of sea surface temperature in the Gulf of Maine on June 28, 1988. The darker shades correspond to cooler surface water temperatures. The tidally well-mixed areas with cooler surface water temperatures include the Maine coast and the eastern Maine coastal current/plume system, the Bay of Fundy and southwest Nova Scotian shelf, Browns Bank, Georges Bank, and Nantucket Shoals.

mal" position as the slope water spread to the west over the following 3-week period. A secondary, divergent upwelling of nutrient-rich waters resulted when the coastal current was "steered" offshore further east than normal.

Slope water represents the major source of inorganic nutrients to the Gulf of Maine[1] and has nitrate concentrations as high as 20 μM,[14] which underscores the biological significance of slope water dynamics, in addition to its importance in driving the residual circulation. It is clear that a proper understanding of the biological and chemical oceanography of the Gulf of Maine depends in turn on a more complete understanding of those processes that affect slope water entry and spreading throughout the Gulf. Most of the slope water-derived nutrients occur in the eastern Gulf, reflecting the proximity to the Northeast Channel source (Figure 6). Vigorous tidal mixing along the southwest Nova Scotian shelf and along the eastern Maine coast[15,16] is responsible for lifting some of this nutrient-rich water into the surface layers where it becomes part of the coastal surface circulation. This was demonstrated by Townsend *et al.*[8] for the eastern Maine coastal current and its ensuing offshore-directed plume (Figure 4). They calculated that about 44% of the nitrate entering with slope water through the Northeast Channel (based on concentrations reported by Schlitz and Cohen[17]) makes its way into the tidally mixed surface waters of Grand Manan area of the eastern Gulf, and thus is made

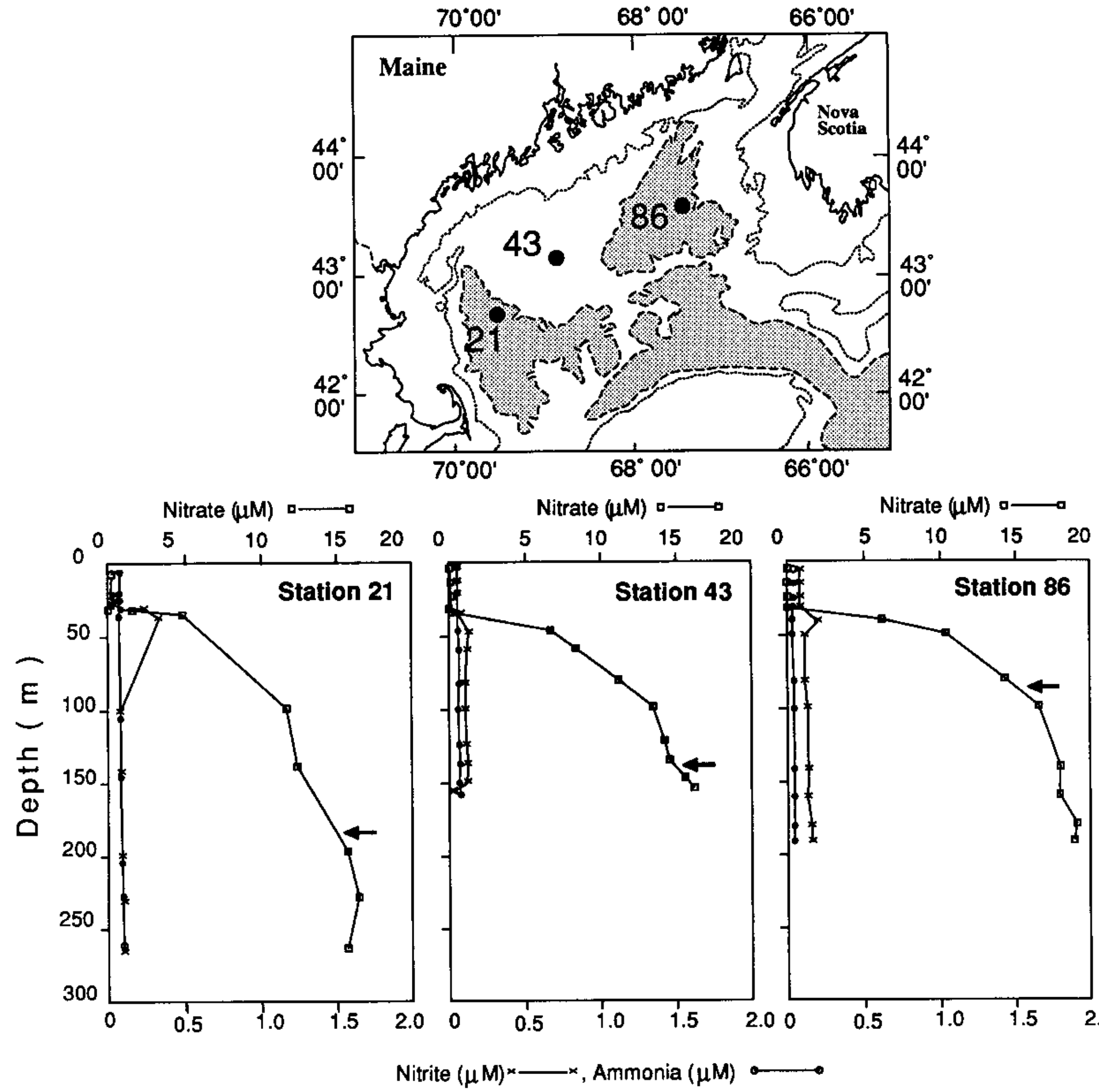

FIGURE 6. Vertical distributions of nitrate, nitrite, and ammonia from west to east in the offshore Gulf of Maine for three stations during July 1985 (data from Townsend and Christensen[14]). Notice the subsurface maximum in nitrite concentrations in the west, indicating nitrification in the intermediate water layer, and that the concentration of nitrate is greatest in the eastern Gulf, reflecting the proximity to the Northeast Channel, which is the slope water source for the Gulf. The arrows mark the depths of the 15 μM nitrate for each station.

