FLUX OF ENERGY AND ESSENTIAL ELEMENTS THROUGH
THE CONTINENTAL SHELF ECOSYSTEM

PROGRESS REPORT

MASTER

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Table of Contents

I. Scope of the Research of the Past Three Years	1
Abstract	1
1. Cooperative studies of Gulf Stream intrusions	2
1.1 The research program	2
1.2 The physical regime	3
1.3 The planktonic community	4
1.4 Analysis of microbiological methods	6
1.5 GABEX I	11
1.6 EASTWARD Cruise E3B-79	16
1.7 R/V GILLIS Cruise, April 19-May2, 1979	20
1.8 R/V ISELIN Cruise, April 24-25, 1978	25
1.9 R/V ISELIN Cruise, August 3-10, 1978	25
2. Coastal fronts	27
2.1 Cooperative front study, May 9-12, 1978	28
2.2 FRNFLX I, November 6-9, 1979	32
3. Microbial populations and the detritus food web	37
3.1 Methods of microscopy	38
3.2 Utilization of dissolved substrates by bacteria in Gulf Stream intrusions	39
3.3 Interactions of populations of free bacteria, attached bacteria, and aggregates	40
3.4 Production of fecal aggregates	42
3.5 A simulation model of the shelf ecosystem	42
4. The effect of copper on photosynthesis of marine phytoplankton	69
Literature cited	70
5. Publications and reports resulting from this contract	74
Appendix: reprints and preprints of publications	
Jacobsen, T. R. 1978. A quantitative method for the separation of a and b from phytoplankton by high pressure liquid chromatography.	
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- Jacobsen, T. R. (in press). Comparison of chlorophyll a measurements by fluorometric, spectrophotometric, and high pressure liquid chromatographic methods in aquatic environments.
- Berman, T. (ms.) Phosphorus uptake by microplankton in estuarine and coastal shelf water near Sapelo Island, Ga., U. S. A.
- Berman, T., R. B. Hanson, and W. J. Wiebe (ms.). Effects of organic substrate addition on size partitioning and respiration of 'single' versus clumped or 'attached' marine bacteria.
- Wood, A. M. and D. W. Evans (ms.) Copper chelating capacity in the Sargasso Sea and on the continental shelf of the southeastern United States.

I. Scope of the Research of the Past Three Years

Abstract

There are three distinct but not mutually exclusive areas of research in this contract, studies of intrusions of the west wall of the Gulf Stream onto the outer continental shelf, studies of the flux of materials across near-shore density fronts, and advances in our understanding of the planktonic food web of the continental shelf. Our studies of frontal events on the outer and inner continental shelf involve distinctive physical and chemical regimes and have proven to require distinctive biological approaches. The studies of the food web run through our work on both of the frontal regimes, but certain aspects have become subjects in their own right. We have developed a simulation model of the flux of energy through the continental shelf food web which we believe to be more realistic than previous ones of its type. It represents realistically both details of the energy transfers within the plankton community and the terminal production of fishes. In a serendipitous, almost accidental way, we discovered that the fecal ribbons of pelagic tunicates break up into flocculent material visually and chemically identical with the flocculent organic aggregates present in sea water. Subsequent experimental work with tunicate fecal matter indicates that some of the naturally occurring aggregates are indeed fecal. This makes it possible to understand and quantify for the first time the production and fate of that population of seston. We have examined several of the many roles of dissolved organic compounds in sea water which originate either from release by phytoplankton, digestive processes or metabolites of zooplankton, or extracellular digestion of microorganisms. We have found that the uptake of dissolved materials, in this instance represented by dissolved adenosine triphosphate, is nearly proportional to bacterial biomass, and that free-living minibacteria and large bacteria attached to particles are equally active in scavenging that material from the water. Many naturally occurring dissolved organic compounds are chelators of heavy metals, and it has been realized for some time that much of the total metal content of sea water is in a chelated form. This would have a significant effect on the toxicity of metals to plankton. Methods have been developed under this contract to measure both the chelating capacity of naturally occurring organic materials and the copper concentration in the water. Using these methods in

conjunction with the Schindler modification of the ^{14}C method of measuring photosynthesis, it has been possible to characterize the effects, both toxic and stimulatory, of copper on photosynthesis of naturally occurring phytoplankton populations.

Our understanding of biological, as well as physical and chemical, events on the outer continental shelf is now on a firm basis. Thanks to our knowledge of the physical forcing of the regime by the west wall of the Gulf Stream, it is possible to characterize in considerable detail the course of biological events associated with meanders of the Gulf Stream. Although there are a number of variations on the theme, the general course of events is a predictable one. We are now in a position to explain the limits to biological productivity of the outer continental shelf of the southeastern U.S. and the reasons why that biological production moves through the food web in the characteristic way that it does.

1. Cooperative Studies of Gulf Stream Intrusions

1.1 The Research Program

During the past three years we have participated in five cooperative studies of intrusions of nutrient-rich water from the cold wall of the Gulf Stream over the outer continental shelf off Georgia and northern Florida. On four of these occasions the scientific party included physical oceanographic contractors as well as other biological DOE contractors and ourselves. This cooperative work between physical and biological oceanographers has contributed significantly to the success of the biological research program. We have been able to find the physical events we are seeking with minimal loss of valuable ship time. The use of infrared imagery from weather satellites, processed and relayed from Miami (RSMAS), was particularly helpful not only in determining the position of the Gulf Stream but in finding intrusions from the west wall of it, so the ship could be positioned in advance of a northward-moving eddy. This permitted us on several occasions to obtain daily observations of the succession of planktonic populations as an intrusion event arrived and was subsequently drawn back over the shelf break. We have, of course, learned the basic pattern of events from the physical oceanographers, and on EASTWARD cruise E1B-79 we were readily able to locate and follow an intrusion off Jacksonville, Florida without the participation of physical oceanographers.

1.2 The Physical Regime

While the detailed information on physical processes on the outer continental shelf of the southeast will be found in the reports to DOE by Atkinson, Lee, and Pietrafesa, we present here an outline of the general features of the system which are important to an understanding of biological processes on the outer shelf.

Meanders of the Gulf Stream appear to be perturbations of the Rossby wave type generated downstream of topographic features, such as Cape Canaveral or the so-called Charleston bump (Atkinson 1977; Blanton et al. 1979; Lee and Brooks 1979; Pietrafesa et al. in press). Because of this relationship to fixed physical features, the intensity and frequency of intrusions varies along the coast, with a region of high frequency of intrusion events off St. Augustine and Jacksonville, Florida, and in Onslow Bay, in North Carolina. The Georgia shelf is a region of comparatively low activity, although many events take the form of moving eddies which sweep up the shelf break through both Florida and Georgia. The period of Gulf Stream meanders is about 5 days, and complete cycles of intrusion and relaxation occur in the active areas at about that rate. South winds during an intrusion may have an Ekman effect, causing the intruded water to remain on the shelf. It is not unusual in summer, when consistent, brisk southerly winds occur, to observe one intrusion move in under a former one, and even a third move in under the others. Cold water stranded on the continental shelf may remain for a week or more as a distinct water body, isolated by density differences from the water above it and around it. Such bodies of nutrient-rich water are the sites of phytoplankton and zooplankton blooms, because they are a persistent source of nutrients (Atkinson et al. 1978). Intrusions which do not strand on the shelf will be drawn back over the shelf break into deep slope water after two or three days, just as a phytoplankton and bacterial bloom is well established.

With the possible exception of Onslow Bay and Raleigh Bay, the impact of intrusions of nutrient-rich water is less than might be expected. This is because those which strand are, except in the North Carolina bays, rare events, and those which do not are swept back out into the Gulf Stream, with most of the productivity going back down into relatively deep water. Nevertheless, intrusions are the major source of new nitrogen for phytoplankton production on the southeastern continental shelf (Dunstan and Atkinson 1977). While frontal intrusions and related frontal processes are widespread (Savidge

and Foster 1978; Pingree et al. 1979; Floodgate et al. 1981), these take a unique form on the southeastern continental shelf because of the proximity of the west wall of the Gulf Stream to the shelf break. It is curious that the positive effect on productivity of intrusions of the west wall is nearly nullified by the relaxations which follow closely, before secondary production of plankton larger than bacteria can occur. The northerly and westerly regional wind fields, which predominate except in summer, tend to reenforce the loss of intruded water rather than its retention. This is in contrast to the typical regime of coastal upwellings in which edge waves interact positively with the regional wind field to induce upwelling of nutrient-rich water to the surface, where it remains, allowing primary and secondary biological production processes to go to completion.

1.3. The Planktonic Community

Because of their short generation times, microbial populations respond to even the most transitory intrusions of nutrient-rich water over the continental shelf. As this water enters the zone of $>1\%$ of surface solar illumination, a bloom of phytoplankton begins to develop. The initial bloom organisms are small, one of those repeatedly found being Thalassiosira subtilis (J. Yoder, pers. comm.), a 5 μm diatom. This is accompanied by blooms of bacteria, although these are not usually congruent in space. The greatest bacterial densities are typically above or toward the land with respect to the center of the bloom of phytoplankton. It is not clear what causes this physical separation of the bacterial and phytoplankton blooms but it has also been observed in the Irish Sea by Floodgate et al. (1981). In the case of Gulf Stream intrusions, the blooms of bacteria are not in the intrusion itself but in the old shelf water adjacent to it. There is, of course, some diffusion of water between the intrusion and the old shelf water as a result of the combined action of internal waves running on the top of the intruded water, tidal currents on the continental shelf, and eddy diffusion.

Bacteria of the shelf waters are composed of two morphologically distinct groups, the large ($>1 \mu\text{m}$) bacteria usually associated with particulate organic material, and the minibacteria ($<0.5 \mu\text{m}$), originally described by Watson et al. (1977), which are free in the water. The latter may be seen doubling but never form colonies in the water. The former often form colonies on seston particles. There are 10^5 minibacteria/ml in continental shelf water. The number may reach 10^6 /ml in blooms associated with intrusions. Minibacteria

are more abundant than large, attached bacteria by about two orders of magnitude, but because of their small size they constitute only about half of the bacterial biomass, and probably they are responsible for half of the production of new bacterial biomass (Hodson et al. in press).

What is surprising is that free and attached bacteria vary in numbers together, and in fact both vary synchronously with populations of flocculent organic seston. The greatest population densities of chroococcoid cyanobacteria (Johnson and Sieburth 1979; Waterbury et al. 1979) also are associated with dense concentrations of flocculent organic matter. The flocculent organic matter is frequently associated with intrusions but is in the water above them as well as in the intrusions proper. We have associated some of this seston with feces of pelagic tunicates, which are also abundant at the interfaces of intrusions with shelf water and above them. It is reasonable to suppose that the pelagic tunicates are responding to the bloom of bacteria, as well as phytoplankton, by feeding actively and producing feces. According to King et al. (1980), pelagic tunicates can be expected to derive significant nutrition from bacteria but not to greatly influence the total numbers of bacteria in the water. However, the most dense populations of tunicates encountered on the outer shelf may even depress bacterial numbers (Deibel 1980). While the activity of pelagic tunicates may explain the increase in both the numbers of flocs and of bacteria, other mechanisms of production of flocculent aggregates are known (Johnson and Cooke 1980; Kranck and Milligan 1980), it is not clear how they operate in the regime of the outer continental shelf to produce distinctive, localized populations of flocculent seston. Whatever the mechanism, there is an increase in populations of bacteria and flocculent aggregates associated with intrusions of nutrient-rich Gulf Stream water. Secondary production in these water bodies involves the production of bacterial biomass and probably the production of organisms which consume bacteria, such as ciliates and pelagic tunicates. The role of the ciliates in consuming bacteria in fecal flocs has been described by us elsewhere in this report (Pomeroy and Deibel 1980, included as a part of this report).

The picture which emerges from our experience with about ten intrusions over the past six years is one of a rapid increase in primary production during the first 24 hours with a phytoplankton bloom localized in the intrusion or at the interface between the intrusion and the shelf water above it.