available for biological uptake via the eastern Maine coastal current/plume. They demonstrated that the nutrients become depleted by phytoplankton uptake as the waters become increasingly stratified some distance downstream within the coastal current/plume system and that zooplankton then propagate in response to that bloom. The result is a chain of events transporting first dissolved, then particulate, nitrogen to the central and western Gulf of Maine, depending on the variable steering of those plume waters as affected by slope waters in Jordan Basin. Furthermore, Cammen[57] has documented the correspondence between the locations of these planktonic events in the coastal plume to the presence of phytoplankton-derived organic matter in the bottom sediments, which argues for a close coupling of benthic-pelagic processes associated with the coastal current/plume system.

B. Tidal Mixing

Because of the Gulf of Maine's morphometry it is in near resonance with the M2 tide and exhibits semidiurnal tides that range from about 2 to 3 m in Massachusetts, 5 m in eastern Maine, and >15 m in the upper reaches of the Bay of Fundy. These tides give rise to swift tidal currents that can, depending on the depth and bottom roughness, effectively mix the water column and prevent thermal stratification in the warmer months. The result is the maintenance of cool, tidally mixed areas throughout the shallower parts of the Gulf that are set apart by sharp thermal fronts from the warmer surface waters over the deeper, vertically stratified regions.[15,16,18,21] The tidally mixed regions of the Gulf of Maine include the southwest Nova Scotia shelf, Georges Bank, the eastern Maine coastal waters, and a narrower coastal band that surrounds the remainder of the Gulf;[16] these features are clearly visible in satellite imagery of sea surface temperature (Figure 5).

Tidal mixing in the Gulf of Maine[19] and the superposition of advective processes on tidally mixed waters[4,8,9,22] affect the overall distribution of less vertically stable waters and their high concentrations of inorganic nutrients. These patterns in turn dictate the spatial distribution of biological production in the Gulf,[1] particularly along the coast where the effects of tidal mixing are most important. The degree of vertical mixing and destratification of the water column can have important effects on phytoplankton production since mixing greatly influences the levels of the two main factors controlling photosynthesis: light and dissolved nutrients. A well-mixed, deep water column often restricts primary production because of light limitation. Nutrients, on the other hand, are usually in plentiful supply in mixed regions, being constantly renewed by a combination of upwelling and benthic regeneration. Yentsch and Garfield[21] suggested that the shallower mixed areas accounted for the majority of primary production in the Gulf of Maine. Stratified waters represent just the opposite situation from mixed waters, and cells tend to be retained in the upper mixed layer above the thermocline/pycnocline and hence are not light-limited. However, surface-water nutrients become rapidly depleted during the spring phytoplankton bloom, a brief period of intense production that begins with the onset of vertical stratification, which isolates phytoplankton cells in a surface layer of relatively high light and nutrient concentrations. After the bloom exhausts the available nutrients in the surface waters, the thermocline acts as an effective barrier to nutrient renewal from below during the remainder of the stratified season and phytoplankton standing stocks remain low throughout the summer. A compromise between the tidally mixed and stratified regions exists in the vicinity of the thermal fronts, where primary production may be enhanced due to the delivery of nutrient-rich deeper waters to an area of shallow stratification existing within the front itself.[8,23-25]

Production in stratified waters during the warmer months proceeds at a much reduced level, apparently confined to a subsurface phytoplankton chlorophyll maximum layer (SCM)[26,27] that derives its nutrients via diffusion through the seasonal pycnocline. Surface production levels are thus set by this diffusion rate and the level of nutrient recycling by the heterotrophs. Conversely, depending on depth and hence light limitation, the spring bloom in tidally mixed regions of the Gulf may exhibit only a muted increase in production, or one confined to only the shallower waters, but production in these shallow areas, as well as in the front, may persist throughout the warmer months.[8,21,25]

Thus, the Gulf of Maine may be characterized not only by regions that stratify or remain mixed by tides or advection of mixed waters, but also by regions that experience a spring bloom or maintain some persistent production level.[28] Considering only the Maine coast out to the 100 m isobath, the dividing line between these two extremes, as discussed above, falls roughly in the vicinity of Matinicus Island to the south of Penobscot Bay (Figure 1). To the east, the waters are more vertically isothermal and show little seasonal stratification, as opposed to the waters to the west that typically become stratified. Depending on the rate, duration, and a real extent of primary production in each region (i.e., comparing the relative importance of a spring bloom in waters that thermally stratify to more steady production in tidally mixed waters and frontal regions), one region may have a greater annual production than the other. Apart from the absolute level of production in each region, the temporal progression of production would also differ between them. It follows that the ensuring trophodynamics that transfer this carbon and energy up the food chain would differ as well, especially as these processes relate to pelagic-benthic coupling.

C. Water Mass Formations

One of the more important features produced in response to the Gulf's pattern of seasonal warming and cooling is the formation of distinct water mass layers. Each winter the Gulf undergoes intense cooling and buoyance extraction that leads to convective sinking of near-surface waters and overturn across the shallow seasonal pycnocline.[29] This vertical homogenization of the upper water column produces a uniformly cool and relatively freshwater mass that extends from the surface to the top of the dense bottom water layer, at about 150 m.[1,30] Such vertical mixing of the upper water column results in an upward delivery of deep nutrients, producing relatively high concentrations that often, in the early stages, initiates a fall phytoplankton bloom. The resulting nutrient concentrations in the upper water column in winter reach about 8 μM nitrate throughout the Gulf, with somewhat greater concentration in the bottom waters.[8,31]

Vertical stratification of the water column in spring and summer isolates a remnant of the previous winter's upper water mass to form a cold and somewhat fresh intermediate water layer sandwiched between a warmer, fresher surface layer and a relatively warm but salty bottom water layer of slope water origin.[30] The intermediate water layer is too deep to be warmed from the surface by solar insulation over the relatively short summer period and is sufficiently removed from the bottom to be tidally mixed.[30] This intermediate layer is colder and denser that the warm surface waters, but lighter than the warm, but salty bottom waters that enter from outside the Gulf (Figure 2 shows the intermediate water layer as a temperature minimum in the western Gulf). The intermediate waters serve as a trap for sinking carbon and nitrogen that has been biologically fixed at the surface, as reflected in the distributions of particulate maximum layers[32,33] and nitrite and ammonium maxima[26] (Figure 6), and is very likely important to the nutrient dynamics in the Gulf. The importance of this intermediate layer in nutrient cycling and to the ratio of new to recycled primary production remains unknown.

The greater volume of slope water in the eastern Gulf of Maine, as well as the greater tidal mixing, results in a more efficient erosion of the intermediate water layer in the eastern Gulf. Hopkins and Garfield[30] showed that the intermediate water layer is thickest and disappears latest from Wilkinson Basin and the western Gulf. This may become a clue to understanding the relative nature of nutrient dynamics in the eastern and western Gulf, as discussed later.

The three-layered system in the Gulf of Maine[30] further complicates the role of water mass exchanges between the Gulf and the open Atlantic in the Gulf-wide nutrient budget. The intermediate water layer is a site of significant nitrification (note the nitrite maximum in Figure 6) as organic matter from above is decomposed in transit to the bottom.[26] Much of the waters that exit the Gulf through the Northeast Channel are from the intermediate water layer, and thus while slope water intrusions provide the bulk of new nitrate entering the Gulf, some internally recycled nitrate, as well as particulate and dissolved organic carbon, may be exposed to the slope.

D. Freshwater Runoff

Numerous rivers of various sizes enter along the northern coastline of the Gulf, resulting in a significant spring freshet each year. This freshwater runoff is important to setting up the coastal circulation in spring[1,4] and in imparting stratification to nearshore waters which may be important for the initiation of inshore phytoplankton blooms.[10] Most of the freshwaters emptying from the rivers hug the coast in response to the Coriolis effect and flow into the western Gulf. The surface waters of the western Gulf typically are fresher and, in summer, significantly warmer than the eastern Gulf. In addition, a significant source of freshwater enters the Gulf around southwest Nova Scotia as relatively cold Scotian Shelf water,[34] which also contributes to horizontal property gradients and can affect the circulation in the eastern Gulf of Maine by providing a sharp contrast with the more dense waters residing offshore in Jordan Basin.

III. NUTRIENT SOURCES AND BIOLOGICAL PRODUCTION

There are only a few published accounts of the rates of primary production in the Gulf of Maine. The most complete set of measurements is provided by O'Reilly and Busch,[35] who reported an average annual rate of primary production of 290 g C m^{-2}. This compares to their estimates of 300 to 470 g C m^{-2} for Georges Bank. It is interesting to note that estimates of zooplankton production are greater for the Gulf of Maine than on Georges Bank, despite lower levels of primary production.[36]

By building upon the above discussion of the physical workings of the Gulf of Maine, we can perhaps add some insight into the rates of primary production as they might vary seasonally and spatially in response to the nutrient dynamics. Such exercises can be instructive since a more complete understanding of the spatial/temporal nature of nutrient fluxes might, in turn, help to explain the apparently significant difference in the nature of plankton trophodynamics that led to the observed differences in zooplankton production between the Gulf and Georges Bank, and add to our understanding of processes affecting fisheries production.

A. Nutrient Fluxes

The data available to undertake an evaluation of nutrient fluxes in the Gulf of Maine are by no means complete, but are certainly adequate for this overview. Much of the information stems from a review by Schlitz and Cohen,[17] who presented a useful compilation of data and calculations to produce an annual nutrient budget for the Gulf. Taken further, we can see that the timing and locations of these nutrient fluxes may hold important implications for the ensuing trophic dynamics.

Fluxes of nutrients into the euphotic zone of the Gulf of Maine can be placed into a number of categories: winter convective overturn, vertical eddy diffusion through the seasonal pycnocline, coastal upwelling, the eastern Maine coastal current/plume system (also the result of upwelling), and recycled production. The relative contributions of each of these to the total annual primary production estimate of O'Reilly and Busch[35] are discussed briefly in the sections that follow.