Concurrent with this is a bloom of bacteria in the water above or inshore of the intrusion. Where these events persist for several days, dense populations of pelagic tunicates develop in the water in the vicinity of the thermocline between intrusion and shelf water. These are often associated with an increase in flocculent seston in the water. They are extremely dynamic events in both space and time. Because water is usually moving laterally along the shelf as well as in and out over the shelf break, it is not possible to follow events in exactly the same body of water through time. Doing so would require threedimensional mapping on a local scale, and would require more personnel and ship time than we have at our disposal.

1.4. Analysis of Microbiological Methods

On several cruises over the past three years we have done microscopic counts of bacteria as well as the more rapid biochemical analyses which are much less costly in processing time. Because there appears to be no perfect biochemical indicator of bacterial numbers or biomass at this time, we have done a partial correlation analysis of data from three cruises, EASTWARD E3B-79, FRNFLX I (GILLISS and BLUE FIN), and BLUE FIN 10-80. These data cover the entire width of the continental shelf, from the nearshore front to the Gulf Stream (Table 1). While this approach is a relative one, and one which says nothing about causation, it gives some indication of the interpretation which can be placed on the biochemical parameters of microbial abundance that we are using.

Correlation of total bacteria and free bacteria with ATP concentration was 0.72, while correlation of total and free bacteria with total adenylates was 0.82 (Table 3). Thus, the analysis of total adenylates does offer some improvement over ATP alone, but perhaps not one that is commensurate with the additional costs and processing time involved.

Chlorophyll has a rather high correlation (0.60) with both free and total bacteria, suggesting that although the peak densities of the two populations, phytoplankton and bacteria, appear to be offset in plots of oceanographic sections, bacteria do occur where phytoplankton (as indicated by chlorophyll concentration) are most abundant. This is what one would expect. However, it unfortunately tends to nullify any attempt to seek correlations of chlorophyll with ATP or adenylates, since bacteria and phytoplankton converge in our data

Table 1. Combined data from cruises E3B-79, FRNFLX I, and BLUE FIN 10-80.

FREEBAC = free bacteria	NO3 = nitrate
ATTBAC = attached bacteria	SAL = salinity
TBAC = total bacteria	CHL-A = chlorophyll a
PC-ATT = per cent of bacteria attached	PHEO-A = pheophytin a
FLOCFEC = fecal-type floc. aggregates	ATP = extracted ATP
PHYTO = phytoplankton (counted)	AXP = extracted total adenylates
NVPHYTO = non-viable phytoplankton	EC = adenylate energy charge
CYANO = chroococcoid cyanobacteria	HPINDEX = heterotrophic-photoauto- trophic index (AXP/CHL-A)

VARIABLE	N	MEAN	STD DEV
FREEBAC	219	5041598.1735160	7040572.5699707
ATTBAC	219	17205.4794521	21453.4714610
TBAC	219	5058803.6529680	7045409.2209031
PC_ATT	219	2.4889947	4.4174227
FLOCFEC	219	8017.8082192	11349.8778533
PHYTO	219	5431.9634703	12516.9676135
NVPHYTO	112	918.7500000	1116.5851456
CYANO	219	1310.9589041	2641.9982174
DEPTH	217	15.8027650	16.9150490
TEMP	147	21.1948980	3.9925122
NO3	83	4.1659036	5.2491934
SAL	143	34.1124182	2.1497517
CHL_A	187	0.5701632	0.6528446
PHEO_A	112	1.4439040	2.4625830
ATP	144	0.5842549	0.3754986
AXP	144	1.6820093	1.1388165
EC	144	0.5741583	0.1179670
HPINDEX	140	32.3308069	75.9859062

Table 2. Combined data from cruises E3B-79, FRNFLX I, and BLUE FIN 10-80.
Pearson correlation coefficients, probability, and number of observations.
Variables are the same as in Table 1.

EC								
PHYTO	TBAC	FREEBAC	CYANO	NVPHYTO	PC_ATT	FLOCFEC	ATTBAC	
-0.13931	-0.12654	-0.12652	0.06715	-0.06557	0.08438	0.05315	-0.03309	
0.0923	0.1307	0.1306	0.2989	0.5897	0.4433	0.5266	0.6938	
144	144	144	144	70	144	144	144	
HP INDEX								
TBAC	FREEBAC	FLOCFEC	PHYTO	NVPHYTO	PC_ATT	ATTBAC	CYANO	
-0.36030	-0.36025	0.23989	-0.19824	0.16404	0.11562	-0.06325	-0.02044	
0.0001	0.0001	0.0043	0.0189	0.1748	0.1737	0.3231	0.8108	
140	140	140	140	70	140	140	140	
FREEBAC								
FREEBAC	TBAC	PC_ATT	NVPHYTO	ATTBAC	PHYTO	FLOCFEC	CYANO	
1.00000	1.00000	-0.35296	-0.31544	0.22400	-0.17552	-0.10428	-0.10385	
0.0000	0.0001	0.0001	0.0007	0.0008	0.0092	0.1239	0.1255	
219	219	219	112	219	219	219	219	
ATTBAC								
ATTBAC	PC_ATT	TBAC	FREEBAC	PHYTO	CYANO	FLOCFEC	NVPHYTO	
1.00000	0.60635	0.22689	0.22400	0.16339	0.05177	0.05015	-0.05091	
0.0000	0.0001	0.0007	0.0008	0.0155	0.4459	0.4602	0.7463	
219	219	219	219	219	219	219	112	
TBAC								
TBAC	FREEBAC	PC_ATT	NVPHYTO	ATTBAC	PHYTO	FLOCFEC	CYANO	
1.00000	1.00000	-0.35089	-0.31533	0.22689	-0.17491	-0.10406	-0.10362	
0.0000	0.0001	0.0001	0.0007	0.0007	0.0045	0.1247	0.1263	
219	219	219	112	219	219	219	219	
PC_ATT								
PC_ATT	ATTBAC	FREEBAC	TBAC	NVPHYTO	FLOCFEC	CYANO	PHYTO	
1.00000	0.60635	-0.35296	-0.35089	0.26315	0.09006	0.06231	0.05047	
0.0000	0.0001	0.0001	0.0001	0.0051	0.1842	0.3549	0.4574	
219	219	219	219	112	219	219	219	
FLOCFEC								
FLOCFEC	CYANO	NVPHYTO	FREEBAC	TBAC	PHYTO	PC_ATT	ATTBAC	
1.00000	0.21200	0.17622	-0.10428	-0.10406	0.10029	0.09006	0.05015	
0.0000	0.0016	0.0631	0.1239	0.1247	0.1390	0.1842	0.4603	
219	219	112	219	219	219	219	219	
PHYTO								
PHYTO	CYANO	FREEBAC	TBAC	ATTBAC	NVPHYTO	FLOCFEC	PC_ATT	
1.00000	0.22673	-0.17552	-0.17491	0.16339	0.10183	0.10029	0.05047	
0.0000	0.0007	0.0092	0.0095	0.0155	0.2654	0.1290	0.4574	
219	219	219	219	219	112	219	219	
NVPHYTO								
NVPHYTO	FREEBAC	TBAC	PC_ATT	CYANO	FLOCFEC	PHYTO	ATTBAC	
1.00000	-0.31544	-0.31533	0.26315	0.24430	0.17622	0.10183	-0.03091	
0.0000	0.0007	0.0007	0.0051	0.0094	0.0631	0.2854	0.7463	
112	112	112	112	112	112	112	112	
CYANO								
CYANO	NVPHYTO	PHYTO	FLOCFEC	FREEBAC	TBAC	PC_ATT	ATTBAC	
1.00000	0.24430	0.22673	0.21200	-0.10385	-0.10362	0.06231	0.05177	
0.0000	0.0094	0.0007	0.0016	0.1255	0.1263	0.3549	0.4459	
219	112	219	219	219	219	219	219	

Table 3. Combined data from cruises E3B-79, FRNFX I, and BLUE FIN 10-80.
Spearman correlation coefficients, probability, and number of observations.
Variables are the same as in Table 1.

CHL_A

TBAC	FREEBAC	ATTBAC	PC_ATT	PHYTO	NVPHYTO	FLOCFEC	CYANO
0.32531	0.82423	0.41450	-0.58130	0.31780	-0.26493	-0.11826	-0.05448
0.0001	0.0001	0.0001	0.0001	0.0001	0.0043	0.1070	0.4339
167	167	167	167	167	112	137	167

PHED_A

FREEBAC	TBAC	PHYTO	PC_ATT	FLOCFEC	CYANO	ATTBAC	NVPHYTO
0.45770	0.45770	-0.34505	-0.27458	-0.20200	0.15823	0.12035	-0.11217
0.0001	0.0001	0.0002	0.0034	0.0327	0.0956	0.2043	0.2390
112	112	112	112	112	112	112	112

ATP

FREEBAC	TBAC	PC_ATT	ATTBAC	PHYTO	FLOCFEC	CYANO	NVPHYTO
0.72285	0.72020	-0.40858	0.31902	0.26057	-0.21181	-0.09541	0.00477
0.0001	0.0001	0.0001	0.0001	0.0016	0.0108	0.2553	0.9360
144	144	144	144	144	144	144	70

AXP

TBAC	FREEBAC	ATTBAC	PC_ATT	PHYTO	FLOCFEC	NVPHYTO	CYANO
0.81254	0.81156	0.44682	-0.39733	0.33083	-0.12792	0.11949	-0.09321
0.0001	0.0001	0.0001	0.0001	0.0001	0.1265	0.3245	0.2665
144	144	144	144	144	144	70	144

EC

TBAC	FREEBAC	PC_ATT	ATTBAC	NVPHYTO	FLOCFEC	CYANO	PHYTO
-0.28933	-0.28223	0.13484	-0.13295	0.06050	0.03182	0.00556	0.00205
0.0004	0.0008	0.1076	0.1122	0.8188	0.7050	0.9473	0.9806
144	144	144	144	70	144	144	144

HPINDEX

TBAC	FREEBAC	PC_ATT	PHYTO	ATTBAC	FLOCFEC	CYANO	NVPHYTO
-0.55805	-0.54721	0.39529	-0.35680	-0.25931	0.18757	0.14838	0.05602
0.0001	0.0001	0.0001	0.0001	0.0020	0.0266	0.0802	0.6451
140	140	140	140	140	140	140	70

FREEBAC

FREEBAC	TBAC	PC_ATT	ATTBAC	NVPHYTO	PHYTO	FLOCFEC	CYANO
1.00000	0.99834	-0.44722	0.44333	-0.34440	0.25927	-0.11135	0.01432
0.0000	0.0001	0.0001	0.0001	0.0002	0.0001	0.1003	0.8331
219	219	219	219	112	219	219	219

ATTBAC

ATTBAC	TBAC	FREEBAC	PC_ATT	PHYTO	FLOCFEC	CYANO	NVPHYTO
1.00000	0.47215	0.44333	0.43655	0.41727	0.34412	0.18578	0.05200
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0058	0.5861
219	219	219	219	219	219	219	112

TBAC

TBAC	FREEBAC	ATTBAC	PC_ATT	NVPHYTO	PHYTO	FLOCFEC	CYANO
1.00000	0.99834	0.47215	-0.42501	-0.34277	0.27032	-0.10565	0.01808
0.0000	0.0001	0.0001	0.0001	0.0002	0.0001	0.1191	0.7903
219	219	219	219	112	219	219	219

Table 3, continued.