1. Winter Convective Overturn

The level of nutrients available for the spring phytoplankton bloom are the result of vertical overturn the previous winter; this homogenizes the water column from the surface down to about 150 m, or to the top of the slope water layer offshore. This produces a nutrient (nitrate) field in winter on the order of 8 mg-at NO_3-N m^{-3} (or 8 μM) over the upper water column.[37] Assuming that the spring bloom develops when thermal stratification caps off the top 35 m, and that the area of the Gulf of Maine, excluding Georges Bank, is approximately 1.03×10^{11} m^2, this then provides 2.8×10^{10} g-at NO_3-N, or 3.9×10^{11} g N available for primary production. Applying the Redfield ratio of 6.625 for C:N gives an estimate of new primary production in the spring bloom of 26 g C m^{-2}. This assumes that the phytoplankton bloom exhausts the nutrients in the mixed layer above the thermocline and that there is no renewal during the bloom period.

2. The Eastern Maine Coastal Current/Plume System

Townsend *et al.*[8] have estimated the flux of nitrate into the surface waters of the inner Gulf via this system by taking an average nitrate concentration at the origin of the coastal current/plume in the east (approximately 5 mg–at

NO_3-N m^3) multiplied by the volume transport of plume waters to arrive at a flux of 1.51 × 10^{11} mg-at NO_3-N d^{-1}. Assuming that this process is important to primary production over 9 months of the year, when light is not limiting, gives a flux of 5.7 × 10^{11} g NO_3-N. Dividing this value by the approximate area of the inner Gulf of Maine (inside a line from Cape Cod to Nova Scotia; 57,500 km^2) and again applying the Redfield ratio gives a level of new primary production of 56 g C m^{-2} 270 d^{-1} for the inner Gulf, or 36.6 g C m^{-2}, averaged over the entire Gulf of Maine.

3. Vertical Eddy Diffusion

The upward flux of nutrients across the pycnocline fuels the surface chlorophyll maximum (SCM), which is a pervasive feature throughout the stratified regions of the Gulf during the warmer months of the year. Though extremely difficult to measure, the upward diffusion of nutrients to the SCM can be estimated based on the one-dimensional Fickian diffusion equation,[38-42]

$$F = K_z \, dNO_3/dz$$

where F is the nitrate flux, K_z is the vertical eddy diffusivity, and dNO_3/dz is the nitrate concentration gradient with depth, z. This estimate is highly sensitive to the choice of the vertical eddy diffusivitiy, K_z, which can be approximated using the empirical relation of King and Devol,[40]

$$K_z = 643\,(10^6\,E)^{-1.61}$$

where $E = d(\sigma_t)/dz \times 10^{-3}$. This equation gives a typical value for K_z in the offshore waters of the Gulf, using data in Townsend and Christensen[14] for the summer months, of approximately 0.3 $cm^2\,s^{-1}$, or $0.3 \times 10^{-4}\,m^2\,s^{-1}$; a typical value for dNO_3/dz = approximately 0.5 mg-at NO_3-N $m^{-3}\,m^{-1}$. This gives a nitrate flux (F) of 1.5 × 10^5 mg-at NO_3-N $m^{-2}\,s^{-1}$, or 1.29 mg-at N m^{-2} d^{-1}. Multiplying by the area of the Gulf and applying the Redfield ratio gives a potential new primary production of 0.12 g C $m^{-2}\,d^{-1}$, or 32 g C m^{-2} $year^{-1}$ (270 d).

Again, this estimate is extremely sensitive to the selected value of K_z. It could be argued that the eddy diffusion coefficient should be compartmentalized with regard to both season and area, since the estimate of $K_z = 0.3 \times 10^{-4}$ is calculated for stratified stations during summer. The values of K_z and dNO_3/dz will, in fact, be quite different around the Gulf depending on season and location. For instance, values of K_z during summer range from 5.1×10^{-4} in the eastern Gulf near the plume, to 0.3×10^{-4} in the basins, to 0.1×10^{-4} nearshore in the west, and 0.7×10^{-4} off Penobscot Bay and over Jeffreys Bank, etc. Previous workers have used values $\geq 1 \times 10^{-4}$. Garside[42] used $K_z = 4 \times 10^{-4}\,m^2\,s^{-1}$ for open ocean flux calculations based on information in Denman and Garrett.[41] Loder and Platt[43] used 1×10^{-4} for the North Sea, basing their number on results from Pingree and Pennycuick[44] for the English Channel. The point here is that each of the latter estimates gives greater rates of vertical flux than one based on $K_z = 0.3 \times 10^{-4}$. If we use a value of $K_z = 1 \times 10^{-4}$, we arrive at an estimate of new primary production in the SCM in the Gulf of Maine of 108 g C m^{-2}.

Although primary production in the SCM layer is limited by both lower subsurface light levels and by nutrients, which must diffuse upward, it is possible, as the previous estimate suggests, that the SCM is much more productive than generally thought and that it is not the static, elevated-biomass feature sitting atop the pycnocline as it first appears. When associated with frontal regions where the pycnocline is sloped, there can be a shallow baroclinic current along the frontal boundary as well as strong current shears on either side of the front and between the surface and deeper water layers.[9] This is particularly true for tidal fronts, where there is evidence of upwelling between the vertically well-mixed region and the stratified region, causing the sea surface slope to be depressed along the front, and producing a current shear along the front on either side. The result is that the increased phytoplankton standing stocks we see in the SCM in these regions occur despite being constantly eroded and carried away from the point of production by these shallow currents. This then suggests that the SCM is quite dynamic and productive, and could be critical to explaining the differences in style of secondary production between the seasonally stratified Gulf of Maine and the tidally well-mixed Georges Bank.