PC_ATT							
PC_ATT	FLOCFEC	FREEBAC	ATTBAC	TBAC	NVPHYTO	CYANO	PHYTO
1.00000	0.51020	-0.44722	0.43655	-0.42501	0.40740	0.24680	0.19642
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002	0.0035
219	219	219	219	219	112	219	219
FLOCFEC							
FLOCFEC	PC_ATT	NVPHYTO	ATTBAC	PHYTO	CYANO	FREEBAC	TBAC
1.00000	0.51020	0.44522	0.34412	0.33964	0.29946	-0.11135	-0.10563
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.1003	0.1191
219	219	112	219	219	219	219	219
PHYTO							
PHYTO	ATTBAC	NVPHYTO	FLOCFEC	TBAC	FREEBAC	CYANO	PC_ATT
1.00000	0.41727	0.37989	0.33964	0.27032	0.25927	0.24953	0.19542
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002	0.0035
219	219	112	219	219	219	219	219
NVPHYTO							
NVPHYTO	FLOCFEC	PC_ATT	PHYTO	CYANO	FREEBAC	TBAC	ATTBAC
1.00000	0.44522	0.40740	0.37989	0.35967	-0.34440	-0.34277	0.05200
0.0000	0.0001	0.0001	0.0001	0.0001	0.0002	0.0002	0.5361
112	112	112	112	112	112	112	112
CYANO							
CYANO	NVPHYTO	FLOCFEC	PHYTO	PC_ATT	ATTBAC	TBAC	FREEBAC
1.00000	0.35967	0.29946	0.24953	0.24680	0.18578	0.01806	0.01432
0.0000	0.0001	0.0001	0.0002	0.0002	0.0058	0.7905	0.6331
219	112	219	219	219	219	219	219
DEPTH							
FREEBAC	TBAC	PC_ATT	NVPHYTO	CYANO	PHYTO	FLOCFEC	ATTBAC
-0.35347	-0.34457	0.27365	-0.11506	0.02951	-0.01347	0.01137	0.00101
0.0001	0.0001	0.0001	0.2270	0.6655	0.8436	0.8678	0.9882
217	217	217	112	217	217	217	217
TEMP							
PHYTO	FLOCFEC	TBAC	NVPHYTO	ATTBAC	FREEBAC	PC_ATT	CYANO
-0.31461	0.20409	-0.15507	-0.15403	-0.15314	-0.14637	0.10550	0.03617
0.0001	0.0132	0.0607	0.2064	0.0640	0.0769	0.2035	0.6636
147	147	147	69	147	147	147	147
NO3							
PHYTO	FREEBAC	TBAC	PC_ATT	ATTBAC	FLOCFEC	CYANO	NVPHYTO
0.31536	-0.31351	-0.26754	0.21852	0.12323	0.03816	-0.03788	0.00000
0.0037	0.0039	0.0145	0.0472	0.2670	0.7320	0.7334	0
83	83	83	83	83	83	83	0
SAL							
TBAC	FREEBAC	ATTBAC	PC_ATT	PHYTO	NVPHYTO	FLOCFEC	CYANO
-0.78032	-0.78009	-0.38384	0.37792	-0.23269	-0.19483	0.11901	0.06362
0.0001	0.0001	0.0001	0.0001	0.0052	0.2044	0.1569	0.4503
143	143	143	143	143	69	142	143

Table 4 . Net primary production in simulations of various intrusion and upwelling events used for modeling the detrital food web.

	g C m ⁻² yr ⁻¹	K Cal m ⁻² yr ⁻¹	KJ m ⁻² yr ⁻¹
4 intrusions, regular	143	1630	6820
4 intrusions, regular, yr 1	143	1629	6816
yr 2	149	1704	7130
yr 3	150	1706	7140
yr 4	149	1697	7100
yr 5	149	1694	7088
4 intrusions, stochastic	141	1607	6742
constant upwelling	761	8671	36279
Peru upwelling	326	3715	15544
spring bloom 1	182	2069	8657
spring bloom 2	140	1599	6690

set. Therefore, we must continue to fall back on the use of the HP index (Campbell et al. 1979) to separate phytoplankton dominance from microbial heterotroph dominance in individual samples. It is also worth noting that the distribution of bacteria counts is highly contagious (variance $\gg$ mean) while that of ATP and adenylates approaches a Poisson distribution. Therefore, some of the apparent increased precision offered by microscopic counting cannot be realized because of the statistical problems of dealing with a negative binomial distribution.

1.5 GABEX I

In April, 1980 R/V ISELIN and R/V EASTWARD were used concurrently to study mesoscale events on the outer continental shelf between Cape Canaveral and Savannah, Georgia. This was supported by overflights of remote-sensing aircraft (a NASA U-2 high altitude flight and Coast Guard low-altitude flights) and by deployment of an extensive array of current meters by T.N. Lee. The two-ship plan gave continuous coverage of the Georgia and Florida continental shelf while permitting flexibility to follow intrusion events as they occurred. R/V EASTWARD maintained a regular cruise track, repeatedly sampling along a series of transects from Savannah to St. Augustine. R/V ISELIN began by covering the outer portion of the grid out of phase with the EASTWARD, but as the three-week study progressed ISELIN turned to more specialized mapping and intrusion hunting. Our program had three persons on EASTWARD and one on ISELIN. This was the maximum space available to us. One of the inevitable consequences of cooperative studies is the limitation on the size of each of the research teams. As a result, we were unable to sample all transects continuously as we would have liked. We concentrated on the St. Augustine transect, because experience had shown this to be a region of frequent intrusions from the west wall of the Gulf Stream.

April, 1980, proved to be an unusual period of runoff of freshwater from the coast, with 34 ‰ salinity extending far out across the shelf at times. Intrusion activity was weak, without the appearance of prominent eddies, but it was essentially continuous through the period, with some nutrient-rich water on the outer continental shelf much of the time. This is indicated by the presence of lenses of 18° water at the bottom on the outer continental shelf during most of the period (Figure 1).

Figure 1. St. Augustine hydrographic section, GABEX I, April 12-24, 1980. Temperature, °C, provided by L. P. Atkinson.

Figure 2. St. Augustine hydrographic section, GABEX I, April 12-24, 1980. Salinity, ‰, provided by L. P. Atkinson.

Figure 3, St. Augustine hydrographic section, GABEX I, April 12-24, 1980.
Active chlorophyll a, micrograms per liter.

Figure 4. St. Augustine hydrographic section, GABEX I, April 12-24, 1980.
Heterotrophic-photoautotrophic index.

The development of the phytoplankton bloom on the outer continental shelf in April, 1980 was unusually extensive and was not limited to the immediate vicinity of the intrusions. Probably this is related to the presence of brackish water moving across the shelf (Figure 2). On several occasions the bloom extended toward shore beyond the region of the outer shelf that we sampled (Figure 3), and it extended to the surface, or very nearly so in some cases. Day-to-day variation along the section was great, as it usually is on the outer shelf, because water is moving through the section as well as back and forth along it. For example, the absence of bloom conditions in the 19 April section should not be taken to indicate that the bloom seen on the previous section two days earlier had been dispersed or eaten by zooplankton. Rather, it was somewhere else.

The HP index (Campbell et al. 1979) shows autotrophic dominance of the microbial community over most of the shelf waters, including all bloom areas, with small patches of heterotrophic dominance outside the bloom areas. The exception is April 19, when heterotrophic dominance is ubiquitous. The extent of autotrophic dominance is in sharp contrast to typical intrusion situations uncomplicated by fresh-water runoff. Compare, for example the HP index distribution of April 1980 with the of April 20-21 (Figure 4).

The data presented in this report for GABEX I are preliminary and incomplete. Data processing has not been completed at this time.

1.6 Eastward Cruise E3B-79

The EASTWARD cruise of August 7-14, 1979 (Brunswick, Ga. to Beaufort, N.C.) was focused on microbial processes in an intrusion off St. Augustine. This was a situation in which weak intrusions were coming with a high frequency. An intrusion which was located immediately upon arrival at the shelf break off St. Augustine, was already near its maximal advance over the shelf, with 15° water at least 20 km west of the shelf break. Nitrate concentrations of 5 $\mu\text{g atoms N/l}$ extended along the bottom to the west of our section (Figure 5). A midwater chlorophyll maximum above the thermocline or in it remained throughout the three days of observation. Counts of bacteria were done on every sample taken on the section for three days. Included in the enumerations were free minibacteria, large attached bacteria, flocculent aggregates, chroococcoid cyanobacteria, and phytoplankters. Two manuscripts based on the results of this cruise are included as parts of this report (Hodson et al. and

Figure 5. Hydrographic section of the continental shelf at 30° N, August 10, 1979. Left: salinity, ‰ (above); temperature, °C (below). Right: Nitrate, micrograms/liter (above); active chlorophyll *a*, micrograms/liter (below). Bottom: 10⁵ bacteria/ml.

Figure 6. Hydrographic section of the continental shelf at 30° N, August 11, 1979. Left: salinity, ‰ (above); temperature, °C (below). Right: Nitrate, micrograms/liter (above); active chlorophyll *a*, micrograms/liter (below). Bottom: 10⁵ bacteria/ml.

Figure 7. Hydrographic section of the continental shelf at 30° N, August 11, 1979. Left: salinity, ‰ (above); temperature, °C (below). Right: Nitrate, micrograms/liter (above); active chlorophyll *a*, micrograms/liter (below). Bottom: 10^5 bacteria/ml.

Jacobsen), and the results are discussed further in section 3.2. If one can speak of a typical intrusion, this example approaches it, based on our experience to date. Although the bloom of both phytoplankton and bacteria was still active when ship scheduling forced us to depart at the end of the third day, there was evidence that the intrusion was relaxing, and probably the whole thing went over the shelf break on the fourth day. Compare, for example, the isotherms and also the chlorophyll distribution on August 10 (Figure 6) and August 12 (Figure 7).

1.7 R/V GILLISS cruise, April 19-May 2, 1979

An intrusion at the shelf break due east of Jacksonville, Florida was followed for four days by running daily sections at 30° 20' N as the intrusion event moved northward through the position. This was a cooperative study involving Atkinson, Paffenhöfer, and Yoder. Physical and chemical data reported here were collected by Atkinson's group.

The high chlorophyll concentrations on April 21 and 23, with comparatively low concentrations on April 22, probably do not represent a sequence of events in the same water body but are the result of water movement through the section (Figure 8). However, the water on April 11 is under the influence of adjacent intrusion water, because it has unusually high adenylate concentration (Figure 9) due to heterotrophic populations (as indicated by HP index values in Figure 11). This is one of several instances where we have observed striking separation in space, but not in time, of blooms of autotrophs and heterotrophs. In contrast, the section taken on April 24 shows old shelf water or Gulf Stream water throughout the section. Chlorophyll is very low, adenylates are very low, adenylate energy charge is 0.6 or less everywhere, and HP index is below 3 everywhere. Although chlorophyll concentration increased by more than an order of magnitude during the intrusion event, energy charge data, used in conjunction with the HP index, suggest that the phytoplankton population as a whole was not growing actively and was suffering from some kind of stress. The only really high energy charge values occurred in the surface water on April 22, when the upper layer was heterotrophically dominated and chlorophyll was comparatively low.

While the biological response to the intrusion of April 20-24, 1979 was not as intense as some others we have seen, it followed the typical course. Having probably originated on the 20th, when first observed on the 21st there

Figure 8. Distribution of active chlorophyll *a*, micrograms per liter, on a section of the continental shelf at 30° 20' N, April 21 (top) to 24 (bottom), 1979.

Figure 9. Distribution of particulate total adenylates, ATP, ADP, and AMP (10^{-11} moles) on a section of the continental shelf at $30^{\circ} 20' N$, April 21 (top) to 24 (bottom), 1979.

Figure 10. Energy charge ratio on a section of the continental shelf at 30° 20', April 21 (top) to 24 (bottom), 1979.

Figure 11. Heterotrophic-photoautotrophic index on a section of the continental shelf at $30^{\circ} 20' N$, April 21 (top) to 24 (bottom), 1979. Hatched area is mixed autotrophic-heterotrophic biomass ($HP > 3 < 10$). Unshaded area is autotroph-dominated biomass ($HP < 3$).

was already a substantial phytoplankton bloom centered in the intruded Gulf Stream water near the bottom. Patches of less nitrate-rich water, such as that passing through the section on April 22, were nevertheless influenced by productivity in the adjacent water because they contained abnormally high concentrations of adenylates of heterotrophic origin and showed a high energy charge ratio attributable to the population of heterotrophic bacteria. On April 23 the intrusion was beginning to relax, with some cascading of water over the shelf break. This is seen in the distribution of adenylates and chlorophyll. On April 24 the event had wholly passed by and the section was occupied by low-nutrient water of low biological activity and biomass.

1.8 R/V ISELIN Cruise April 25-24, 1978

This was the first combined cooperative cruise by the intrusion research group, in which physical, chemical, and biological oceanographers combined efforts on the study of a single intrusion event. Using satellite imagery, an intrusion was located east of Brunswick, Georgia, and a section was run on two successive days. The first day was that of maximal intrusion, and the water was moving over the shelf break on the second day. This was the first use of our concept of the heterotrophic-photoautotrophic index (HP index) as a qualitative indicator of the relative dominance of autotrophs and heterotrophs in water samples. Data from this cruise, together with a description of the HP index and the rationale behind it are published in the paper by Campbell et al. (1979) which is a part of this report.

While this cruise was short, and only two consecutive sections were run through an intrusion, it was important in establishing a research strategy which has proven very successful for us. This involves the cooperative use of a ship by physical, chemical, and biological contractors, satellite data to locate the Gulf Stream and eddies on the west wall (at least in seasons when temperature differences make this possible), and running daily hydrographic sections at an established latitude. Each station is sampled only once, using an STD and rosette sampler, with all scientists using water from the single cast.

1.9 R/V ISELIN Cruise August 3-10, 1978.

This was a cooperative cruise whose purpose was to follow a stranded intrusion. August is the most favorable time for stranding of intrusions, and

Figure 12. Indices of microbial activity in an intrusion of Gulf Stream water on the outer continental shelf, 30° N, April 21 (top) and 22 (bottom), 1978. Left, temperature, °C; center, adenylate energy charge; right, heterotrophic-photoautotrophic index. Shaded portion is dominated by autotrophic biomass (HP index < 3). Unshaded portion is mixed autotrophic and heterotrophic biomass (HP index 3-10).

indeed one was found off Fernandina which we were able to follow over several days. Unfortunately, it is difficult to set up a two-dimensional sampling regime, such as that used for intrusions at the shelf break, because the movement of stranded intrusions is slow and unpredictable. Moreover, they lie on the bottom, so there are no surface clues. Satellite imagery does not help. We have since developed a towed subsurface thermistor, but at that time the only approach was many STD or XBT casts. Attempts to follow a specific water body with a drogue were of limited success, apparently because of the shear between the intrusion and the overlying shelf water. Therefore, continuity of sampling was not satisfactory.

From the point of view of the DOE mission, this was a useful experience in that it gave us good insight into water movement on the continental shelf. Movement is comparatively slow in the absence of forcing from the Gulf Stream, but when stratification is present surface and bottom waters may not be moving together.

2. Coastal Fronts

Density fronts are a feature of the ocean which has long been recognized. The importance and ubiquity of mesoscale density fronts has been appreciated relatively recently (Savidge and Foster 1978; Floodgate et al. 1981). The water of the inner continental shelf of the southeastern U.S. is well mixed vertically, but it is segmented horizontally by a number of density fronts. The fronts are often prominent on satellite imagery. They can usually be seen from the bridge of a ship as well. This is because the water on the coastal side of a front is typically more turbid. In fact, differences in salinity and temperature are small across most of the fronts, often less than $1 \text{ }^{\circ}/_{\text{oo}}$ and 1° C , which suggests that most of the density difference is caused by the suspended sediments themselves. The fact that there are significant density differences across the fronts is demonstrated by the presence of a convergence at the front, marked by a foam line. While not much seems to be known about their formation, they appear to form in the first 5-10 km of the ocean. Probably they have a lifetime of one to several days (J. Imberger, pers. comm.). Fronts influence the flux of materials, as well as water itself, across the inner continental shelf (Blanton 1980; Blanton and Atkinson 1978). To evaluate that flux and its chemical and biological impact, a series of

cooperative studies have been undertaken which are planned and coordinated by J.O. Blanton.

Three cooperative studies have been completed, and a fourth is planned for April 1981. The first, in 1977, was an anchor station in Wassaw Inlet to evaluate transport through the frontal zone. Two persons from this research group participated in the collection of data. In 1978 two vessels, R/V KIT JONES and R/V BLUE FIN, were anchored in the Wassaw Inlet area. Four persons from our research group participated. In 1979 two vessels, R/V BLUE FIN and R/V ISELIN, were anchored in the Wassaw Inlet area. Five persons from our research group participated. The latter two studies are described in the following sections. It must be emphasized that these studies, at least from our point of view, are preliminary in nature. The objective is as much to define the system as to actually measure it. For this reason we have tried many things, sometimes collecting only partial data sets, to ascertain what measurements will be useful.

2.1. Cooperative Front Study, May 9-12, 1978

Participants in the study included J.O. Blanton, H. Windom, and D. Hayes. The overall objective of the project was to measure water flux through the region of the coastal front off Wassaw Inlet. The primary objective of all participants was to evaluate various tracers of water movement, including tritium (Hayes), trace metals (Windom), and such biological parameters as chlorophyll, pheophytin, and adenylates (Pomeroy). BLUE FIN and KIT JONES were anchored for four tidal cycles in positions which we hoped would provide sequential sampling of the Savannah River plume. The positions and a summary of the physical data are given by Blanton (1979). Measurements of active chlorophyll a, ATP, and total adenylates were made at several depths every two hours. Sample depths were based on temperature and salinity profiles from a CTD cast to place the water samplers in distinct upper and lower water layers associated with the frontal convergence. In addition, in vivo fluorescence was measured with a Turner Designs fluorometer equipped with a submersible pumping system.

Plots of in vivo fluorescence against time (Figure 13) suggest that the two vessels were seeing different water bodies, and the physical data support this. Location A was in the Savannah River plume, while location B was in the Ogeechee River plume as well as frontal and nearshore circulation. The dif-

Figure 13. In vivo fluorescence time series at anchor stations off Wassaw Inlet, May 9-11, 1978. Top: R/V BLUE FIN. Bottom: R/V KIT JONES. Calibrated against purified chlorophyll a.

Figure 14. Time series at BLUE FIN anchor station off Nassaw Inlet, May 9-11, 1978. Top: total adenylates and adenylate energy charge. Center: chlorophyll a (HPLC), mg/m^3 . Bottom: In vivo fluorescence, mg/m^3 .

Figure 15. Time series at KIT JONES anchor station off Wassaw Inlet, May 9-11, 1978. Top: Total adenylates and adenylate energy charge. Center: chlorophyll a (HPLC), mg/m^3 . Bottom: *In vivo* fluorescence, mg/m^3 .

ference between fluorescence of in vivo "chlorophyll" and active chlorophyll a measured by the method of Jacobsen (1978) in the time series (Figures 14 and 15) is striking. In vivo fluorescence at location A remained relatively constant at about 2.5 $\mu\text{g/l}$, while active chlorophyll a was only about 0.5 $\mu\text{g/l}$ but with considerably more variation. The higher concentrations of active chlorophyll a in the bottom samples probably represent highly active phytoplankton which have recently been carried down in the frontal convergence.

While active chlorophyll a is demonstrably a superior parameter of phytoplankton biomass and is useful in understanding the movement of phytoplankton in the frontal zone, in vivo chlorophyll fluorescence was the more useful indicator of different water bodies in this instance. The difference between in vivo chlorophyll fluorescence at location A and location B is one of the best indications that the two vessels were seeing different bodies of water.

2.2 FRNFLX I, November 6-9, 1979.

Two vessels were placed in Wassaw Inlet, one seaward of the other so water would move directly from one station to the other. Their distance was such that some of the same water would be sampled by both vessels. Replacement of the very small and cramped KIT JONES with R/V ISELIN made it possible to have more technical assistance, to undertake more elaborate kinds of measurements, and to set up the Zeiss epifluorescence microscope to look at living microbial samples during the anchor station. Rather than focusing on the identity of water bodies, our goal during this study was to evaluate a number of microbiological parameters which might be indicative of biomass or activity in the nearshore zone. Some of the parameters which had been most useful in our work on Gulf Stream intrusions proved to be of less interest in the nearshore zone, while others showed considerable promise for future studies. In several cases we took only partial data sets during the five tidal cycles of the study. This permitted us to examine more parameters. As in the offshore work, we were limited by the number of personnel the vessels could accommodate.

Absolute numbers of bacteria are nearly an order of magnitude higher in the nearshore zone than in the water of the outer continental shelf. The numbers vary relatively little. In this study the range was from 0.9 to $3 \times 10^6/\text{ml}$ (Figure 17). Most of the bacteria are free-living. Those on particles are much fewer but they are more variable in number. Based on our experience

on this and several other coastal cruises on R/V BLUE FIN, it is necessary to prepare a separate sample, in which more water is filtered, to get a statistically significant count of attached bacteria. There may in fact be some difficulty in getting enough material on the slide for a significant count without incurring a coincidence loss effect from clumping of particulate material. Based on this experience we conclude that counts of total bacteria are not a useful parameter to measure, at least in coastal Georgia, because biomass varies little. If you've seen one sample, you've seen them all.

The alternative approach to measuring microbial biomass, which we found to be quicker and equally precise on the outer continental shelf, is the measurement of ATP or total adenylates. In the nearshore zone we found that total adenylates varied little. Moreover, the H-P index shows that most of that biomass, most of the time, is phytoplankton (Figures 16-17). Therefore, adenylate measurements are telling us essentially the same thing as chlorophyll a measurements in this water. Moreover, energy charge calculated from the adenylate measurements is in most cases that of the phytoplankton. We cannot ascertain the energy charge of the bacterial population in the presence of so many phytoplankton. For these reasons we probably will not measure adenylates in the future in studies of the nearshore zone in Georgia.

Chlorophyll a measurements showed more phytoplankton in the bottom layer than in the surface (Figure 17 and 18). Measurements of photosynthetic potential showed these phytoplankters near the bottom to have a higher potential than those near the surface, all being exposed to the same, moderate illumination from a fluorescent light source (Figure 17). Evidently the phytoplankton in the bottom water have recently been drawn down in the frontal convergence. However, something more than that has occurred to increase their photosynthetic potential. Enhanced nutrients seem unlikely in this nutrient-rich coastal water. Possibly there is an infusion of a different phytoplankton population from the other side of the front. While the measurement of photosynthetic potential produced some interesting and unexpected results, probably it is not an item of high priority for future work in the frontal zone.

Heterotrophic uptake of ^{14}C -labeled glucose showed as much variation as any parameter of microbial activity we investigated (Figure 17). It varied a full order of magnitude over the course of the three tidal cycles in which the measurements were done. This makes heterotrophy a parameter of interest for

Figure 16. FRNFLX I anchor station A, 7-9 November, 1979. Top, total adenylates. Center, adenylate energy charge ratio. Bottom, heterotrophic-photoautotrophic index. Shaded areas are mixed autotrophic-heterotrophic biomass ($HP > 3 < 10$). Unshaded areas are autotroph-dominated ($HP < 3$).

Figure 17. FRNFLX I anchor station A, 7-9 November, 1979. Top left, A0 counts of total bacteria, 10^6 cells/ml. Bottom left, heterotrophic uptake of ^{14}C -labeled glucose, $\mu\text{g C l}^{-1} \text{ hr}^{-1}$. Top right, chlorophyll a, mg m^{-3} . Bottom right, potential photosynthesis, $\text{mg C m}^{-3} \text{ hr}^{-1}$. Shaded portions are times when samples were not taken.