4. Coastal Upwelling

Graham[45] has argued that coastal upwelling is the most important physical process operating in Maine coastal waters. Quantifying it is difficult, but we can arrive at its relative magnitude by first considering estuarine upwelling and then boldly assuming that Eckmann upwelling is of the same order. Upwelling at the mouths of Maine's estuaries can be based on an average annual freshwater discharge into the Gulf of 95 km^3 $year^{-1}$ [46] and a crude salt balance argument whereby the seaward extension of the estuaries has a salinity of roughly 1.5 to 4 ppt less than the source salinity of about 33 ppt. Therefore, from 8 to 22 times as much Gulf of Maine source water as freshwater mixes at the mouths of the estuaries (Dyer,[47] for instance, uses an average dilution factor of 19). If the source waters are from 20 to 30 m depth, as is the case in the Shepscot River estuary,[48] and the source nitrate concentrations are those of Maine Intermediate Water (5 to 8 mg-at NO_3-N m^{-3}), then we can estimate the new primary production to be 8.3 $\times 10^{11}$ g C $year^{-1}$; averaged over the entire area of the Gulf, this converts to about 8 g C m^{-2} $year^{-1}$, which is very little. However, if viewed as local primary production restricted to the very small areas of the estuaries and waters immediately offshore, this level of production appears very important.

It is interesting to speculate here. Most of the freshwater runoff in Maine occurs in April, which is after the early spring phytoplankton bloom triggered simply by increasing daylength and controlled by bathymetry.[10] This could mean that an early bloom can continue longer in some cases when runoff occurs earlier than normal, thus providing a secondary source of nutrients, or it can cause a second bloom that spring, which is what appears to happen.[49,50]

On a Gulf-wide scale, the estuaries appear to be unimportant to the total fisheries production in the Gulf of Maine, but if we apply their local production to serve the needs of only a select group of consumers, perhaps a particular life his-

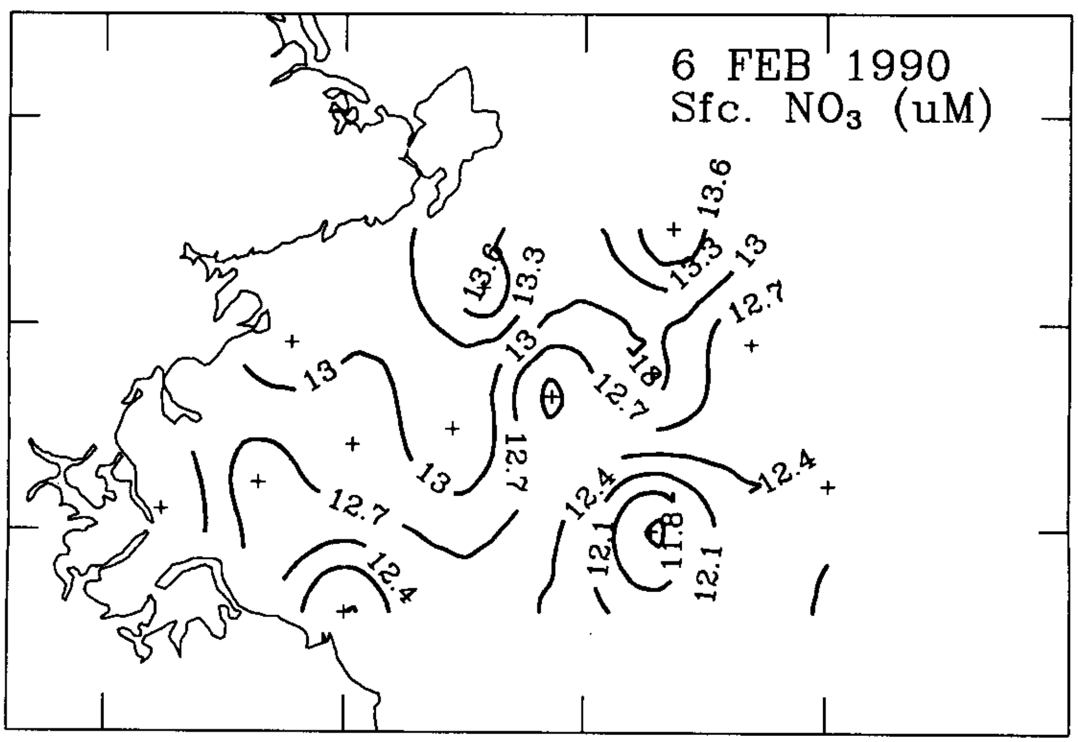

FIGURE 7. Contours of surface nitrate concentrations in northern Massachusetts Bay on February 6, 1990 (from Townsend et al.[56]). Concentrations were nearly uniform with depth throughout the well-mixed water column. Note the highest concentrations at the northeasternmost stations.

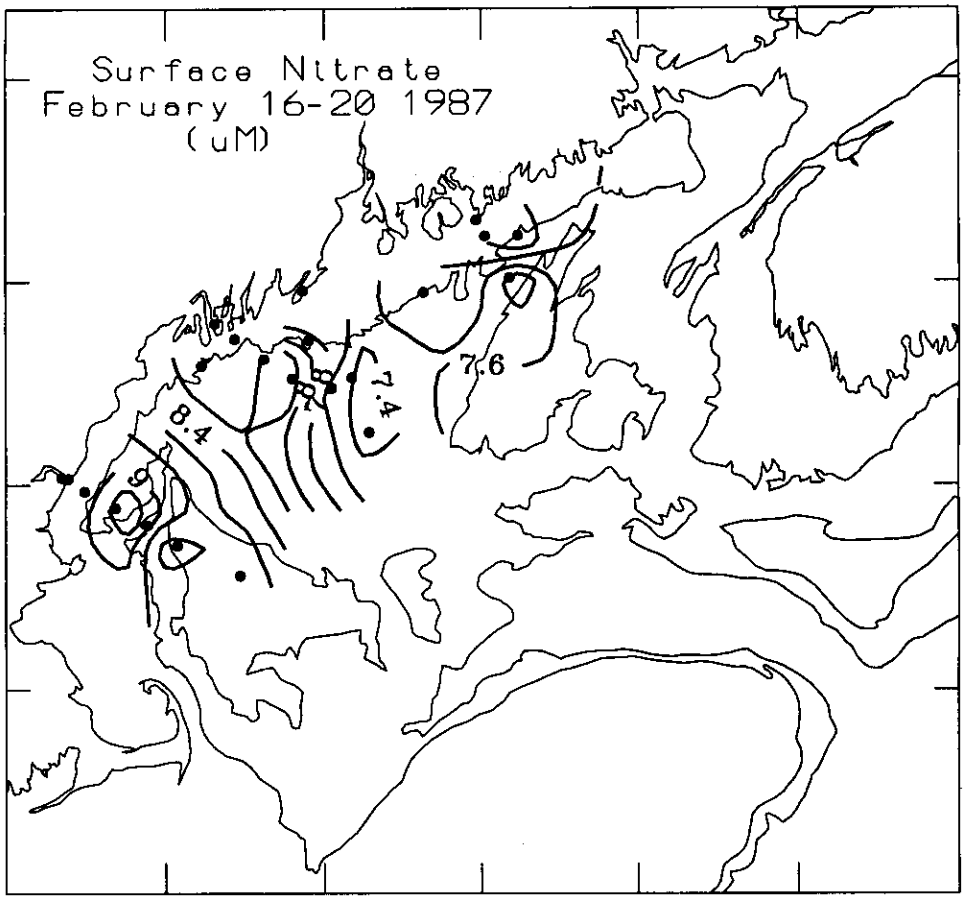

FIGURE 8. Contours of surface nitrate concentrations in the Gulf of Maine during February 16 to 20 1987 (from Townsend et al.[37]). Concentrations were nearly uniform with depth throughout the well-mixed water column. Note the highest nitrate concentrations in the western Gulf over Bigelow Bight and Jeffreys Basin. The 100 and 200 m bottom contours are given.

tory stage such as the juveniles of certain commercial species, then one could make a strong argument for the importance of the intense production at the mouths of the estuaries in supporting nursery areas, even though they represent only a very small fraction of the total Gulf of Maine production.

In addition to Graham's[45] study of upwelling on the Maine coast, Denman and Herman[51] and Garrett and Loucks[52] have demonstrated significant upwelling on the southwestern Nova Scotian shelf. Lauzier[53] showed that the bottom currents were about 2 cm^{-1} shoreward there. It appears, as summarized by Denman and Herman,[51] that "the supply of nutrient-rich slope water onto the continental shelf in the eastern Gulf of Maine and the subsequent phytoplankton production are most likely controlled by a combination of centrifugal upwelling, wind events and tidal mixing." It is difficult to assign a value to the upwelling of nitrate here, but as a first guess we can assume it is of the same order as that upwelling in the Grand Manan area, i.e., 57 g N $year^{-1}$, giving rise to a new primary production of 36.6 g C m^{-2} $year^{-1}$ (if averaged over the entire Gulf).

5. Recycled Production

King et al.[54] used an enzyme method to estimate recycling of nitrogen by a number of size