Figure 18. FRNFLX I anchor station B, 7-9 November, 1979. Top left, total adenylates. Bottom left, heterotrophic-photoautotrophic index. Shaded portion is mixed autotrophic-heterotrophic biomass ($HP > 3 < 10$). Remainder is autotrophic-dominated biomass ($HP < 3$). Top right, chlorophyll a, mg m^{-3} . Bottom right, adenylate energy charge.

future studies. Uptake of labeled glucose, however, may not be the best possible approach. It is not indicative of total uptake of organic matter, and probably it underestimates it by more than an order of magnitude (Wiebe and Smith 1979). While routine use of even an abbreviated measurement of uptake of a defined labeled compound is almost prohibitively time consuming for a fast-paced series of samples at an anchor station, the possibly more realistic approach of Smith and Wiebe (1978) of using labeled naturally occurring dissolved organic compounds (but chemically undefined) is even more time consuming. Perhaps the ideal parameter would be the measurement of respiration, although this would have a substantial phytoplankton bias. We shall probably consider doing that if a method can be set up that is sufficiently sensitive without being too time consuming for sampling closely spaced in time.

3. Microbial Populations and the Detritus Food Web

Because this contract is concerned with the flux of energy and materials, particularly as mediated by microorganisms, in the water over the continental shelf, it is concerned with the production and fate of particulate and dissolved organic matter that is non-living as well as living. While this work emphasizes the non-living components to some degree, any complete separation of living and non-living would be artificial and unworkable. Therefore, we have to begin with primary production, as do Paffenhöfer and Yoder, who are concerned with the flux of energy through the zooplankton. We also have to consider some aspects of zooplankton ecology, particularly the production of fecal material which is a major input of non-living particulate organic matter to the system. Since we are working cooperatively in a coordinated research program, unnecessary duplication can be avoided.

The flux of energy through non-living components of the pelagic ecosystem involves both very rapid responses and stabilizing influences. The dissolved organic matter, produced both as a primary source by phytoplankton and as a secondary energy source by zooplankton and bacteria, is utilized by bacteria very rapidly. In fact, utilization is so rapid that evaluation of the rate of production of DOM is difficult. This is one of several reasons why its significance as an energy flux in planktonic ecosystems has been underestimated. Most of the particulate matter in the sea is non-living, indicating that much of it has a comparatively long residence time in the water. Since it is both

a substrate and a structural component of the environment for microorganisms, its production and fate are important considerations. However, we know surprisingly little about the non-living seston. Both biological and abiotic origins have been postulated (Riley 1963; 1970; Wiebe and Pomeroy 1972; Zimmermann 1977; Pomeroy and Deibel 1980). Probably both occur in the real world, but the actual rates are not known. Chemical analysis of seston has been of little help, because all of it probably originates from phytoplankton, and therefore its chemistry is all much alike and like the phytoplankton themselves. While it is not the major thrust of this contract to develop new ideas or data on the detritus food web for its own sake, these are questions which have to be taken into consideration in our interpretations of processes on the continental shelf. In the course of understanding processes on the southeastern continental shelf some new ideas and information on the detritus food web have emerged.

The turnover of dissolved organic matter and its relation to bacterial populations in the water has been examined. The nature, source, and fate of particulate seston has been re-examined, and some of it identified as the fecal material of zooplankton. A simulation model of the food web has been constructed which includes the major features of the flux of dissolved organic matter and detritus.

3.1 Methods of Microscopy.

Although we are routinely using the acridine orange epifluorescence method for counting marine bacteria, it does have some limitations, and we are continually exploring new methods. We have modified the acridine orange method somewhat to increase the time samples can be stored before they are counted. This is a significant problem. It is not feasible to count samples in large numbers at sea. They must be brought back to the laboratory and counted later. Samples preserved in formalin last only about two weeks after collection, not long enough to count a large set. We have extended the storage time to about six weeks by preserving the samples in buffered glutaraldehyde, just as one would for scanning electron microscopy. The time can be extended further by preparing the stained filters, mounting them on slides in immersion oil, and storing them in the refrigerator.

We have also worked with Karen Porter on the development of DAPI staining for epifluorescence counting (Porter and Feig 1980). Although DAPI staining

has some advantages, we will not switch to it as a routine counting procedure unless data we are now collecting indicate that there is a significant difference in total counts. One of the minor disadvantages of DAPI staining is the necessity to prepare stained filters immediately at sea. The filters must then be kept cold until they are returned to the laboratory and counted.

3.2 Utilization of Dissolved Substrates by Bacteria in Gulf Stream Intrusions

To evaluate microbial responses to intrusions it is necessary to develop methods and criteria of activity appropriate for the populations in question. We have found that specific (per cell) uptake rates (Wright 1978) present a problem when cell volumes vary over two orders of magnitude, as they do in oceanic bacteria. Using dissolved adenosine triphosphate (DATP) labeled with ^{32}P as a tracer, we measured uptake of naturally occurring DATP by natural populations of free and attached bacteria in a Gulf Stream intrusion and in adjacent Gulf Stream and continental shelf water. Free bacteria in the ocean, including the outer continental shelf are, with rare exceptions, less than 0.5 micrometers in size, while attached bacteria are usually greater than one micrometer in size. The greater size is generally taken to indicate greater metabolic activity and active growth on the part of attached bacteria.

DATP is a convenient naturally occurring organic compound to study, because a good analytical method exists (Azam and Hodson 1977), and ^{32}P -labeled ATP can be used as a sensitive tracer. Hodson and Azam (1977) have shown that DATP is biologically active: it is readily taken up by bacteria. Uptake by free and attached bacteria can be distinguished in ocean water by counting ^{32}P activity retained on 0.2 and 0.6 μm Nuclepore filters. Aliquots from the same water samples were also preserved in cold glutaraldehyde for counting free and attached bacteria by acridine orange fluorescence.

Specific uptake of DATP was highly correlated with ambient DATP concentration. Specific uptake of DATP by large, attached bacteria was 4-430 times that of small, free-living bacteria. Specific uptake by both free and attached bacteria increased up to 200 times within 24 hours of the arrival of an intrusion on the continental shelf. Uptake rates of free and attached bacteria are significantly correlated ($r^2 = 0.8$), suggesting that both are dissolved substrates and both are stimulated by intrusion events.

While on a per-cell basis the rate of uptake of DATP by attached bacteria was 66 times higher than that by free bacteria, the uptake per unit of biomass was essentially the same for both populations, because attached bacteria have approximately 40 times the volume of free bacteria. Therefore, on the basis of equal units of biomass, attached bacteria do not appear to be more active than free minibacteria. Of course, this may be because a significant fraction of the population of free bacteria is inactive. However, when bacterial populations are widely divergent in size, as are the free and attached bacteria of the ocean, the best basis of comparison appears to be activity per unit biomass rather than per cell.

A more complete account of this is in the manuscript by Hodson, Maccubbin and Pomeroy (in press) which is a part of this report.

3.3. Interactions of populations of Free Bacteria, Attached Bacteria, and Aggregates

The work of Hodson et al. (in press) showed that both free and attached bacteria respond to Gulf Stream intrusions by increasing their numbers and their uptake of dissolved substrates. In a further examination of the interactions of these populations we examined the relationship of bacteria, phytoplankton, and chroococcoid cyanobacteria to the abundance of flocculent aggregates. The abundance of flocs varies greatly, sometimes dominating the population of particulate matter and sometimes being a comparatively rare component. In general, dense populations of flocs are associated with intrusions of Gulf Stream water (but are in surface water as well as in the subsurface intrusion) and with biologically productive nearshore fronts.

A set of 45 samples from all parts of the continental shelf was examined. Each sample was counted with acridine orange epifluorescence for free and attached bacteria, phytoplankton, chroococcoid cyanobacteria, and flocculent aggregates. In each case a sample was categorized as having a dense flocculent background or not having one. Because a dense population of flocs may obscure free bacteria, this in itself might tend to reduce the count of free bacteria in the presence of dense flocs. Of the 45 samples examined, 29 had a dense flocculent background and 16 did not. Using the Wilcoxon two-sample test, the following parameters were tested with respect to the two categories of samples.

1. Number of free bacteria per ml.
2. Variance of the free bacteria counts as a per cent of the mean.
3. Per cent of flocs with attached bacteria.
4. Mean number of attached bacteria per floc.
5. Per cent of time viable phytoplankton occur with flocs.
6. Per cent of time flocs occur with viable phytoplankton.
7. Ratio of viable phytoplankton to flocs.
8. Per cent of time cyanobacteria occur with flocs.
9. Per cent of time flocs occur with cyanobacteria.
10. Ratio of cyanobacteria to flocs.
11. Floc/free bacteria ratio.
12. Viable phytoplankton/free bacteria ratio.

The number of free bacteria was significantly greater at the 99% confidence level for samples with a dense flocculent background, in spite of the likely possibility that some free bacteria were obscured by the flocs. The per cent of flocs with attached bacteria on them was significantly greater at the 95% confidence level in samples with a dense flocculent background. Also, the per cent of flocs that occur with cyanobacteria is significantly greater at the 95% confidence level in samples with a dense flocculent background. Particularly when viewed in the light of the findings of Hodson et al., these additional findings suggest that dense populations of flocculent aggregates are a phenomenon of productive conditions where bacterial numbers have increased. There is no substantial agreement in the literature on the nature and origin of flocculent aggregates. Over the years they have been postulated to be condensations of dissolved organic matter, extracellular products of bacteria, and fecal matter. Very likely they are all of the above in various proportions. Their presence in situations of high productivity and their relative absence elsewhere suggests that they have a comparatively short residence time in the water, either because they aggregate further and sink or because they are degraded by bacteria. Again, these may not be mutually exclusive fates, and both fates provide flocculent aggregates with a potential role in the food web of the continental shelf. These potential roles are explored in a different manner in the simulation model of the food web (section 3.5).

3.4. Production of Fecal Aggregates by Zooplankton

A novel finding in the course of our work on microbial processes in continental shelf water was that some of the flocculent organic aggregates which are a common feature of the seston of productive surface water are fecal. Some of them are identifiable as the fecal ribbons of pelagic tunicates (salps, doliolids, and appendicularians) which have broken up in the water (Pomeroy and Deibel 1980). Our assertions about finding this fecal material in the water in small (50 μ m) fragments has been contested by some workers on the grounds that salp feces are found in sediment traps, and some other studies of salp feces have shown that they sink rapidly. What these investigators do not seem to appreciate is that pelagic tunicates do not produce fecal pellets but a fecal ribbon which break away. Within the ribbon are boluses of material which do remain intact and do sink rapidly. This is the material found in sediment traps and, because it is big enough to see with the unaided eye, it is what other workers have studied exclusively. These large boluses are only a part of the fecal matter however. Studies of the respiratory rate of fecal material (Pomeroy, in prep.) and of the uptake of adenine by the material (R. Hanson, pers. com.) show that there is more activity in the small fragments which remain in suspension than in the large boluses which sink out of the water column. Since the fragments are seen only by oil immersion microscopy, they have been missed by other workers. A second publication describing this is in preparation.

Probably a number of other zooplankton contribute to the fecal aggregate population in the seston, including the smaller larval stages of copepods (Paffenhofer and Knowles 1979, Klinck et al. in press). We find very dense populations of what appear to be fecal aggregates in the nearshore zone where pelagic tunicates do not live. These may be benthic or may be produced by meroplankton. A proposal to continue work on aggregates has been submitted to the National Science Foundation. It is not our intention to continue along this line under this contract.

3.5. A Simulation Model of the Shelf Ecosystem

In 1978 a conceptual model of the detritus food web on a continental shelf subject to intrusions of nutrient-rich water was developed in connection with this contract (Pomeroy 1979). The conceptual model demonstrated that, using recent estimates of gross growth efficiency of oceanic organisms, it was

possible to have production of higher trophic levels, including fishes, while much of the energy of primary production was channelled through a detrital food web. This was in sharp contrast to the North Sea model of Steele (1974) in which all production was directed through a short, linear chain of grazing and predation, with fecal pellets going quantitatively to the benthos. The latter was not based on observed fate of fecal pellets but rather on the necessity to provide a sufficient flux of energy to the benthos in the model to support a reasonable production of demersal fishes. Pomeroy's continental shelf model demonstrated that it is possible to support fishes, both demersal and pelagic, without drastic and unrealistic assumptions about transfer of fecal pellets to the benthos, and indeed without such unrealistic assumptions about the flux of energy through a short, linear food chain, in which copepods eat 100% of the phytoplankton production. Not all of phytoplankton production is available to copepods. Much of it is rather small for them. On the other hand, Steele's model clearly demonstrated that the so-called ecological efficiency of 10% per trophic level cannot work in the real world, even if the world is constrained to clear-cut trophic levels, as was Steele's model. In the real marine environment trophic levels are blurred by bacteria, mucus net feeders, protozoans, and other omnivores.