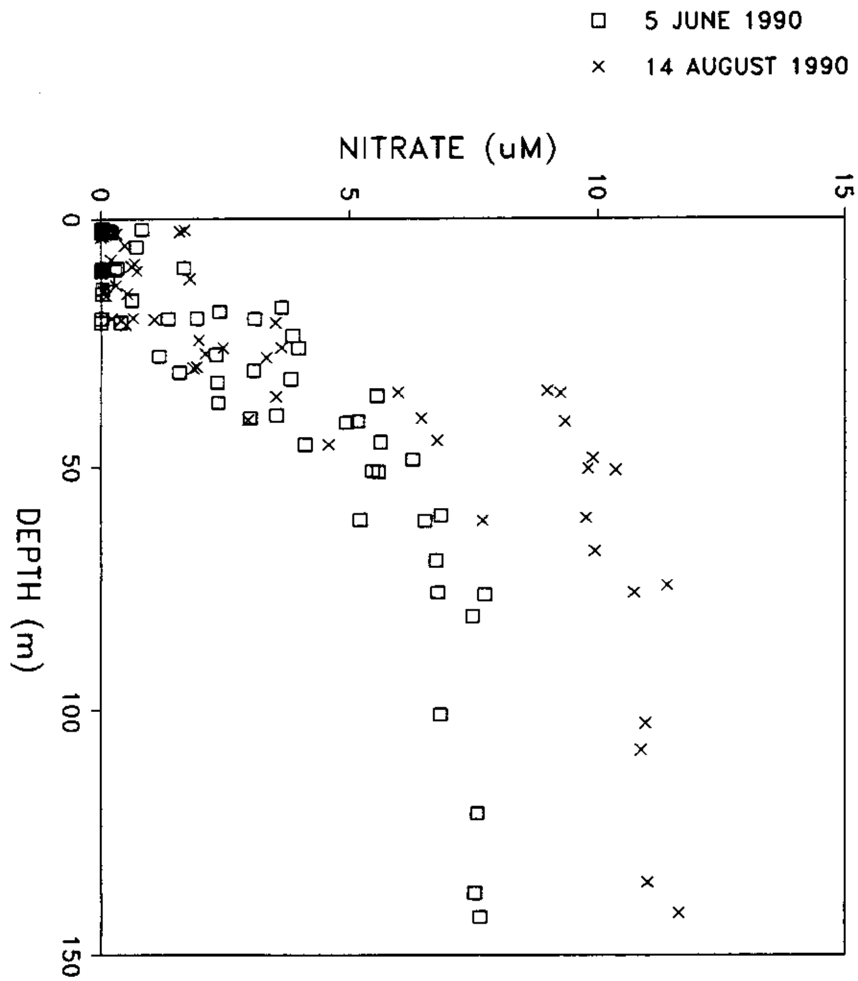

FIGURE 9. Nitrate concentrations as a function of depth for the Massachusetts Bay area shown in Figure 7, in June and August 1990 (from Townsend et al.[56]). Note the higher nitrate concentrations at depth in August. Those higher concentrations were from the northeasternmost stations, suggesting an influx of higher nutrient waters from the north.

fractions of zooplankton at a few summertime stations in the Gulf of Maine. They calculated an average recycling rate of 0.622 mg-at N m^{-2} d^{-1} for the inner Gulf stations, which converts to a primary production level of about 16 g C m^{-2} $year^{-1}$. Schlitz and Cohen[17] have also presented estimates of recycled production levels in the Gulf of Maine, but using relations in Vidal and Whitledge[55] in which between 0.42 and 0.71 μg-at N/mg dry weight of zooplankton per day is regenerated. A mean zooplankton biomass of approximately 7.85 g dry weight m^{-2} for the Gulf of Maine[17] gives about 1.18 g-at N m^{-2} 270 d^{-1}, or a corresponding primary production of about 110 g C m^{-2} $year^{-1}$, which is quite a bit greater than King et al.[54] measured using an enzyme assay. King et al.[54] did not effectively sample the larger copepods in their study, such as *Calanus finmarchicus,* however, which would mean that recycled production was underestimated. It is possible that the true value lies closer to that predicted by Schlitz and Cohen.[17]

6. A Nutrient Trap in the Western Gulf

There are limited data showing that winter nutrient levels are sometimes highest in the Bi-

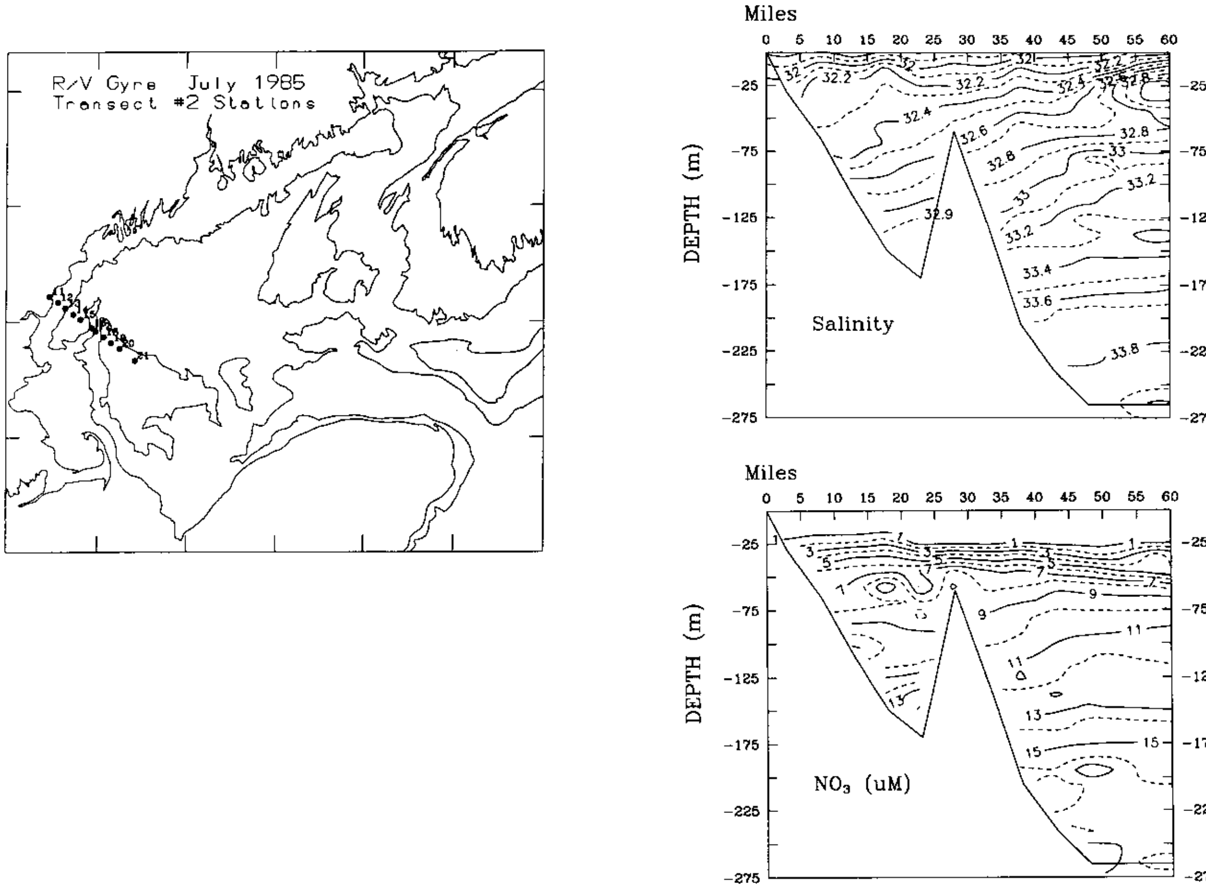

FIGURE 10. Vertical sections of salinity and nitrate for a transect from the coast across Bigelow Bight, Jeffreys Basin, Jeffreys Bank, and the offshore Gulf of Maine (from Townsend and Christensen[14]). Note the elevated nitrate concentrations at depth in Jeffreys Basin, which do not correspond with the nitrate concentrations at similar salinities offshore.

gelow Bight portion of the western Gulf (Figure 1) — far removed from the suspected slope water source in the eastern Gulf [37,56] (Figures 7 and 8). These high nutrient concentrations could result from a nutrient trap that may be operating in the western Gulf of Maine, particularly the Bigelow Blight-Jeffreys Basin area, whereby nutrient recycling at depth acts in concert with the overlying surface flow of productive waters. The evidence comes from Townsend et al.,[56] who have shown that relatively high-nutrient waters appear to enter Massachusetts Bay from the north both in winter (Figure 7) and in summer (Figure 9), but those high-nutrient waters did not reflect an influx into Massachusetts Bay of bottom water of immediate slope water origin.[56] In addition, earlier survey work in this area[14] has shown that the higher nutrient concentrations in the deeper waters of Bigelow Bight in summer (Figure 10) were not associated with higher salinity waters, again suggesting that slope waters are not the direct source. The nutrient trap that may account for these elevated nutrient concentrations operates as carbon and nitrogen are biologically fixed in the surface waters over the western Gulf and, in particular, Bigelow Bight. As these waters flow in a general southwest direction along the coast, the biogenic particles sink to the more sluggish waters beneath where the nitrogen is regenerated, thereby enriching the deep waters over time. Surface nutrient concentrations in the Gulf during winter are thus often greatest here as a result of vertical convective mixing with the deeper, nitrogen-enriched waters in Bigelow

TABLE 1
Summary of Nitrogen Sources and Resulting Rates of Primary Production in the Gulf of Maine

Nitrogen source	Resulting primary production (g C m^{-2} $year^{-1}$)
New nitrogen	
Winter convective overturn	25.2
Eastern Gulf plume	36.6
Vertical eddy diffusion	32.3—108
Upwelling	
Coastal Maine	
Estuarine	8.0
Eckmann	8.0
Southwest Nova Scotia	36.6
Recycled nitrogen	16—110
Total primary production	162—364

Bight. These waters appear to escape the area throughout the year and flow to the south, thus affecting the nutrient budget of Massachusetts Bay. Furthermore, depending on the nature of the coastal currents, as discussed above, as well as interannual variability in freshwater runoff, there may be significant interannual variability in the level of nutrients accumulating at depth. Because of the present uncertainties in the exact nature and variability of this nutrient trap in recycled primary production in the Gulf of Maine, it is not included in the the production estimates reported here.

B. Estimated Primary Production

The above-estimated primary production rates based on nutrient fluxes in the Gulf of Maine are summarized in Table 1. These estimates of primary production give a wide bracket to the measurements of O'Reilly and Busch[35] of 290 g C m^{-2} $year^{-1}$, which does not help to redefine the Gulf's overall biological productivity; however, this exercise is valuable in that it points to the times and places where primary production is important and it helps to illuminate those aspects of the biological oceanography where we lack information. Two areas most in need of further research as revealed here relate to the level of primary production resulting from vertical diffusion and that resulting from recycling, each of which can have important ramifications for the nature of the ensuing trophodynamics.

IV. CONCLUSIONS

The oceanography of the Gulf of Maine is made up of a complex assortment of physical processes that drive water mass exchanges with the open Atlantic, and drive the vertical mixing and residual circulation inside the Gulf. Superimposed on these is the seasonal warming and cooling of the upper water column. All of these processes act to control primary production in subtle but very important ways, many of which we know very little about. The relative proportions of primary production consumed by secondary producers in the water column vs. the benthos, for example, will depend on where and when there is significant primary production.

Our examination of production during the summer stratified season strongly suggests that it is higher than we might have at first assumed, due to what may be a high rate of production within the SCM, as a result of increased vertical diffusion of nutrients, especially in frontal regions where current shears are important. In some ways, this might have been expected since there is evidence of higher zooplankton aggregations and presumably increased grazing in these layers. It is also likely that the source of nutrients that diffuse upward throughout much of the western Gulf, at least, derive from nitrification in the intermediate water layer, where a subsurface nitrite maximum is commonly observed. Further support of the idea of significant nitrification and the importance of nutrient recycling in the Gulf of Maine is revealed in the unbalance between the nitrogen supplied through the Northeast Channel and both the estimated and measured rates of primary production reported here. The nitrogen flux through the Northeast Channel can account for only about 85 g C m^{-2} $year^{-1}$, [8,17] leaving the remainder to be driven by recycled nutrients. Moreover, we can speculate that nitrification and nutrient recycling are more important in the western Gulf of Maine which typically exhibits greater standing stocks of zooplankton.[8]

The message here is that an increased understanding of the biological oceanography of the Gulf of Maine and the variability in its commercial fisheries, for example, will depend on future research efforts that take an interdisciplinary approach to the problems touched upon here.

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