After the crude demonstration that a model could be constructed which would produce fishes through various detrital food webs (Pomeroy 1979), J.E. Hagner was supported through this contract to develop a simulation model of such a food web. A 17-compartment model was developed (Figure 19) which has a number of unusual features. Phytoplankton are divided into two size groups. Phytoplankton produces dissolved as well as particulate organic matter. Some of the former becomes detritus directly. There are three bacterial populations: free, attached, and benthic. There are four zooplankton populations: grazers, carnivores, mucus-net feeders, and Protozoa. This model provides for the possibility of many alternative pathways for energy and materials between primary producers and terminal consumers (benthic and demersal fishes, other carnivores, and benthic invertebrates). The proposition is that indeed the pathways probably do vary with the circumstances. For example phytoplankton blooms are situations in which much of the primary production is not being grazed and is going to detritus production.

Hagner developed a model along the lines of those developed for other ecosystems by Wiegert (1975; 1979a; 1979b; Wiegert and Wetzel 1979; Wiegert et

Figure 19. Simulation model of the flux of energy through continental shelf food webs. Continuous lines = trophic fluxes. Dotted lines = dissolved fluxes. Broken lines = detrital fluxes. Wavy lines = respiratory fluxes. Arrows to or from a number are additional fluxes to the compartment numbered.

al. 1975). Non-linear equations describe growth, assimilation, mortality, refuge levels, upper population limits, and other known parameters of organisms. The groups thus described are trophic groups of similar species, not individual species populations. We are postulating that ecosystem function will be similar in the presence of certain trophic groups, regardless of the species that predominate at any time. The models thus are intended to simulate ecosystem function, not species population dynamics.

There are several subsets within the model which can be varied individually to explore their effect on the entire model. There is a pelagic subset which is very similar to Steele's (1974), except for the division of phytoplankton into two categories based in size (and the properties which go with

size, such as K_s and r). There is benthic subset which includes benthic bacteria, benthic detritus, meiofauna, macrofauna, predators, and demersal fishes (Figure 20). There is a detritus subset (Figure 21) and a dissolved organic matter subset (Figure 22). By varying these sets, as well as components of them, it is possible to simulate many situations which have been documented in the literature and others which are postulated. Assimilation efficiency can be set to correspond with values in the recent literature or the model can seek efficiencies which lead to a stable system.

Unfortunately, Hagner had to leave the work before it was completed, and after a lapse of about a year the work was taken up again by Michael Pace, who is now completing work with the first-generation model. It is an energy model with nitrogen forcing on primary production. Productivity is adjusted to reasonable levels by varying the number or intensity of intrusions of nitrate-rich water. The model is space-averaged and does not simulate the two-layered

Figure 20. Subset of benthic energy fluxes on the 17-compartment model of energy flux on continental shelves.

Figure 21. Pathways of energy to and from detritus in the simulation model of the flux of energy in a continental shelf ecosystem.

Table 5. Simulated zooplankton production, K Cal m⁻² yr⁻¹ in a mixed detritus and phytoplankton based food web.
 A. Four pulses of nitrogen at regular intervals. B. Short pulses of nitrogen at 20-day intervals.

	grazers	mucus-net feeders	Protozoa	Total
A				
Ingestion	561	404	393	1358
Assimilation	393	263	275	931
Respiration	181	117	117	415
Excretion: loss of DOC	82	61	70	212
Physiological mortality	41	30	7	78
Predatory mortality	96	58	85	239
Egestion	168	142	118	428
Gross growth efficiency	0.24	0.22	0.30	0.25
Production	137	89	118	343
B				
Ingestion	633	422	488	1543
Assimilation	443	274	342	1059
Respiration	178	115	149	442
Excretion	84	60	96	240
Physiological mortality	42	30	10	82
Predatory mortality	137	69	87	294
Egestion	190	147	147	484
Gross growth efficiency	0.28	0.24	0.20	0.24
Production	180	100	97	376

condition of an intrusion on the outer continental shelf. This is a potential refinement for a second generation model. There are no lags in responses of populations in the present model, so there is some foreshortening of time of the responses to the pulses of nitrogen.

By varying the nitrogen forcing, the model can be made to simulate various coastal upwelling situations, as well as the spring bloom conditions of temperate oceans and epicontinental seas (Table 4 and Figure 24). At this level of aggregation there is really nothing unique about a particular marine ecosystem, so long as it is at least 50 meters deep. The model is very stable, as indicated by the means of each of five years of simulation, and this stability carries on through the food web.

In a preliminary run of the simulation, secondary production is divided between various zooplankton groups in what is, so far as we know, a realistic way. We cannot validate the relatively large production of Protozoa at this time, either from our own work or from the literature, although there are indications that it probably is realistic. Gross growth efficiencies are similar to those in the recent literature (Pomeroy 1979; Mills 1980; Banse and Mosher 1980). Secondary production of bacteria is nearly as high as that of zooplankton (Tables 6 and 7). Although this would be missed by a highly condensed model such as Steele's, probably it is a realistic representation of the partitioning of energy fluxes in a planktonic ecosystem. The recent estimates of bacterial production using tritiated thymidine (Fuhrman and Azam 1980) tend to support it. Various levels of production in the simulation model compare favorably with data from continental shelf ecosystems (Table 8). When run as an intrusion model, the simulation yields of demersal fishes are low. Everything we know about the outer continental shelf of the southeastern U.S. supports this (Tenore et al. 1978). The brief nature of intrusions is not conducive to development of demersal fish populations, and except for some small populations associated with ledges and rock outcrops, there is little demersal fish production, so far as we know at present.

The simulation model of the continental shelf ecosystem will serve several functions. It provides a richer simulation of the pelagic food web than most extant models, allowing us to explore the potential fluxes of energy and materials through detritus, bacteria, non-crustacean zooplankton, and even dissolved materials. This in turn serves as a heuristic device to show us the populations and processes not well represented in the present DOE research

Figure 22. Fluxes of dissolved organic carbon in the 17-compartment simulation model of the flux of energy through continental shelf ecosystems.

program in the southeast. Protozoa immediately appear as one such under-investigated group. The reader should, of course, be careful not to ask this model to perform simulations it was not designed to do. Response times of trophic groups may not be realistic, although they will be in relative proportion to each other. Of course, any model wuch as this suggests what is possible or impossible and does not tell us what indeed happens in the real world. Prediction is not an immediate goal of this modeling effort.

Table 6. Simulated bacterial production, K Cal m⁻² yr⁻¹ in a mixed detritus and phytoplankton based food web.

A. Four pulses of nitrogen at regular intervals. B. Short pulses of nitrogen at 20-day intervals.

A	Benthic	Planktonic		Total	Plankton Total
		attached	free		
Ingestion	1695	209	684	2589	893
Respiration	257	99	239	595	338
DOM loss	90	36	86	212	122
Physiological mortality	26	10	25	61	35
Predatory mortality	1321	66	335	1722	402
Gross growth efficiency	0.79	0.37	0.53	0.69	0.49
Production	1347	76	361	1784	437
B					
Ingestion	1891	250	753	2894	1004
Respiration	286	109	248	643	356
DOM loss	103	39	86	228	125
Physiological mortality	30	11	26	67	37
Predatory mortality	1470	93	393	1956	486
Gross growth efficiency	0.79	0.42	0.56	0.70	0.52
Production	1500	104	419	2023	523

Table 7. A comparison of metabolic rates and production of zooplankton and bacteria in a simulated food web which includes both phytoplankton and detrital components ($\text{K Cal m}^{-2}\text{yr}^{-1}$).

	Four regular pulses of nitrogen per year		Short pulses of nitrogen every 20 days	
	Zooplankton	Bacteria	Zooplankton	Bacteria
Ingestion	1358	893	1543	1004
Respiration	415	338	442	356
Production	343	437	376	523

Table 8. A comparison of production data ($\text{K Cal m}^{-2}\text{yr}^{-1}$) from studies of several ecosystems (from Mills 1980) with production values from a simulation model of a mixed phytoplankton and detritus food web in a continental shelf subject to periodic intrusions of nitrate-rich water.

System	Net Primary Production	Zooplankton	Macro- benthos	Demersal Fishes	Pelagic Fishes
Scotian Shelf	1160	89	35	4	4
Scotian Slope	1148	79	27	2	16
North Sea	1026	128	20-50	3.3	10
Intrusion model	1630	137	36	1	3
Spring Bloom model	1599	141	39	2.5	4.4
Peru upwelling model	3715	701	141	1.2	55

YEAR= 5

VARIABLE= 1 Nitrogen inputs

LOGARITHMS

RMAX=	0.17600	RMIN=	-0.10103
RMAX=	1.00000	RMIN=	-4.00000
7.50	0.50000		
15.00	0.50000		
22.50	0.50000		
30.00	0.50000		
37.50	0.50000		
45.00	0.50000		
52.50	0.50000		
60.00	0.50000		
67.50	0.50000		
75.00	0.50000		
82.50	0.50000		
90.00	0.50000		
97.50	0.50000		
105.00	0.50000		
112.50	0.50000		
120.00	0.50000		
127.50	0.50000		
135.00	0.50000		
142.50	0.50000		
150.00	0.50000		
157.50	0.50000		
165.00	0.50000		
172.50	0.50000		
180.00	0.50000		
187.50	0.50000		
195.00	0.50000		
202.50	0.50000		
210.00	0.50000		
217.50	0.50000		
225.00	0.50000		
232.50	0.50000		
240.00	0.50000		
247.50	0.50000		
255.00	0.50000		
262.50	0.50000		
270.00	0.50000		
277.50	0.50000		
285.00	0.50000		
292.50	0.50000		
300.00	0.50000		
307.50	0.50000		
315.00	0.50000		
322.50	0.50000		
330.00	0.50000		
337.50	0.50000		
345.00	0.50000		
352.50	0.50000		
360.00	0.50000		

YEAR= 5

VARIABLE= 2 phytoplankton

LOGARITHMS

RMAX=	1.10222	RMIN=	0.18614
RMAX=	2.10000	RMIN=	-3.00000
7.50	3.26260		
15.00	3.38120		
22.50	3.47141		
30.00	3.54143		
37.50	3.60178		
45.00	3.65777		
52.50	3.70266		
60.00	3.74771		
67.50	3.79310		
75.00	3.83899		
82.50	3.88536		
90.00	3.93221		
97.50	3.97961		
105.00	4.02756		
112.50	4.07606		
120.00	4.12511		
127.50	4.17471		
135.00	4.22487		
142.50	4.27559		
150.00	4.32687		
157.50	4.37870		
165.00	4.43108		
172.50	4.48401		
180.00	4.53749		
187.50	4.59152		
195.00	4.64610		
202.50	4.70123		
210.00	4.75691		
217.50	4.81314		
225.00	4.86992		
232.50	4.92725		
240.00	4.98513		
247.50	5.04356		
255.00	5.10254		
262.50	5.16207		
270.00	5.22215		
277.50	5.28278		
285.00	5.34396		
292.50	5.40569		
300.00	5.46797		
307.50	5.53080		
315.00	5.59418		
322.50	5.65811		
330.00	5.72259		
337.50	5.78762		
345.00	5.85320		
352.50	5.91933		
360.00	5.98601		

Figure 23a. Output of 5th year of simulation of four intrusions per year.

[illegible]

```

* 2 5
VARIABLE= 9
100011015
NAME 0.55951 0.11111 -2.16944
NAME 1.00000 0.11111 -4.00000
  3 0.71517
15.17 0.72367
22.60 0.71514
30.20 0.71337
37.57 0.71514
45.10 0.71674
52.47 0.71742
59.00 0.71746
67.57 0.71517
76.30 1.02938
82.59 1.20922
89.20 0.60315
95.58 0.60315
103.38 0.60312
112.43 0.70437
117.27 0.71212
124.47 0.71576
131.37 0.71212
142.57 0.71757
147.97 0.71747
157.47 1.34957
167.96 0.62797
177.44 0.67452
179.74 0.60620
187.44 0.70623
197.44 0.70071
207.45 0.71518
217.25 0.71732
217.45 0.71677
231.45 0.71916
237.45 0.71715
247.44 0.73142
255.91 0.60321
265.42 0.60312
269.10 0.70310
277.14 0.71215
285.41 0.71650
292.10 0.71663
297.22 0.71330
307.14 0.71713
315.71 1.31613
325.13 1.00954
329.45 0.60051
337.12 0.60840
345.20 0.60770
351.20 0.60701
359.20 0.71650

```

Figure 23d. Output of 5th year of simulation of four intrusions per year.

YEAR = 5
 VARIABLE = 13 attached bacteria

LOGARITHMS

MAX = 0.3 MIN = -0.46895
 MAX = 1.00000 MIN = -6.00000

1.0	0.3213	
1.5	0.3119	
2.0	0.3024	
2.5	0.2929	
3.0	0.2834	
3.5	0.2739	
4.0	0.2644	
4.5	0.2549	
5.0	0.2454	
5.5	0.2359	
6.0	0.2264	
6.5	0.2169	
7.0	0.2074	
7.5	0.1979	
8.0	0.1884	
8.5	0.1789	
9.0	0.1694	
9.5	0.1599	
10.0	0.1504	
10.5	0.1409	
11.0	0.1314	
11.5	0.1219	
12.0	0.1124	
12.5	0.1029	
13.0	0.0934	
13.5	0.0839	
14.0	0.0744	
14.5	0.0649	
15.0	0.0554	
15.5	0.0459	
16.0	0.0364	
16.5	0.0269	
17.0	0.0174	
17.5	0.0079	
18.0	-0.0016	
18.5	-0.0121	
19.0	-0.0226	
19.5	-0.0331	
20.0	-0.0436	
20.5	-0.0541	
21.0	-0.0646	
21.5	-0.0751	
22.0	-0.0856	
22.5	-0.0961	
23.0	-0.1066	
23.5	-0.1171	
24.0	-0.1276	
24.5	-0.1381	
25.0	-0.1486	
25.5	-0.1591	
26.0	-0.1696	
26.5	-0.1801	
27.0	-0.1906	
27.5	-0.2011	
28.0	-0.2116	
28.5	-0.2221	
29.0	-0.2326	
29.5	-0.2431	
30.0	-0.2536	
30.5	-0.2641	
31.0	-0.2746	
31.5	-0.2851	
32.0	-0.2956	
32.5	-0.3061	
33.0	-0.3166	
33.5	-0.3271	
34.0	-0.3376	
34.5	-0.3481	
35.0	-0.3586	
35.5	-0.3691	
36.0	-0.3796	
36.5	-0.3901	
37.0	-0.4006	
37.5	-0.4111	
38.0	-0.4216	
38.5	-0.4321	
39.0	-0.4426	
39.5	-0.4531	
40.0	-0.4636	

YEAR = 5
 VARIABLE = 14 dissolved organic matter

LOGARITHMS

MAX = 1.33692 MIN = -1.70853
 MAX = 2.00000 MIN = -1.00000

1.0	0.640102	
1.5	0.630101	
2.0	0.620100	
2.5	0.610099	
3.0	0.600098	
3.5	0.590097	
4.0	0.580096	
4.5	0.570095	
5.0	0.560094	
5.5	0.550093	
6.0	0.540092	
6.5	0.530091	
7.0	0.520090	
7.5	0.510089	
8.0	0.500088	
8.5	0.490087	
9.0	0.480086	
9.5	0.470085	
10.0	0.460084	
10.5	0.450083	
11.0	0.440082	
11.5	0.430081	
12.0	0.420080	
12.5	0.410079	
13.0	0.400078	
13.5	0.390077	
14.0	0.380076	
14.5	0.370075	
15.0	0.360074	
15.5	0.350073	
16.0	0.340072	
16.5	0.330071	
17.0	0.320070	
17.5	0.310069	
18.0	0.300068	
18.5	0.290067	
19.0	0.280066	
19.5	0.270065	
20.0	0.260064	
20.5	0.250063	
21.0	0.240062	
21.5	0.230061	
22.0	0.220060	
22.5	0.210059	
23.0	0.200058	
23.5	0.190057	
24.0	0.180056	
24.5	0.170055	
25.0	0.160054	
25.5	0.150053	
26.0	0.140052	
26.5	0.130051	
27.0	0.120050	
27.5	0.110049	
28.0	0.100048	
28.5	0.090047	
29.0	0.080046	
29.5	0.070045	
30.0	0.060044	
30.5	0.050043	
31.0	0.040042	
31.5	0.030041	
32.0	0.020040	
32.5	0.010039	
33.0	0.000038	
33.5	-0.010037	
34.0	-0.020036	
34.5	-0.030035	
35.0	-0.040034	
35.5	-0.050033	
36.0	-0.060032	
36.5	-0.070031	
37.0	-0.080030	
37.5	-0.090029	
38.0	-0.100028	
38.5	-0.110027	
39.0	-0.120026	
39.5	-0.130025	
40.0	-0.140024	

Figure 23g. Output of 5th year of simulation of four intrusions per year.

YEAR = 5
 VARIABLE = 15 free-living bacteria in water

LOGARITHMS

MAX = 0.22576 MIN = -0.19924
 MAX = 1.70010 MIN = -4.00000

1.00	1.14773
1.01	1.14773
1.02	1.14773
1.03	1.14773
1.04	1.14773
1.05	1.14773
1.06	1.14773
1.07	1.14773
1.08	1.14773
1.09	1.14773
1.10	1.14773
1.11	1.14773
1.12	1.14773
1.13	1.14773
1.14	1.14773
1.15	1.14773
1.16	1.14773
1.17	1.14773
1.18	1.14773
1.19	1.14773
1.20	1.14773
1.21	1.14773
1.22	1.14773
1.23	1.14773
1.24	1.14773
1.25	1.14773
1.26	1.14773
1.27	1.14773
1.28	1.14773
1.29	1.14773
1.30	1.14773
1.31	1.14773
1.32	1.14773
1.33	1.14773
1.34	1.14773
1.35	1.14773
1.36	1.14773
1.37	1.14773
1.38	1.14773
1.39	1.14773
1.40	1.14773
1.41	1.14773
1.42	1.14773
1.43	1.14773
1.44	1.14773
1.45	1.14773
1.46	1.14773
1.47	1.14773
1.48	1.14773
1.49	1.14773
1.50	1.14773
1.51	1.14773
1.52	1.14773
1.53	1.14773
1.54	1.14773
1.55	1.14773
1.56	1.14773
1.57	1.14773
1.58	1.14773
1.59	1.14773
1.60	1.14773
1.61	1.14773
1.62	1.14773
1.63	1.14773
1.64	1.14773
1.65	1.14773
1.66	1.14773
1.67	1.14773
1.68	1.14773
1.69	1.14773
1.70	1.14773
1.71	1.14773
1.72	1.14773
1.73	1.14773
1.74	1.14773
1.75	1.14773
1.76	1.14773
1.77	1.14773
1.78	1.14773
1.79	1.14773
1.80	1.14773
1.81	1.14773
1.82	1.14773
1.83	1.14773
1.84	1.14773
1.85	1.14773
1.86	1.14773
1.87	1.14773
1.88	1.14773
1.89	1.14773
1.90	1.14773
1.91	1.14773
1.92	1.14773
1.93	1.14773
1.94	1.14773
1.95	1.14773
1.96	1.14773
1.97	1.14773
1.98	1.14773
1.99	1.14773
2.00	1.14773

VARIABLE = 16 mucus net feeders

LOGARITHMS

MAX = 1.26765 MIN = 0.76001
 MAX = 2.03000 MIN = -3.00000

1.00	2.03000
1.01	2.03000
1.02	2.03000
1.03	2.03000
1.04	2.03000
1.05	2.03000
1.06	2.03000
1.07	2.03000
1.08	2.03000
1.09	2.03000
1.10	2.03000
1.11	2.03000
1.12	2.03000
1.13	2.03000
1.14	2.03000
1.15	2.03000
1.16	2.03000
1.17	2.03000
1.18	2.03000
1.19	2.03000
1.20	2.03000
1.21	2.03000
1.22	2.03000
1.23	2.03000
1.24	2.03000
1.25	2.03000
1.26	2.03000
1.27	2.03000
1.28	2.03000
1.29	2.03000
1.30	2.03000
1.31	2.03000
1.32	2.03000
1.33	2.03000
1.34	2.03000
1.35	2.03000
1.36	2.03000
1.37	2.03000
1.38	2.03000
1.39	2.03000
1.40	2.03000
1.41	2.03000
1.42	2.03000
1.43	2.03000
1.44	2.03000
1.45	2.03000
1.46	2.03000
1.47	2.03000
1.48	2.03000
1.49	2.03000
1.50	2.03000
1.51	2.03000
1.52	2.03000
1.53	2.03000
1.54	2.03000
1.55	2.03000
1.56	2.03000
1.57	2.03000
1.58	2.03000
1.59	2.03000
1.60	2.03000
1.61	2.03000
1.62	2.03000
1.63	2.03000
1.64	2.03000
1.65	2.03000
1.66	2.03000
1.67	2.03000
1.68	2.03000
1.69	2.03000
1.70	2.03000
1.71	2.03000
1.72	2.03000
1.73	2.03000
1.74	2.03000
1.75	2.03000
1.76	2.03000
1.77	2.03000
1.78	2.03000
1.79	2.03000
1.80	2.03000
1.81	2.03000
1.82	2.03000
1.83	2.03000
1.84	2.03000
1.85	2.03000
1.86	2.03000
1.87	2.03000
1.88	2.03000
1.89	2.03000
1.90	2.03000
1.91	2.03000
1.92	2.03000
1.93	2.03000
1.94	2.03000
1.95	2.03000
1.96	2.03000
1.97	2.03000
1.98	2.03000
1.99	2.03000
2.00	2.03000

Figure 23h. Output of 5th year of simulation of four intrusions per year.

Figure 24a. First year of simulation of a temperate spring bloom.

free living bacteria

1.47712	RMIN=	-0.13710
0.00000	RMIN=	-4.00000
3.00000		
0.72529		
1.41452		
1.47878		
1.44624		
1.38067		
1.35608		
1.35603		
1.25528		
1.28742		
1.28054		
1.27640		
1.26656		
0.84709		
1.03183		
1.39050		
1.94072		
1.92063		
1.32309		
1.46431		
1.50706		
1.43222		
1.72719		
1.56419		
1.49288		
1.43854		
1.38740		
1.33556		
1.38792		
1.35358		
1.50011		
1.37945		
1.36880		
1.35667		
1.34826		
1.33520		
1.32131		
1.29734		
1.28000		
1.26685		
1.25551		
1.24206		
1.23473		
1.22823		
1.22411		
1.21718		

mucus net feeders

1.46624	RMIN=	0.59226
2.00000	RMIN=	-3.00000
9.95895		
10.04212		
9.36291		
8.24332		
7.67545		
7.23259		
7.00900		
6.81951		
6.67926		
6.58114		
6.50036		
6.43543		
6.41638		
6.39339		
6.36546		
6.34122		
6.31501		
6.28792		
6.26072		
6.23274		
6.20472		
6.17666		
6.14859		
6.12044		
6.09227		
6.06407		
6.03582		
6.00751		
5.97916		
5.95078		
5.92238		
5.89395		
5.86549		
5.83700		
5.80848		
5.77993		
5.75135		
5.72274		
5.69411		
5.66546		
5.63679		
5.60810		
5.57939		
5.55066		
5.52191		
5.49314		
5.46435		
5.43554		
5.40671		
5.37786		
5.34899		
5.32010		
5.29119		
5.26226		
5.23331		
5.20434		
5.17535		
5.14634		
5.11731		
5.08826		
5.05919		
5.03010		
5.00100		
4.97188		
4.94274		
4.91358		
4.88440		
4.85520		
4.82599		
4.79676		
4.76751		
4.73824		
4.70895		
4.67964		
4.65031		
4.62096		
4.59159		
4.56220		
4.53279		
4.50336		
4.47391		
4.44444		
4.41495		
4.38544		
4.35591		
4.32636		
4.29679		
4.26720		
4.23759		
4.20796		
4.17831		
4.14864		
4.11895		
4.08924		
4.05951		
4.02976		
4.00000		

Figure 24c. First year of simulation of a temperate spring bloom.

demersal fishes

feces

Figure 24d. First year of simulation of a temperate spring bloom.

benthic bacteria

VSAB = 1			
VARIABLE = 9			
LOGARITHMS			
OMAX = 0.62787	OMIN = -0.62434		
RMAX = 1.00000	RMIN = -1.00000		
0.0	0.23750		
7.50	1.06284		
15.00	1.51378		
22.50	1.62706		
30.00	1.62948		
37.50	1.50001		
45.00	1.45451		
52.50	1.40555		
60.00	1.35209		
67.50	1.32307		
75.00	1.29050		
82.50	1.26080		
90.00	1.23413		
97.50	1.20992		
105.00	1.18742		
112.50	1.16674		
120.00	1.14788		
127.50	1.13076		
135.00	1.11542		
142.50	1.10181		
150.00	1.08987		
157.50	1.07954		
165.00	1.07078		
172.50	1.06355		
180.00	1.05781		
187.50	1.05353		
195.00	1.05068		
202.50	1.04923		
210.00	1.04915		
217.50	1.05043		
225.00	1.05371		
232.50	1.05896		
240.00	1.06619		
247.50	1.07547		
255.00	1.08785		
262.50	1.10330		
270.00	1.12183		
277.50	1.14350		
285.00	1.16838		
292.50	1.19654		
300.00	1.22808		
307.50	1.26309		
315.00	1.30167		
322.50	1.34392		
330.00	1.38995		
337.50	1.43987		
345.00	1.49377		
352.50	1.55174		
360.00	1.61398		

benthic invertebrates

1.16707	OMIN = -0.65887	
2.00000	RMIN = -3.00000	
5.00000		
7.11130		
10.36566		
11.34136		
10.30739		
10.11592		
9.45596		
8.67653		
7.87775		
7.05268		
6.20669		
5.34167		
4.46759		
3.58347		
2.68865		
1.78587		
0.87000		
14.70900		
13.31546		
12.85857		
13.10828		
13.65000		
14.52177		
15.38407		
16.23532		
17.07610		
17.90617		
18.72488		
19.53149		
20.32619		
21.10884		
21.87951		
22.63876		
23.38707		
24.12489		
24.85262		
25.57072		
26.27962		
26.97979		
27.67146		
28.35592		
29.03349		
29.70659		
30.37573		
31.04149		
31.69427		
32.34370		

Figure 24e. First year of simulation of a temperate spring bloom.

11

other carnivores

0.0	FMIN=	-1.01808
1.00000	AMIN=	-4.00000
0.50000		
0.46287		
0.44806		
0.44035		
0.43255		
0.42366		
0.41367		
0.40279		
0.39123		
0.37793		
0.36256		
0.34576		
0.32806		
0.30987		
0.29282		
0.27720		
0.26745		
0.25602		
0.24398		
0.23068		
0.21355		
0.20732		
0.20111		
0.27760		
0.27718		
0.27538		
0.27282		
0.26909		
0.26451		
0.25941		
0.25376		
0.24772		
0.24138		
0.23481		
0.22801		
0.22075		
0.21246		
0.20337		
0.19337		
0.18354		
0.17313		
0.16253		
0.15203		
0.14196		
0.13166		
0.12231		
0.11306		
0.10425		
0.05592		

detritus in the water

2045	RMIN=	2.13305
0000	AMIN=	-2.00000
249.99944		
257.22827		
259.25501		
223.41029		
210.05576		
197.47171		
184.15302		
173.35736		
173.35275		
169.07362		
164.91743		
161.22284		
157.87989		
225.35152		
235.02234		
229.39838		
225.54829		
221.60853		
239.87447		
259.48007		
254.92030		
263.30151		
258.40088		
240.42765		
240.24431		
231.55833		
223.51492		
216.12488		
209.32126		
203.00595		
197.08444		
191.43097		
184.15613		
181.05589		
176.20448		
171.55856		
161.24837		
163.16420		
159.35092		
156.00853		
152.53052		
149.50615		
146.72213		
144.16113		
141.80968		
139.64934		
137.65626		
135.04613		

Figure 24f. First year of simulation of a temperate spring bloom.

YEAR = 1
VARIABLE = 5
LOG4FITMS

carnivorous zooplankton

PMAX	1.25014	PMIN	-1.1433M
BMIX	1.00000	BMIN	-3.00000
0.0	1.39559		
7.50	2.53276		
15.00	4.02745		
22.50	4.15075		
30.00	3.75249		
37.50	1.20356		
45.00	2.18135		
52.50	2.24643		
60.00	1.07493		
67.50	1.57150		
75.00	1.37047		
82.50	1.11480		
90.00	0.95557		
97.50	0.80550		
105.00	0.65266		
112.50	0.50487		
120.00	0.36186		
127.50	0.22334		
135.00	0.09346		
142.50	0.27013		
150.00	0.48393		
157.50	0.74065		
165.00	0.77732		
172.50	0.59612		
180.00	0.35287		
187.50	0.24553		
195.00	0.45010		
202.50	0.77411		
210.00	0.66697		
217.50	0.53761		
225.00	0.40000		
232.50	0.11450		
240.00	0.36212		
247.50	0.71243		
255.00	0.58508		
262.50	0.48510		
270.00	0.41250		
277.50	0.31158		
285.00	0.30156		
292.50	0.26912		
300.00	0.22302		
307.50	0.15378		
315.00	0.12793		
322.50	0.15267		
330.00	0.12644		
337.50	0.10678		
345.00	0.06533		
352.50	0.07270		
360.00	0.07188		

YEAR = 1
VARIABLE = 6
LOG4FITMS

pelagic fishes

PMAX	0.40148	PMIN	-0.05674
BMIX	1.00000	BMIN	-4.00000
0.0	2.02477		
7.50	2.03687		
15.00	2.05978		
22.50	2.01808		
30.00	1.99112		
37.50	1.91802		
45.00	1.86737		
52.50	1.78609		
60.00	1.70052		
67.50	1.61545		
75.00	1.53419		
82.50	1.45859		
90.00	1.38940		
97.50	1.32664		
105.00	1.26996		
112.50	1.21844		
120.00	1.17109		
127.50	1.12823		
135.00	1.08967		
142.50	1.05167		
150.00	1.01463		
157.50	0.97842		
165.00	0.94311		
172.50	0.90804		
180.00	0.87416		
187.50	0.84087		
195.00	0.80796		
202.50	0.77607		
210.00	0.74407		
217.50	0.71186		
225.00	0.68019		
232.50	0.64850		
240.00	0.61686		
247.50	0.58512		
255.00	0.55319		
262.50	0.52112		
270.00	0.48904		
277.50	0.45696		
285.00	0.42487		
292.50	0.39279		
300.00	0.36071		
307.50	0.32863		
315.00	0.29655		
322.50	0.26447		
330.00	0.23239		
337.50	0.20031		
345.00	0.16823		
352.50	0.13615		
360.00	0.10407		

Figure 24g. First year of simulation of a temperate spring bloom.

Figure 24h. First year of simulation of a temperate spring bloom.

Figure 24i. First year of simulation of a temperate spring bloom.

Because the first generation simulation model is space averaged, it would have limited value if coupled with more detailed physical models of intrusion phenomena. However, a two-layered model, which could easily be developed as a second generation, would not only add interesting biological details but could be meaningfully coupled to models or data sets of the physical regime of the southeastern continental shelf. The inherent strength of this kind of model is its basis in biological principles. It is not a curve-fitted model which simply reproduces in any convenient mathematical way the behavior of the ecosystem. Rather, the equations are developed as descriptions of biological function, just as good physical oceanographic models are descriptions of physical functions. The fact that the model produces realistic production values is therefore, a first-stage validation.

4. The Effect of Copper on Photosynthesis of Marine Phytoplankton

The interaction of naturally occurring dissolved organic matter with heavy metals in solution in sea water may significantly modify the uptake of the metals by organisms. Therefore, analysis of total concentration of a metal in sea water does not permit inferences about its toxicity. A.M. Wood, who is now a Research Associate in the Biology Department of the University of Chicago, completed a doctoral dissertation on the effect of naturally occurring chelators on photosynthesis of naturally occurring phytoplankton populations while she was associated with this contract as a research assistant (Wood 1980).

To evaluate the effect of binding capacity of dissolved organic materials on copper toxicity it is necessary to measure binding capacity as well as copper toxicity. In collaboration with David Evans and James Alberts of the Savannah River Ecology Laboratory, Wood developed an ion-exchange method for measuring copper binding capacity in sea water. Toxicity was evaluated with a bioassay which consisted of a ^{14}C measurement of photosynthetic carbon assimilation in the presence of known copper additions. This is the first time that a copper bioassay has been combined with a binding capacity measurement in a marine environment.

Binding capacity was highly correlated with total dissolved organic carbon concentration. Therefore, coastal waters and estuaries showed the highest binding capacities. At one station in Doboy Sound, Georgia, the binding capacity was so high that no copper toxicity could be demonstrated at

600 $\mu\text{g Cu l}^{-1}$. Other stations in Doboy Sound showed 50% inhibition at Cu concentrations greater than 100 $\mu\text{g l}^{-1}$. A series of samples from the Gulf of Mexico in the vicinity of Barataria Bay and the Mississippi River plume showed 50% inhibition of photosynthesis at Cu concentrations of 50-100 $\mu\text{g l}^{-1}$. In contrast, Sargasso Sea samples showed 50% inhibition at 15-25 $\mu\text{g l}^{-1}$.

These findings have implications for anthropogenic copper inputs into the ocean and continental shelves, such as those associated with the cooling systems of power plants. The binding capacity on the southeastern continental shelf shows the full range of values, with very high capacity near shore to very low at the edge of the shelf. Release of equal amounts of copper on the inner and outer shelf would have very different biological consequences. The principle will apply to other heavy metals. Therefore this work should prove to be a benchmark in the bioassay of heavy metal toxicity in the ocean.

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5. Publications and Reports Resulting from this Contract

A. Published

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- Campbell, W. B. 1981. Adenylate analysis in natural waters. Georgia Marine Science Center Tech. Report. DOE report No. DOE/EV/00639-21

B. Dissertations

- Wood, A. M. *Biological and Chemical Factors Regulating the Response of Natural Marine Phytoplankton Communities to Copper Addition*. University of Georgia. 139 pp.

C. In press

- Hodson, R. E., A. E. Maccubbin and L. R. Pomeroy. Dissolved Adenosine triphosphate and its utilization by free-living and attached bacterioplankton. *Marine Biology*.*

Jacobsen, T. R. Comparison of chlorophyll a measurements by fluorometric, spectrophotometric, and high pressure liquid chromatographic methods in aquatic environments. Arch. Hydrobiologie, Beih. Ergebn. Limnol. In press.*

D. Manuscripts

Berman, T. Phosphorus uptake by microplankton in estuarine and coastal shelf water near Sapelo Island, Ga., U. S. A.*

Berman, T., R. B. Hanson, and W. J. Wiebe. Effects of organic substrate addition on size partitioning and respiration of 'single' versus clumped or 'attached' marine bacteria.*

Wood, A. M. and D. W. Evans Copper chelating capacity in the Sargasso Sea and on the continental shelf of the southeastern United States.*

*Publications marked with an asterisk are included as appendices to this report.

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